

Social and Environmental Factors in the Evolution of Signalling

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DECLARATION

I declare that this thesis was composed by myself and that the work contained herein is my own except where explicitly stated in the text. The work has not been submitted for any degree or professional qualification except as specified.

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PUBLICATIONS AND CONTRIBUTIONS

The following publications have arisen from this thesis and are presented in Chapters 2, 4 and 5. The published versions are appended.

Chapter 2:

- **Caro, S. M.**, Griffin, A. S., Hinde, C. A. & West, S. A. 2016. Unpredictable environments lead to the evolution of parental neglect in birds. *Nature Communications* 7, 1–10, doi:10.1038/ncomms10985.
 - Stu West, Ashleigh Griffin, Camilla Hinde and I conceived of the comparative analysis. I formulated the hypotheses, collected the data, ran analyses, and prepared the figures. All co-authors contributed to the interpretation of results and commented on the manuscript.

Chapter 4:

- **Caro, S. M.**, West, S. A. & Griffin, A. S. 2016. Sibling conflict and dishonest signalling in birds. *Proceedings of the National Academy of Sciences* 113, 13803–13808, doi: 10.1073/pnas.1606378113.
 - Ashleigh Griffin, Stu West and I conceived of the comparative analysis and formulated the hypotheses. I collected the data, ran analyses and prepared the figures. All co-authors contributed to the interpretation of results and commented on the manuscript.

Chapter 5:

- Wild, G.*, **Caro, S. M.***, & West, S. A. 2017. Signaling about information that is neither cryptic nor private. *Journal of Evolutionary Biology*, doi: 10.1111/jeb.13049. *These authors contributed equally.
 - I conceived of the theoretical model and prepared Figure 1. Geoff Wild carried out the modelling work and prepared Figures 2-4. All co-authors contributed to the interpretation of results and wrote the manuscript.

The following manuscripts have arisen from this thesis, and are presented in Chapters 3 and 6. These are collaborative efforts, although in each case the majority of work is my own.

Chapter 3:

- **Caro, S. M.**, Griffin, A. S., West, S. A., & Hinde, C. A. Environmental conditions and facultative adjustment of parent-offspring communication. *In preparation*.
 - Camilla Hinde, Stu West, Ashleigh Griffin and I conceived of the study and formulated hypotheses. I collected the comparative data, and Camilla Hinde collected the empirical data. I ran analyses and prepared the figures. All co-authors contributed to the interpretation of results and commented on the manuscript.

Chapter 6:

- **Caro, S. M.**, Griffin, A. S., West, S. A., & Hinde, C. A. Gape size and its function as a signal of non-cryptic information in great tits. *Under review at Behavioural Ecology*.
 - Camilla Hinde and I conceived of the study. Camilla Hinde collected the empirical data. I formulated hypotheses, ran analyses and prepared the figures. All co-authors contributed to the interpretation of results and commented on the manuscript.

ABSTRACT

Offspring across the animal kingdom have evolved a variety of vocalizations, postures and structural ornaments to help them solicit more food from their parents. These signals are typically assumed to convey information about offspring state that helps parents decide which offspring to feed, and the dominant framework holds that begging is a signal of need. However, species differ both in how they beg and how they respond to begging, and signalling theory has been unable to account for this variation. In this thesis, I use a combination of comparative, observational and theoretical data to explore how the degree of within-family conflict leads to differences in parent-offspring signalling systems both across and within bird species. I also explore the possibility that some signalling systems function differently because the information they transmit is not cryptic. Specifically: 1) I show that offspring signals of need are more likely to evolve in species living in predictable and/or unusually good environments, while signals or cues of quality are more likely to evolve in unpredictable and/or unusually poor environments, when conflict over food is greater because brood reduction is probable; 2) I show that the same patterns hold within-species, indicating that parents can facultatively adjust their responsiveness based on the risk of brood reduction; 3) I show that offspring signals of need are less honest when sibling competition is greater, due to offspring number and/or relatedness; 4) I argue, using a simple game, that signals of non-cryptic condition can be stable if signalling provides an efficiency benefit compared to parents' using cues; and 5) I provide a potential example of such a signal in nature, gape size, and show that its honesty fluctuates based on local conditions.

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FOREWORD

I have not provided a detailed review of the literature in the introduction, because I review the relevant literature in Chapters 2-6.

INTRODUCTION

The vulnerabilities of signalling

Communication allows organisms to share information in a mutually beneficial way (Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). Communication can take diverse forms and functions across the tree of life: a honeybee performing a waggle dance shows its sisters where to find honey, a wolf baring its teeth shows it's ready for a fight, a bacterium releasing quorum-sensing molecules announces its presence, a bird displaying more colourful plumage highlights its quality as a mate, an infant crying shows its mother how much it needs milk. In all these cases, one individual produces a trait—a signal—that alters the behaviour of another individual, and which evolved in the signaller because of the receiver's response (Maynard Smith & Harper 2003). In general, signals reflect some internal or environmental condition experienced by the signaller, and receivers are selected to respond if they would benefit from behaving differently based on those conditions (Maynard Smith & Harper 2003).

Signals are only stable when signallers benefit from signalling and when receivers benefit from responding to those signals, on average (Hamilton 1964; Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). Producing and responding to signals entails at least some costs, and so the benefits of both producing and responding to signals must outweigh those costs. Signalling systems therefore face a double vulnerability: they are exploitable by individuals who signal dishonestly, and they can collapse if individuals stop responding to signals. All else being equal, honest signallers could be outcompeted by dishonest signallers who manipulate receivers into

responding inappropriately (Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011; Flower *et al.* 2014; Mokkaenen & Lindstedt 2015). Individuals may stop responding to signals if they become too unreliable, or if conditions change and it no longer benefits them to respond (Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). Determining how organisms overcome communication's double vulnerability remains the key question in the study of signalling.

Several solutions to this vulnerability have been proposed, including mechanisms which enforce honesty through costly handicaps, punishment for dishonesty, and indices (Zahavi 1975; Grafen 1990; Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). Mechanisms that promote common interest may also favour the evolution of signalling. If all parties share a preferred outcome, there is no incentive to being dishonest or to ignoring signals (Maynard Smith & Harper 2003). For example, common interest can arise from high relatedness, since organisms will gain inclusive fitness from outcomes that benefit their relatives, or from mutual benefits from the response to signalling (Hamilton 1964; Maynard Smith & Harper 2003). Unless organisms are clonal, they will experience some degree of conflict of interest, which could lead to an arms race between signallers and receivers, or even destabilise communication to the point of collapse.

My thesis focuses how signalling systems are influenced by the degree of conflict amongst communicators. Using parent-offspring communication in birds as a framework, I investigate how the intensity of conflict, determined by variation in social

and ecological factors, impacts the information content of signals and how receivers respond to those signals.

Key terms

Models of honest signalling frequently contradict each other as well as the biological data. Some of this confusion may arise, ironically, through miscommunication about terminology, and so I will begin by defining some key terms. These following definitions are mainly adapted from Maynard Smith and Harper's (2003) overview of the literature on communication.

Communication is the transfer of information through signals. A **signal** is a phenotype that alters the behaviour of another individual in a way that benefits the receiver, and which evolved in the signaller because the receiver's response benefits the signaller (Maynard Smith & Harper 2003). This phenotype can be a physical structure, behaviour, or chemical excretion. The only constraint is that it had to evolve in the signaller *because* its effect on the receiver benefits the signaller on average. For instance, a snake may see the heat signature of a mouse and thus discover its prey's location, but body temperature in mice did not evolve in order to transmit information to snakes. This type of information transfer is better called a **cue**: a feature of another organism that receivers benefit from responding to, but that did not evolve for the purpose of transferring information (Maynard Smith & Harper 2003). Typically, signals are assumed to contain **cryptic** or **private** information, which is only accessible to the signaller and not to the receiver (Grafen 1990; Godfray 1991; Johnstone & Grafen 1993; Kilner & Johnstone 1997; Hinde & Godfray 2011). This contrasts with **non-cryptic** or **public** information, which the receiver has access to through its own senses or through

cues from other individuals. For example, body size is public information, but blood glucose level is cryptic.

Reliable or **honest** signals accurately reflect the state of the world as perceived by the signaller (Johnstone & Grafen 1993; Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Broom *et al.* 2013; Carazo & Font 2014; Flower *et al.* 2014). **Dishonest** or **unreliable** signals are the opposite: inaccurate information that benefits the sender but not the receiver of that (mis)information. Imagine a bird that gives a specific call whenever a dangerous cat is near. When other birds hear that call, they respond by fleeing. There is a clear benefit to responding to this signal when cats are around: the receiver does not get eaten. However, if a bird gives the alarm when no cats are near and uses that opportunity to steal the fleeing birds' food, only the signaller benefits. Thus, these alarm calls could be considered honest when predators are near, but dishonest when no predators are near. There is an evolutionary incentive to be dishonest if signallers benefit more from exaggerating their signals than from signalling in a way that accurately reflects the state of the world. Dishonesty requires no intent on the part of the signaller. For example, bacterial cells with a mutation causing them to over-produce quorum-sensing molecules, which cause their neighbours to over-produce costly public goods, would be considered dishonest despite their lack of intention.

An **index** or **performance-based signal** is a signal that is honest by default, because its intensity is physically constrained (Maynard Smith & Harper 2003; Biernaskie *et al.* 2014). If the pitch of a bullfrog's croak is determined wholly by the size of its throat, which is proportional to its overall body size, bullfrogs of a certain size are physically unable to make deeper croaks. Indices are similar to **handicaps**, which are signals that

could be faked, but which are reliable because the cost of faking them is greater than the benefit, and this cost-benefit ratio differs based on signaller state (Zahavi 1975; Grafen 1990; Biernaskie *et al.* 2014). There are two kinds of costs important to signalling theory: efficacy and strategic costs. These fitness costs are generated by proximate mechanisms such as energy expenditure. **Efficacy costs** are the baseline costs required to transmit signals: in noisy environments birds must sing more loudly to be heard (Guilford & Dawkins 1991). **Strategic costs** are the additional costs that are required to ensure honesty of handicaps: complex songs require hours of practice that only high quality birds can spare from foraging (Guilford & Dawkins 1991).

In this thesis, signals produced by offspring which appear to act as solicitations for food from parents are called **begging** when they are behavioural, and are called **structural** when they are morphological features. **Condition** (or **long-term condition**) refers to an offspring's total requirement for food to improve overall quality before fledging—the ultimate fitness effects of receiving additional food (Price *et al.* 1996; Wells 2003; Searcy & Nowicki 2005). An offspring in low condition has high **need** and an offspring in good condition has high **quality**. Higher quality individuals are more likely to survive and be recruited to the breeding population. Condition differs from **hunger** (or **short-term condition**), an immediate desire for food, in that offspring may be more or less hungry in a given moment without influencing their total required parental investment. Hunger and condition may not be completely separable, but they represent different pressures. For example, we would consider a chick that is plump and healthy but currently has an empty stomach as being higher quality than a chick that is emaciated and sickly but currently has a full stomach (Price *et al.* 1996; Wells 2003). Both hunger and condition may influence signalling, but this thesis explores the effects of condition.

Begging in birds

Begging is an ideal model for examining the evolution and stability of signalling when communicators are in conflict. Offspring produce a variety of calls, postures and physical structures that serve to solicit food from parents, termed begging (Wright & Leonard 2002). We can assume that parents and offspring would both prefer it if offspring survive, and so signals facilitating provisioning could be in everyone's best interests (Grodzinski & Lotem 2007). However, there could be conflict over optimal parental investment levels: while parents are equally related to all their offspring, offspring are more related to themselves than to their siblings (Hamilton 1964; Trivers 1974; Kilner & Hinde 2012). This conflict means that offspring and parents may have different optimal investment strategies. As the interests of parents and offspring diverge, parent-offspring signalling becomes more vulnerable: offspring may have an incentive to exaggerate their signals to get a bigger share of resources, and parents may have an incentive to ignore those signals (Johnstone & Grafen 1993; Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). Begging thus allows researchers to examine the role of conflict in determining what information signals should contain, how honest those signals should be, and when individuals should respond to them (Trivers 1974; Grafen 1990; Godfray 1995b; Rodríguez-Gironés *et al.* 1996; Kilner & Johnstone 1997; Wright & Leonard 2002; Kilner & Hinde 2008; Grodzinski & Johnstone 2012). I investigate these questions in Chapters 2-6.

Birds provide an ideal lens through which to study whether this conflict actually determines how parents and offspring communicate. While begging can be observed across the animal kingdom from burying beetles to marmosets, the most detailed studies have been on birds (Wright & Leonard 2002). Research has been conducted on parental

care and communication in more than a hundred bird species, revealing variation both across- and within-species. Variation in conflict permits comparative analyses that explore the overarching pressures governing the evolution of begging across species, as well as detailed analyses within populations to determine whether individuals exhibit facultative adjustment of signalling. The phylogenetic relationships within birds are fairly well resolved: Jetz *et al.* (2012) published a resource with 10,000 bird phylogenies. These data allow us to conduct comparative analyses controlling for the non-independence of closely related species and accounting for uncertainty in the phylogeny.

Despite the extensive literature on begging in birds, its exact function remains under debate (Wright & Leonard 2002; Hinde & Godfray 2011; Johnstone & Kilner 2011; Kölliker 2011; Mock *et al.* 2011; Wright 2011). The benefit of begging could be to increase total parental investment in the current brood (whole-brood begging), to increase the signaller's share of parental investment (within-brood begging), or some combination of these (Johnstone 2004). In this thesis, I focus on how begging influences the distribution of food, so that I can investigate how parents divide investment within their existing brood. This can reveal, for example, whether parents are prioritising the survival of a few, high-quality offspring, or trying to produce as many offspring as possible, even if those offspring are lower quality. Understanding how begging influences overall provisioning effort also deserves research, as it could reveal, for example, how much parents value their current brood over saving energy for future reproduction. I intend to address this function of begging in future research (see Discussion).

Begging is most frequently assumed to convey information about offspring condition, and has been put forward as a handicap signal (Godfray 1991; Kilner & Johnstone 1997; Wright & Leonard 2002; Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). The majority of models that address whether begging can be stable in the face of parent-offspring conflict allow the cost-benefit ratio of signalling to differ based on chick condition, so that the strategic cost of signalling keeps begging honest (Grafen 1990; Godfray 1991; Maynard Smith 1991a; Godfray 1995b; Johnstone 1996; Kilner & Johnstone 1997; Nöldeke & Samuelson 1999; Godfray & Johnstone 2000). Other models have allowed cost-free or low-cost begging based on relatedness, identical rank orders of preferences, or partially informative signalling (Lachmann & Bergstrom 1998; Bergstrom *et al.* 2002; Maynard Smith & Harper 2003; Zollman *et al.* 2012). Begging does appear quite costly: loud vocalizations attract predators, posturing and flapping waste valuable energy, and carotenoid-based signals pull nutrients away from immune responses, though evidence for its costs are mixed (Leech & Leonard 1996; McCarty 1996; Kilner & Johnstone 1997; Weathers *et al.* 1997; Kilner 2001; Chappell & Bachman 2002; Fenoglio *et al.* 2002; Wright & Leonard 2002; Wells 2003; Moreno-Rueda 2006; Haff & Magrath 2011; Martin-Galvez *et al.* 2011; Sternalski *et al.* 2012; Soler *et al.* 2014). This thesis sets aside the issue of costliness, focusing instead on what information is contained in offspring signals and how parents respond to those signals.

The majority of research on offspring signals has assumed that the information conveyed through offspring signals is need, where offspring in the worst condition signal the most intensely (Godfray 1991; 1995b; Kilner & Johnstone 1997; Wright & Leonard 2002; Searcy & Nowicki 2005). It is also possible that offspring signals

function as a signal of quality, where offspring in the best condition signal the most intensely (Grafen 1990; Mock *et al.* 2011). Under both signal-of-need and signal-of-quality frameworks, condition is assumed to be cryptic, and so parents gain information about offspring condition through paying attention to begging behaviours and structural ornaments (e.g. Grafen 1990; Godfray 1991; Kilner & Johnstone 1997; Bergstrom *et al.* 2002; Johnstone 2004; Hinde & Godfray 2011). Some theorists, such as Johnstone (1996b) and Bro-Jørgensen (2010), have explored when multiple signals providing redundant information can be stable, but these also assume that quality cannot be directly observed. In other words, models assume that the information in offspring signals is not available via non-signalling means, or else why would parents and offspring pay the costs of producing and responding to signals?

Begging behaviours and structural ornaments may also function as scramble competition (Rodríguez-Gironés *et al.* 1996; 1998; Parker *et al.* 2002a; Royle *et al.* 2002). In this framework, offspring control resource allocation and parents passively respond to the chick presenting the largest stimulus. It is difficult to distinguish between whether begging is a signal of quality or scramble competition because these hypotheses make the same predictions about which offspring beg the most intensely (Royle *et al.* 2002). However, by passively deferring to the winner of scramble competition, parents are essentially following the same strategy as if they actively fed the offspring signalling the highest long-term quality (Royle *et al.* 2002). Although it is likely that the balance between parental or offspring control of resource distribution varies in nature, this thesis assumes that parents control distribution to some extent, and thus treats begging and structural ornaments as signals, rather than direct sibling competition.

Finally, begging may be a signal to nestmates rather than to parents. The sibling negotiation hypothesis posits that chicks vocalize and jostle each other to signal their readiness to fight for the next piece of food (Roulin *et al.* 2000; Johnstone & Roulin 2003). Barn owls (Roulin *et al.* 2000; Dreiss *et al.* 2010), spotless starlings (Bulmer *et al.* 2007), and barn swallows (Romano *et al.* 2012) vocalize extensively in the absence of parents. Yet it is possible that parent-absent begging occurs when chicks mistakenly believe a parent is present (Dor *et al.* 2006) or because parents can actually still hear and respond to chicks' calling (Jimeno *et al.* 2013). It is also possible that chicks are participating in two distinct conversations, one with their parents and one with their siblings (Bulmer *et al.* 2007). Comparatively little work has been done on parent-absent offspring behaviour, and this thesis will only evaluate offspring to parent signalling models.

Thesis and chapter aims

This thesis explores signalling when it is extremely vulnerable: when conflict between communicators is high and when the information included in signals is redundant. I assess how well patterns in nature conform to the predictions of signalling theory. When the empirical data contradicted predictions from theory or other empirical data, I attempted to identify which model assumptions were violated. I employ a three-pronged approach, combining comparative meta-analyses to explain broad-scale patterns in evolution across species, observational data on wild great tits, *Parus major*, to assess fine-scale variation within species, and theoretical modelling to explore the potential for the evolution of a novel function of offspring signals.

In Chapters 2 and 3, I investigate whether ecological variation leads to variation in parent-offspring signalling in birds. In Chapter 2, I explore how two key ecological factors—predictability and quality—influence the evolution of both offspring signalling strategies and parental response strategies across species, using phylogenetic comparative analyses. In unpredictable and in unusually poor environments, partial brood starvation becomes more likely, violating a common assumption in signal-of-need models that parents are attempting to rear all their offspring. In Chapter 3, I explore whether we can observe the same shifts in communication within-species as we observed across-species. This chapter combines within-species comparative data and detailed observational data on a wild population of great tits. Overall, I found that as the likelihood of brood reduction increases, based on ecological factors and brood size, parents become less likely to respond to offspring signals of need. Correspondingly, parents become more likely to distribute food based on offspring cues or signals of quality than on signals of need, both across- and within-species.

In Chapter 4, I investigate how the degree of conflict within-families influences the honesty of offspring signals of condition, using phylogenetic comparative analyses. Specifically, I found offspring produce less honest signals of need in species with higher numbers of siblings or broods and lower relatedness between broods. This suggests that as signaller and receiver interests become less aligned, signals of need become more likely to collapse.

In Chapter 5, I challenge the common and explicit assumption in signalling theory that signals must contain cryptic or private information. Using a simple game-theoretic model, I showed that offspring signals containing publically-available information can

be stable—if responding to a signal is more efficient than investigating the publically-available cue of offspring condition. This suggests that the biological function of signals may be broader than is currently considered.

In Chapter 6, I explore a potential example of a signal of non-cryptic information: gape size in nestling great tits. Using observational data from a wild population, I address whether gape size can act as signal, and whether the honesty of this putative signal is affected by within-family conflict. This chapter also explores how pre- and post-hatching parental investment patterns shift based on the likelihood of brood reduction. I found that gape size may act as a signal of body size, that its honesty varies with within-family conflict, and that parents adjust multiple aspects of investment based on the likelihood of brood reduction.

In Chapter 7, I summarize the main results and conclusions of Chapters 2-6. I then discuss implications for the field of signalling and future research directions.

2. UNPREDICTABLE ENVIRONMENTS LEAD TO THE EVOLUTION OF PARENTAL NEGLECT IN BIRDS^{*†}

Abstract

A nest of begging chicks invites an intuitive explanation: needy chicks want to be fed and parents want to feed them. Surprisingly, however, in a quarter of species studied, parents ignore begging chicks. Furthermore, parents in some species even neglect smaller chicks that beg more, and preferentially feed the biggest chicks that beg less. This extreme variation across species, which contradicts predictions from theory, represents a major outstanding problem for the study of animal signalling. We analyse parent–offspring communication across 143 bird species, and show that this variation correlates with ecological differences. In predictable and good environments, chicks in worse condition beg more, and parents preferentially feed those chicks. In unpredictable and poor environments, parents pay less attention to begging, and instead rely on size cues or structural signals of quality. Overall, these results show how ecological variation can lead to different signalling systems being evolutionarily stable in different species.

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† This chapter is presented in the narrative format of *Nature Communications*, with detailed methods following the main text.

Introduction

In many species, including our own, the production of offspring represents the most energetically demanding stage of an animal's life. Raising a brood successfully puts a metabolic demand on breeding birds that is the equivalent to a human cycling the Tour de France (Peterson *et al.* 1990). Success or failure often depends on parents' ability to determine which offspring to invest in, when to invest in them and how much to invest. Offspring attempt to influence the feeding behaviour of their parents by begging for food through a variety of mechanisms, including vocal calls, behavioural displays and physical structures (Wright & Leonard 2002).

Different species, however, appear to beg and respond to begging in different ways (Figure 2.1) (Kilner & Johnstone 1997; Davis *et al.* 1999; Hinde & Godfray 2011; Johnstone & Kilner 2011; Kölliker 2011; Mock *et al.* 2011; Wright 2011). In many species, such as the tree swallow, smaller nestlings beg more, and are preferentially fed by their mothers (Leonard & Horn 1996; 2001). In other species, such as the hoopoe, mothers sometimes force food into the beaks of larger, silent chicks, ignoring the persistent begging from their smaller offspring (Martin-Vivaldi *et al.* 1999). In many siblicidal species, such as the blue-footed booby, the largest offspring beg and are fed the most (Drummond & Garcia Chavelas 1989).



Figure 2.1. Variation in parental provisioning. In every species of bird with parental care, chicks appear to have evolved signals designed to maximize their chance of being fed, such as vocalizations, begging postures and bright mouths. However, the way parents respond to information about their offspring differs markedly across species. Tree swallows *Tachycineta bicolor* feed the chick begging the most (a). Others sometimes neglect begging offspring, such as the blue-footed booby *Sula nebouxii* (b) and the hoopoe *Upupa epops* (c), which instead preferentially feed larger chicks. Gouldian finch *Erythrura gouldiae* parents (d) may preferentially feed offspring with elaborate structural ornaments around their mouths. (Photos courtesy of (a) M. Sodicoff. (b) Damschen/ARCO/naturepl.com. (c) L.M.R. Gordón; and (d) G. Grall, National Aquarium, Baltimore)

Evolutionary theory has been unable to account for this diversity across species, as highlighted by Mock *et al.* 2011. The dominant paradigm, ‘signal of need’, predicts that

chicks in worse condition beg with greater intensity and that parents respond to this begging (Godfray 1991; 1995b; Godfray & Johnstone 2000; Mock *et al.* 2011). However, these signal of need models assume that parents are trying to rear all their offspring and that offspring in better condition reduce their begging (Godfray 1991; Kilner & Johnstone 1997; Godfray & Johnstone 2000; Hinde & Godfray 2011; Mock *et al.* 2011). This is clearly not the case in species where parents let the neediest offspring starve and offspring in better condition beg more (Drummond & Garcia Chavelas 1989; Grafen 1990; Mock & Parker 1997; Cotton *et al.* 1999; Royle *et al.* 2002; Mock *et al.* 2011). The pattern in those species may be better explained by ‘signal of quality’ models (Grafen 1990; Royle *et al.* 2002; Mock *et al.* 2011). However, most signal of need and quality models do not predict that parents should flexibly ignore begging, as the hoopoe does (Cotton *et al.* 1999; Martin-Vivaldi *et al.* 1999; Godfray & Johnstone 2000). Parker and Macnair (1979), however, do find that ignoring offspring solicitation can be an evolutionary stable strategy, which can shift the level of investment closer to parents’ optima. While each model is consistent with observations in some species, it is inconsistent with others (Mock *et al.* 2011).

A possible explanation for this diversity is that different ecological conditions, in different species, favour different signalling systems (Johnstone 1995; Davis *et al.* 1999; Fawcett & Johnstone 2003; Bro-Jørgensen 2010; Grodzinski & Johnstone 2012). When food is relatively plentiful, parents can be selected to preferentially feed the offspring signalling the greatest need (Davis *et al.* 1999). In contrast, when food is scarce, parents can be predicted to ignore begging and preferentially feed bigger chicks (Davis *et al.* 1999). Consequently, a single factor—the extent to which parents can acquire enough food to feed all their offspring—could lead to the stability of different signalling

systems, and hence explain the extreme variation across species in who begs and how parents respond to begging (Figure 2.2) (Davis *et al.* 1999; Mock *et al.* 2011; Grodzinski & Johnstone 2012).

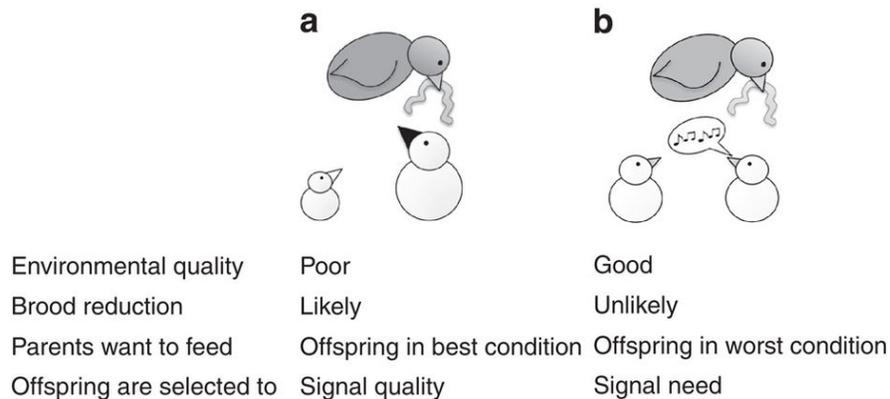


Figure 2.2: Ecological variation and diversity in signalling systems. (a) In unpredictable environments, parents may produce a larger brood than future environmental conditions will support. This selects for parents to preferentially feed the offspring with the highest chance of survival. We predict parents will assess quality by cues such as body size, or structural signals such as dark mouths. Offspring may still beg, but parents should ignore begging in favour of other information. (b) In contrast, in predictable environments, parents will lay an appropriate number of eggs and food will be plentiful enough to rear all their offspring. Here parents will be selected to preferentially feed offspring in the worst condition. We predict offspring should signal need through begging, and parents will feed those begging more.

There has, however, been no empirical test of whether different signalling systems have evolved in response to differences in relative food availability. While many studies have been conducted within species, it is hard to generalize their findings because of differences in environmental context and life history variables between species. We therefore conducted a comparative study to test whether signalling and provisioning correlate with the likelihood that parents can acquire enough food to rear a complete brood. We collected data on 143 bird species, examining how offspring signalling relates to their condition, and how parents respond to signals and cues of offspring

condition. Our aim was to test the hypothesis that variation in food availability can explain variation in offspring communication and parental provisioning strategies.

We examined two possible determinants of parents' ability to acquire enough food to rear all their offspring: environmental predictability and environmental quality (Lack 1954; Forbes & Ydenberg 1992; Stoleson & Beissinger 1995; Mock & Parker 1997; Davis *et al.* 1999). First, in species where environmental conditions are more predictable, parents are more likely to produce the clutch size that leads to all of their offspring surviving (Lack 1954; Magrath 1990; Stoleson & Beissinger 1995). Conversely, in unpredictable environments, parents may lay an optimistic number of eggs, and are only be able to rear all their offspring in particularly good years (Lack 1954; Magrath 1990; Stoleson & Beissinger 1995; Mock & Parker 1997; Cotton *et al.* 1999). Such species often begin egg incubation before they have completed a clutch, creating a size hierarchy: when conditions are worse, only the biggest and best quality chicks survive to fledge (Lack 1954; Magrath 1990; Stoleson & Beissinger 1995; Mock & Parker 1997). We classified species as 'brood reducing' if hatching is asynchronous or if the later-hatched offspring die at greater rate, as is expected with low environmental predictability (Lack 1954; Magrath 1990; Stoleson & Beissinger 1995; Mock & Parker 1997). If this information was not available, we used a conservative cut-off of 75% broods in the population typically experiencing the starvation of at least one chick. We classed all other species as having a 'whole-brood survival' strategy, as is expected with relatively high environmental predictability.

Our second determinant of food availability was current environmental quality (Davis *et al.* 1999). In unusually good conditions, parents are more likely to be able to acquire

enough food to feed all their offspring, even if they are typically brood reducing. We categorized environmental quality as good, average or poor compared with the norm for that population, dependent upon ecological measures or experimental manipulations. For example, owls experiencing a crash in the vole population (Lockie 1955) are in a poor environment, and pigeons supplemented with mealworms and grain (Mondloch 1995) are experiencing a good environment.

We found that the strategies of both offspring and parents are associated with upon environmental predictability and quality. In relatively stable and unusually good environments, offspring signal their need and parents distribute food according to begging. In contrast, in relatively unpredictable and unusually poor environments, offspring signal their quality and parents are more likely to feed offspring based on signals or cues of quality. These results allow us to explain why opposite patterns have been observed in different species, with parents preferentially feeding offspring in either worse or better condition.

Results and Discussion

Offspring signalling strategies

To determine what information is encoded in chick signals, we calculated the correlation coefficient (effect size) between offspring long-term condition and (1) begging and (2) structural signals (Figure 2.3). The coefficient varies between ± 1 , with positive values meaning that chicks in better condition beg more or have larger structural signals, and negative values implying that chicks in worse condition beg more or have larger structural signals. Long-term condition, or the likelihood that offspring will survive to adulthood and reproduce, is information that obviously influences

parents' fitness (Price *et al.* 1996; Godfray & Johnstone 2000; Mock *et al.* 2011; Wright 2011). Long-term condition was captured by health, body condition, changes to food intake over multiple days, weight and rank within the brood. These different measures reflect factors that parents may or may not be able to assess directly to different degrees (Godfray 1991; Hinde & Godfray 2011; Mock *et al.* 2011).

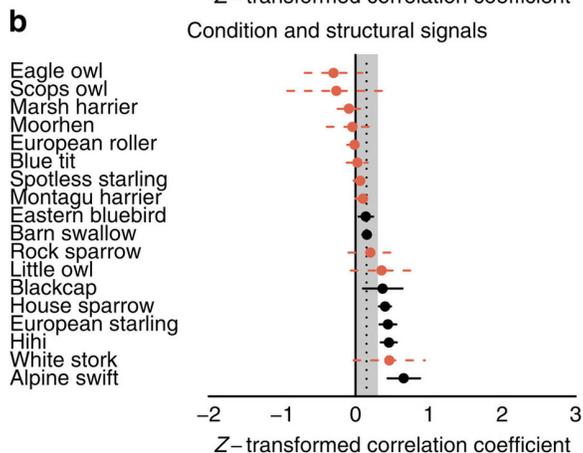
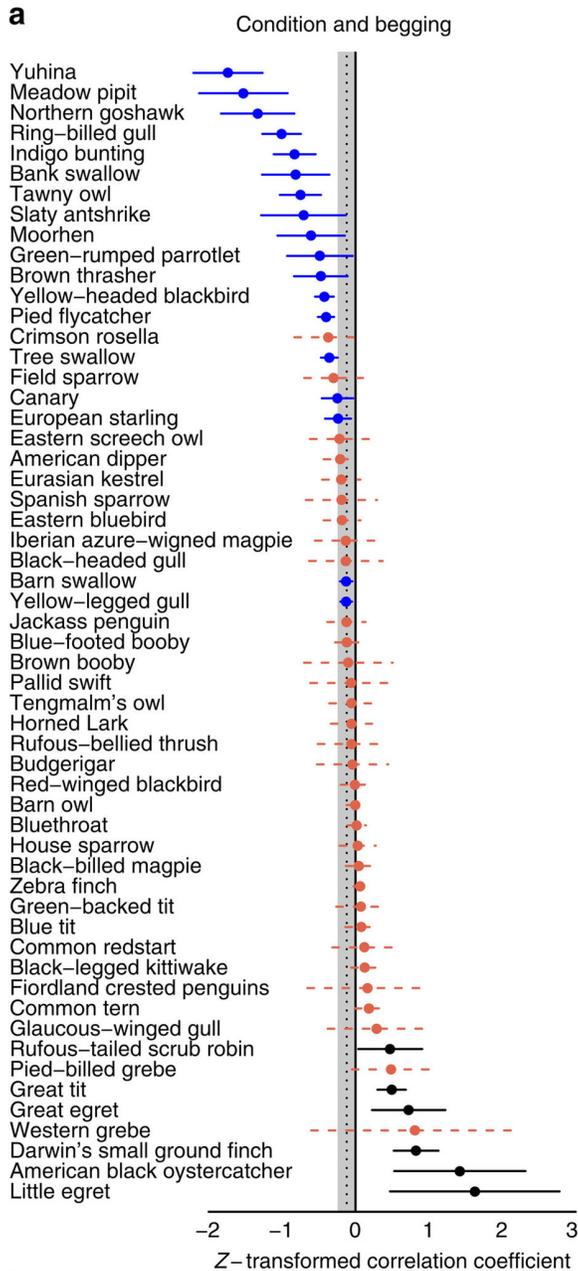


Figure 2.3: Variation in offspring signals across species. Circles represent species' mean z-transformed correlation coefficient between condition and (a) begging intensity (n=56 species) and (b) structural signal intensity (n=18 species). The grand mean and 95% credible interval (CI) are denoted by the shaded bar. Blue, solid lines indicate that chicks that in worse condition signal more. Black, solid lines indicate that chicks in better condition signal more. Red, dashed lines indicate no effect of condition on signals. Lines show 95% CI (\pm s.e. $\times t_{critical}$). s.e. was estimated from the pooled number of broods across all studies.

Our first prediction was that chicks in worse condition should be more likely to beg, or beg more intensely, in better environmental contexts and in species that generally rear the whole brood. Under these conditions, all offspring will be more likely to survive to maturity, and hence honest signalling of need can be favoured. We examined vocal begging and posture, as birds could adjust these behaviours flexibly in response to need.

As predicted, we found that chicks in worse condition were more likely to beg in species that rear a complete brood (phylogeny-based, Bayesian generalized linear mixed models with Markov chain Monte Carlo methods: $pMCMC=0.001$; Table 2.1a; Figure 2.4a). In contrast, in brood-reducing species, there is no general correlation between chick long-term condition and begging intensity ($pMCMC=1$; Table 2.1a). Furthermore, across all species, chicks in worse condition were more likely to beg more intensely in better environments ($pMCMC=0.001$; Table 2.1a). None of our results were influenced by the measure of condition or begging used in the original studies (Supplementary Tables 2.1 and 2.2). These results are consistent with a greater likelihood of signalling of need in species trying to rear all their offspring.

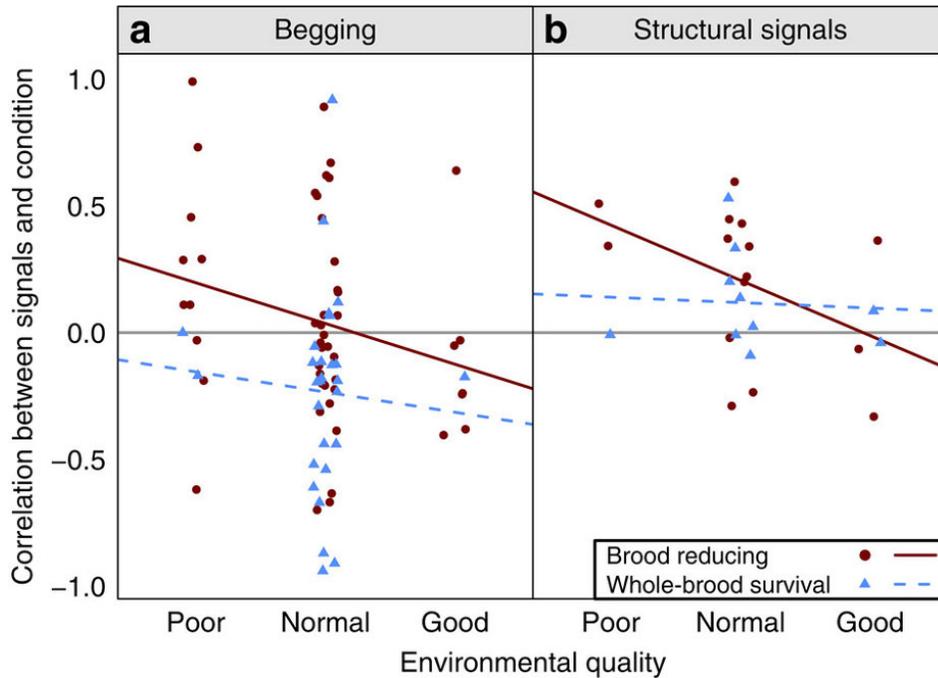


Figure 2.4: Brood reduction likelihood determines whether low or high condition chicks signal more. Data points represent each species' mean correlation coefficient (effect size) of offspring condition on signal intensity in that environment. Positive correlations indicate chicks in better condition signal at a higher intensity, and negative correlations indicate chicks in worse condition signal more. This is a graphical simplification; analyses were run on the full data set per effect size reported, not species' means. **(a)** Chicks in worse condition were more likely to beg the most in good environments (MCMCglmm, $p_{MCMC}=0.001$), and in species which tend to raise the whole brood (MCMCglmm, $p_{MCMC}=0.02$, $n=56$ species). This represents the scenario where brood reduction is least likely. **(b)** Chicks in better condition were more likely produce more intense structural signals in brood-reducing species in poor environments (MCMCglmm, $p_{MCMC}=0.003$, $n=18$ species). This represents the scenario where brood reduction is most likely.

Table 2.1. Environmental and life history influences on offspring signalling strategies.

	Posterior mean Z	95% Credible Interval	pMCMC
(a) Begging			
Brood-reducing	0.01	-0.19 to 0.17	0.95
Whole brood survival	-0.30	-0.47 to -0.14	0.001***
Reduction difference	-0.37	-0.66 to -0.05	0.02*
Environment	-0.29	-0.50 to -0.07	0.001**
Reduction * Environment	-0.07	-0.33 to 0.22	0.62
<i>Grand mean</i>	<i>-0.12</i>	<i>-0.26 to 0.01</i>	<i>0.09.</i>
(b) Structural signals			
Brood-reducing	0.31	0.08 to 0.57	0.02*
Whole brood survival	0.10	-0.13 to 0.36	0.4
Reduction difference	-0.21	-0.47 to 0.09	0.18
Environment	-0.53	-0.77 to -0.28	0.0001***
Reduction * Environment	0.49	0.16 to 0.80	0.003**
<i>Grand mean</i>	<i>0.15</i>	<i>-0.00 to 0.32</i>	<i>0.06.</i>

Results of MCMCglmm analyses on Fisher's Z-transformed correlation coefficients (manuscript and figures report correlation coefficients). $.p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (a) Behavioural begging: $n=56$ species, 96 studies, 247 effect sizes. (b) Structural signals: $n=18$ species, 33 studies, 140 effect sizes.

We then examined a mode of parent–offspring communication that we predicted could function as a signal of quality: structures such as mouth colour, ultraviolet reflectance and mouth size (Johnstone 1995; Kilner 1997; Hill & McGraw 2006). These require a relatively long-term investment of resources such as carotenoids, and so are more likely to reflect long-term quality rather than short-term need (Hill & McGraw 2006). Consequently, these structural signals are more likely to be used as signals of quality, and so we predict that they will be greater in species living in unpredictable and poor environments, where only a fraction of the brood will be reared.

As predicted, we found that chicks in better condition tended to produce more intense structural signals in brood-reducing species (pMCMC=0.02), but not in species that rear

the whole brood (pMCMC=0.4; Table 2.1b; Figure 2.4b). This is consistent with structural signals being used to signal quality when brood reduction is possible. Furthermore, there was a significant interaction between brood reduction strategy and environmental quality in the predicted direction (pMCMC=0.003; Table 2.1b). Specifically, brood-reducing species showed an increased tendency for better condition chicks to produce greater structural signals in poorer environments, which is when brood reduction is most likely. These results are consistent with a decrease in relative food availability selecting for chicks to signal quality to their parents, to avoid being the chick left to starve.

Our analyses support our hypothesis that when raising a complete brood is likely, selection should favour chicks that signal need through behavioural begging. In contrast, when parents are unlikely to raise a complete brood, selection appears to favour chicks that signal quality through structural signals. However, caution is required when interpreting these results, because signalling theory predicts that signals must transmit information about a cryptic aspect of quality that parents cannot otherwise detect (Grafen 1990; Godfray 1995b; Hinde & Godfray 2011). While researchers may have captured this with measures such as immunocompetence (Saino *et al.* 2001; Hill & McGraw 2006), measures such as body mass may be less likely to reflect some cryptic aspect of condition. A stronger approach to test our hypothesis would be to examine parental response to begging signals, structural signals and body size cues, in terms of how parents distribute food among offspring.

Parental feeding strategies

To determine what information parents use when allocating food, we estimated the strength of the correlation between feeding and three sources of information about chick condition: begging, structural signals and body size cues (Figure 2.5). Parents may respond to all, none or a combination of these signals and cues when allocating food. As far as possible, we included only data that isolated the individual effects of each of these information sources; for example, begging height, which combines both body size and begging posture, was excluded. The direction of each correlation coefficient was based solely on whether chicks signalling more were fed more, and our analyses of parental response made no assumptions about what information was included in the signal or cue.

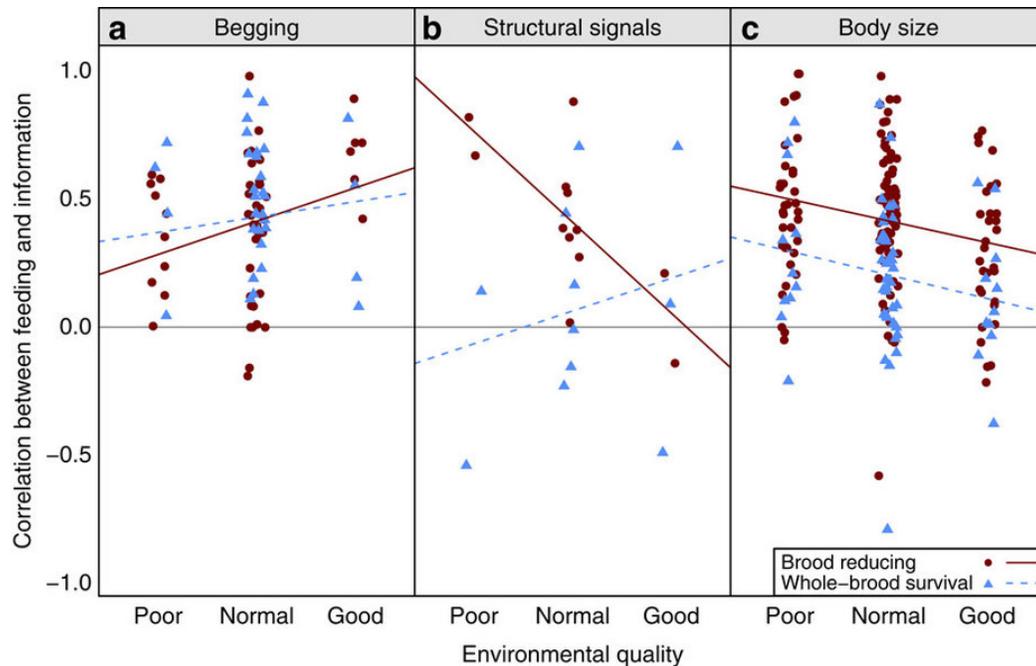


Figure 2.5. Brood reduction likelihood determines how parents respond to chick signals and cues. Data points represent species' mean correlation coefficient (effect size) of signal intensity or body size on food allocation in that environment. Positive correlations indicate larger chicks or those signalling more intensely receive more food. This is a graphical simplification; analyses were run on the full data set per effect size reported, not species' means. **(a)** Parents respond more to begging as the environment improves (MCMCglmm, $p\text{MCMC}=0.01$, $n=61$ species). **(b)** Brood-reducing species paid more attention to structural signals in poorer environments, whereas species that rear the whole brood show a consistently low response, though low sample size keeps this interaction non-significant (MCMCglmm, $p\text{MCMC}=0.09$, $n=15$ species). **(c)** Parents showed a stronger preference for larger chicks in poorer environments (MCMCglmm, $p\text{MCMC}=0.006$) and brood-reducing species (MCMCglmm, $p\text{MCMC}<0.0002$ and $n=120$ species).

On average, parents preferentially feed chicks that beg more ($p\text{MCMC}<0.0001$; Table 2.2a), have brighter and more saturated mouths ($p\text{MCMC}=0.009$; Table 2.2b), and are larger ($p\text{MCMC}<0.0002$; Table 2.2c). The responsiveness to begging varied across species, with parents not preferentially feeding the chicks that beg the most in 17 of the 61 species studied (Figure 2.6a; total heterogeneity (I^2), the proportion of observed variance that reflects true differences in correlation coefficients: 23.2%; Supplementary

Table 2.6). Responsiveness to structural signals was also variable across species, with no effect of signal intensity on feeding in almost half of species studied ($I^2=16.9\%$; Figure 2.6b; Supplementary Table 2.6). Surprisingly, given the common assumption that parents want to feed the neediest offspring, parents almost universally prefer feeding larger offspring: only 2 of 120 species feed smaller chicks more ($I^2=15.4\%$; Figure 2.7; Supplementary Table 2.6). None of our results were influenced by the measure of feeding preference used in the original studies (Supplementary Tables 2.3, 2.4 and 2.5).

Table 2.2. Environmental and life history influences on parental response strategies.

	Posterior mean Z	95% Credible Interval	pMCMC
(a) Begging			
Brood-reducing	0.70	0.52 to 0.89	0.0004***
Whole brood survival	0.61	0.38 to 0.87	0.0002***
Reduction difference	-0.11	-0.40 to 0.16	0.5
Environment	0.35	0.05 to 0.61	0.01*
Reduction * Environment	-0.16	-0.67 to 0.33	0.5
Grand mean	0.62	0.48 to 0.76	<0.0001***
(b) Structural signals			
Brood-reducing	0.79	0.34 to 1.2	0.0006***
Whole brood survival	0.34	-0.09 to 0.80	0.12
Reduction difference	-0.45	-0.97 to 0.08	0.09.
Environment	-0.71	1.22 to -0.20	0.007**
<i>Reduction * Environment</i>	<i>0.70</i>	<i>-0.10 to 1.50</i>	<i>0.09.</i>
Grand mean	0.36	0.10 to 0.61	0.009**
(c) Body size			
Brood-reducing	0.50	0.40 to 0.59	<0.0002***
Whole brood survival	0.19	0.07 to 0.32	0.003**
Reduction difference	-0.30	-0.43 to -0.17	<0.0002***
Environment	-0.14	-0.25 to -0.04	0.006**
Reduction * Environment	0.001	-0.20 to 0.18	0.98
Grand mean	0.43	0.31 to 0.54	<0.0002***

Results of MCMCglmm analyses on Fisher's Z-transformed correlation coefficients. . $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$. (a) Behavioural begging: n=61 species, 92 studies, 301 effect sizes. (b) Structural signals: n=15 species, 20 studies, 60 effect sizes. (c) Body size: n=120 species, 218 studies, 795 effect sizes.

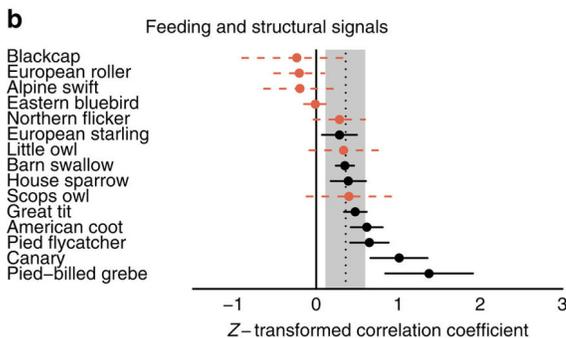
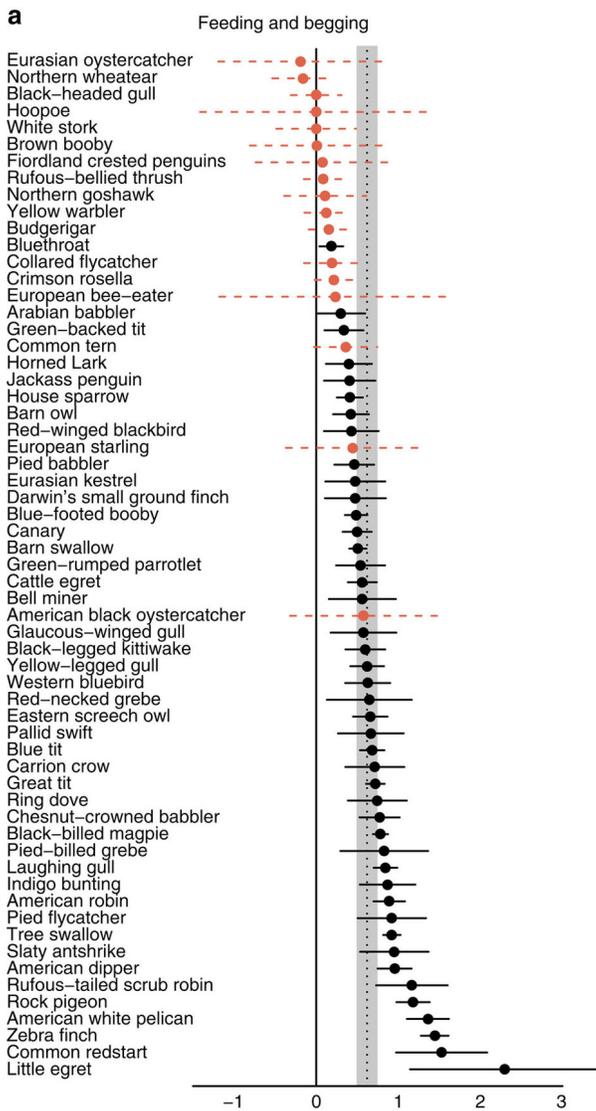


Figure 2.6. Variation in parental responsiveness to offspring signals across species. Circles represent species' mean z -transformed correlation coefficient between feeding and (a) begging ($n=61$ species), and (b) structural signals ($n=15$ species). The grand mean and 95% credible interval (CI) are denoted by the shaded bar. Black, solid lines indicate chicks that signal more are preferentially fed more. Red, dashed lines indicate no effect of signals on feeding. Lines show 95% CI ($\pm s.e. \times t_{critical}$). s.e. was estimated from the pooled number of broods across all studies.

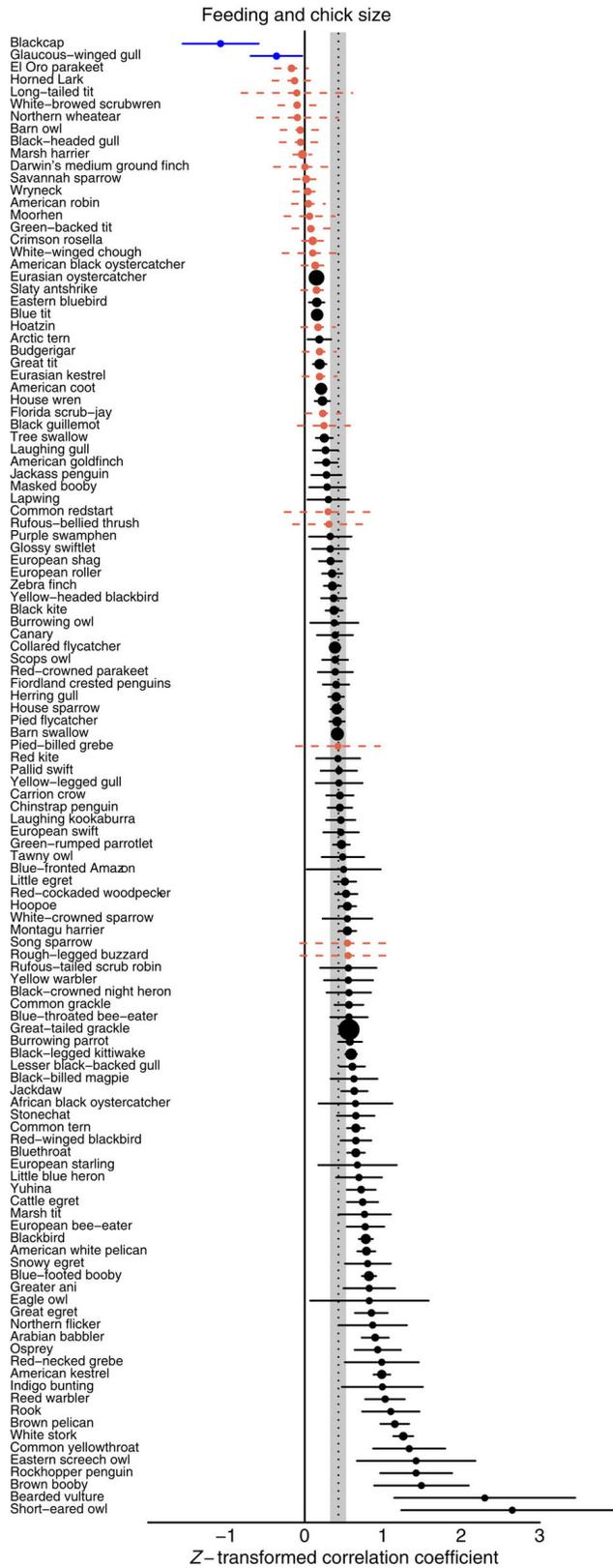


Figure 2.7: Variation in parental responsiveness to offspring size across species. Circles represent species' mean z -transformed correlation coefficient between feeding and chick body size ($n=120$ species). The grand mean and 95% credible interval (CI) are denoted by the shaded bar. Black, solid lines indicate larger chicks are fed more. Blue, solid lines indicate that smaller chicks are fed more. Red, dashed lines indicate no effect of chick size on feeding. Lines show 95% CI ($\pm s.e. \times t_{critical}$). $s.e.$ was estimated from the pooled number of broods across all studies.

We predict that parents will preferentially feed chicks in the greatest need when there is a relatively high likelihood that parents will have enough food to rear a complete brood. Given that chicks signal need behaviourally with vocal calls and posturing (Figure 2.4a), we expect that parents should be more likely to respond to such begging in relatively good environments. In contrast, when parents are unlikely to have enough food to rear a complete brood, we predict that parents should prefer to feed the better quality chicks, irrespective of begging intensity. Quality could be assessed by a cue such as body size or by chicks signalling quality with structures (Figure 2.4b). In this context, we expect a positive correlation between food allocation and offspring size and/or structural signals.

As predicted, we found that parents preferentially fed the chicks that begged the most in good environments, but were less responsive to begging in poor environments ($pMCMC=0.01$; Table 2.2a; Figure 2.5a). This pattern did not differ depending upon whether a species was brood reducing or rears the whole brood ($pMCMC=0.5$; Table 2.2a).

In contrast, we expect the opposite pattern with structural signals of quality and body size: when parents are unlikely to have enough food to rear all of their offspring, we predict they will respond more to structural signals and body size. As predicted, we found that parents preferentially fed chicks with more colourful mouths and/or larger bodies in poor environments, and responded less to structural signals and body size cues in good environments (structural signals: $pMCMC=0.007$; size: $pMCMC=0.006$; Table 2.2b,c; Figure 2.5b,c). Furthermore, the preference for larger chicks was greater in brood-reducing species than in species where the whole brood survives

($pMCMC < 0.0002$; Table 2.2c). Parents in brood-reducing species were also more likely to feed chicks based on structural signals, although not significantly, perhaps because of low sample size for this comparison ($pMCMC = 0.09$, $n = 6$ whole-brood survival species, 9 brood-reducing species; Table 2.2b).

Overall, a clear pattern emerges: the probability of successfully raising all offspring from a nest is correlated with the system of communication between parents and their offspring across species. In predictable and/or unusually good environments, offspring in worse condition are more likely to beg (Figure 2.4a), and parents are more likely to feed individuals begging at a higher rate (Figure 2.5a). These results are predicted by signal of need models, where parents expect to rear a complete brood (Godfray 1991; 1995b; Johnstone 2004; Mock *et al.* 2011). In contrast, in unpredictable and/or poor environments, offspring in better condition have more intense structural signals (Figure 2.4b), and parents are more likely to feed chicks that are larger or have more intense structural signals (Figure 2.5b,c). These results are predicted by signal of quality models, where parents rear only a fraction of their offspring, or by models where signalling is not stable, and parents just respond to cues of quality (Rodríguez-Gironés *et al.* 1996; Davis *et al.* 1999; Royle *et al.* 2002; Parker *et al.* 2002a; Mock *et al.* 2011). Another possibility is that parents respond less to variation in begging when food availability is low simply because all chicks are hungry, and therefore beg at similar rates. Irrespective of whether begging provides less information or parents are selected to ignore it, the outcome is the same: begging appears to become a less useful signal in worse environments, while body size and structural signals appear to become more important. Our findings rely on correlational, across-species data, and so are not conclusive. Experimental selection studies on birds or other model species, such as

burying beetles or earwigs, are a crucial next step for understanding the links between brood reduction and parent-offspring communication.

Our study relied on the fact that there was sufficient variation across species in food availability to produce different evolutionary outcomes. In some cases, there may even be sufficient environmental variation within a species that individuals will be selected to adjust their behaviour conditionally in response to local conditions. For example, hihi parents become less sensitive to their offspring's mouth colour when they are supplemented with additional food (Thorogood *et al.* 2011). Similarly, alpine swifts who breed early in the season, when food availability is greater, prefer nestlings with lower ultraviolet reflectance, while parents who breed later, under worse conditions, switch to preferring nestlings with greater reflectance (Bize *et al.* 2006).

Conclusions

More generally, one of the major outstanding challenges for our understanding of how communication evolves is to explain why species have such diverse communication systems. We have shown how variation in environmental quality can explain differences in communication between offspring and their parents. In relatively good environments, there is less conflict, and offspring can be selected to signal need to their parents. In contrast, in relatively poor environments, there is more conflict, and parents are expected to respond to quality rather than need. Furthermore, this can occur via either offspring signalling quality or parents ignoring signals and instead relying on cues such as body size. This variation is why hundreds of empirical studies on begging and parental response have not yet led to a consensus on exactly what information is transmitted through offspring signals, or how parents respond to various signals (Hinde

& Godfray 2011; Johnstone & Kilner 2011; Kölliker 2011; Mock *et al.* 2011; Wright 2011). Our results suggest that this variation reflects different communication systems being stable in different species.

Methods

Data collection

We conducted a literature search on Web of Science and Google Scholar using the keywords ‘beg’, ‘parent–offspring’, ‘bird’, ‘begging’, ‘communication’ and ‘provision’ (see Supplementary Figure 2.1 for PRISMA flowchart detailing data collection). We performed backwards and forwards citation searches on all studies. We included studies published before August 2014, as well as unpublished data sets from five researchers. We included all papers with any measure relating to the relationship between chick long-term condition and (1) behavioural begging or (2) structural signals, and food allocation and (3) behavioural begging, (4) structural signals or (5) size cues (see Supplementary Table 2.9 for a list of excluded studies). We excluded studies if it was impossible to determine whether parents were responding to begging or to size cues. We excluded effect sizes where the only measure of chick condition was proximate hunger rather than long-term condition. We only included effect sizes for the relationship of begging on within-brood food allocation, rather than on increases in overall parental feeding effort, as these represent fundamentally different aspects of parental care. We excluded data on species that lay only one egg per brood, as selective pressures on these offspring are likely to differ from species laying multiple eggs per brood. If relevant data were given in papers without statistical tests, such as raw means and s.e.’s, we estimated effect sizes. This resulted in a data set of 1,544 effect sizes (correlation coefficients) from 306 studies on 143 species (Data published online:

www.nature.com/articles/ncomms10985). The data set contains a diverse range of species, spanning 51 families in 19 different orders.

Measures of offspring condition

We examined the effect of long-term condition on signalling intensity (Price *et al.* 1996). Our proxies for long-term condition were health (for example, experimental immune challenge, parasite load, carotenoid supplementation), body condition (for example, body mass to skeletal size ratio, blood glucose levels), weight (for example, body mass), rank within the brood (for example, hatching rank, dominance rank, body mass or skeletal size rank) and experimental manipulations that affected food intake over multiple days (for example, experimentally reduced or enlarged broods, with the assumption that chicks in larger broods receive less food per capita).

We excluded studies that examined only the effect of short-term food deprivation, that is, hunger. While hunger and condition may not be truly separable, they represent very different selection pressures (Price *et al.* 1996; Godfray & Johnstone 2000; Wells 2003; Hinde & Godfray 2011; Johnstone & Kilner 2011; Mock *et al.* 2011; Wright 2011). For example, although each piece of food eaten contributes to the likelihood that a chick will survive, the fitness benefit of food to fatally diseased chicks is zero, because they will not live to breed (Kilner 1997; Wells 2003; Mock *et al.* 2011). Furthermore, the influence of hunger on begging is already well established (Wright & Leonard 2002; Mock *et al.* 2011). Consequently, we focused on the influence of long-term condition, and so data on the relationship between hunger and signal intensity were not included in analyses of offspring strategies. For example, we excluded data such as Kilner (1997) finding that canary chicks' mouths get redder as they become hungrier over 40 min.

However, our analyses of parental behaviour made no assumptions about what information was transmitted by signals. Therefore, feeding in response to mouth redness would be included in analyses on parental behaviour, just as the response to begging calls, which may be influenced by both hunger and condition, was included. It would be an interesting task for the future to examine whether and how hunger interacts with measures of long-term condition (Hinde & Godfray 2011).

Measures of signalling and provisioning

Many aspects of the behavioural and structural signalling suite were reported in the literature, such as begging amplitude, duration, latency, likelihood, call structure, posture, ultraviolet reflectance of the gape or flange, carotenoid saturation of the gape or flange, or colouration of specialized skin patches and feathers only present during the nestling period. Different measures of food allocation were also reported, such as weight gain over a short time period, actual food intake, number of food items received, likelihood of being fed, growth rate and mortality. We assumed that all measures of signal intensity and food allocation were driving towards the same biological phenomenon, and so included all reported statistics in our analyses. Parents' responses to begging signals, structural signals and body size cues were analysed separately. Because measures of feeding preference such as mortality could have been partially confounded by how we classified environmental predictability, we tested whether the measure of feeding affected the strength of the correlation coefficient, but found no difference between any of the proxies for feeding preference ($p_{\text{MCMC}} > 0.05$, see Supplementary Tables 2.3, 2.4 and 2.5). Because test statistics were converted to a standardized scale, differences between the various measures of begging intensity or feeding preferences should not influence the overall trends seen. Study methodology,

such as which measure of long-term condition was reported or whether the study was experimental or observational, had no impact on effect size ($p_{MCMC} > 0.05$ in all cases; Supplementary Tables 2.3, 2.4 and 2.5).

Data on brood reduction strategy

We classified species as brood reducing if hatching is asynchronous (24 h or more passes between the hatching of the first and last chick in the brood) and if nestling mortality follows a stereotypical pattern of later-hatched nestlings dying at a greater rate due to starvation, siblicide or infanticide (Lack 1954). If that data were not available, we assessed whether partial brood mortality is typical (at least one chick starves in at least 75% of broods in the population) (Lack 1954; Stoleson & Beissinger 1995; Mock & Parker 1997). Many brood-reducing species experience lower rates of starvation, but this conservative criterion allows us to identify species with a very clear strategy of brood reduction based on environmental factors, rather than incidental starvation. The combination of hatching and mortality patterns allowed us to distinguish between species employing a true brood reduction strategy and those with asynchronous hatching for other reasons, such as spreading offspring demand evenly over the nestling period or avoiding chilling earlier-laid eggs (Stoleson & Beissinger 1995).

Data on environmental quality

To evaluate how environmental conditions interact with life history traits across species, we categorized populations as experiencing normal, better than normal or worse than normal environments, based on experimental manipulations (parents were fed reduced or supplemented diets or chick demand was artificially increased or decreased), ecological measures (such as prey density, date or rainfall), or average mortality across

different years in long-term observational studies. Only long-term manipulations of food availability over multiple days were included, to ensure chick condition, and not simply hunger, was affected by the ecological variation. If no information on environmental quality was available, studies were conservatively classified as normal conditions.

Statistical analyses

To evaluate the strength of the relationships across studies and species, we transformed any test statistic measuring either an effect of long-term condition on signal intensity, or an effect of chick signals or cues on feeding into a standardized effect size (Fisher's Z -transformed correlation coefficient) (Borenstein *et al.* 2011; Grissom & Kim 2011; Koricheva *et al.* 2013; Nakagawa & Schielzeth 2013). These correlation coefficients follow a normal distribution, account for different scales in their original measurements, are well suited to the ordered nature of the data and are more straightforward to interpret than standardized difference in means (Borenstein *et al.* 2011). Before analyses, we decided not to exclude potential outliers. Fisher's Z -transformed correlation coefficients were analysed using the MCMCglmm package in R, which implements Bayesian generalized linear mixed models with Markov chain Monte Carlo methods (Hadfield 2010; R Core Team 2013). Models were weighted by sample size and controlled for phylogeny and repeated measures on the same study and species. Sample size was determined as the number of broods used to generate the original test statistic, because this is a standard measure across studies. It also conservatively avoids pseudoreplication if chick number or number of observations were used as the sample size. Environmental quality was treated as a three-level ordered categorical variable, and brood reduction strategy as a two-level categorical factor. We obtained phylogenies from Birdtree.org, and models were run on 100 random phylogenetic trees with Ericson and Hackett

backbones, and then averaged (Jetz *et al.* 2014). Analyses were run separately for each relationship.

Forest plots and species-level analyses were conducted with the metafor package in R (Viechtbauer 2010; R Core Team 2013). We assessed the heterogeneity of our data using I^2 , which is a descriptive measure of the proportion of observed variance that reflects true differences in correlation coefficients (Higgins *et al.* 2003; Borenstein *et al.* 2011; Nakagawa & Santos 2012). Results related to heterogeneity and random effects can be found in Supplementary Tables 2.6 and 2.7. Example R code can be found in Supplementary Information. We used ASReml analyses to confirm the results of our meta-analysis (Supplementary Methods; Supplementary Table 2.8) (Lee & Song 2004; Butler *et al.* 2009; Hadfield *et al.* 2014).

Tests for publication bias

Although we did not expect to find one true effect size across all studies and species (Borenstein *et al.* 2011), we tested our meta-analysis for publication bias using the regression test for funnel plot asymmetry (Egger's test) in the 'metafor' package in R (Viechtbauer 2010). We calculated the average effect size per study and compared it with its variance to determine whether studies with smaller sample sizes were more likely to show extreme effects. We found no evidence of publication bias in the relationships between: (1) offspring condition and begging ($z=0.54$, $p=0.59$); (2) offspring condition and structural signals ($z=0.93$, $p=0.35$); (3) feeding and begging ($z=-0.49$, $p=0.63$); (4) feeding and structural signals ($z=0.91$, $p=0.36$); and (5) feeding and body size cues ($z=-1.59$, $p=0.11$).

Tests for confounding methodological factors

We recorded additional information on study methodology for each effect size, including the following: the sample size (number of broods) of that measurement; the type of begging variable (three-level factor: whether or not begging occurred; any continuous intensity measure (for example, duration, amplitude and posture); hunger treatment: experimentally deprived or satiated, with the assumption that hungry chicks beg more); the type of feeding variable (four-level factor: whether or not feeding occurred; any continuous measure of feeding (feeding rate or weight of food received); growth of mass or body structures (tarsus and primary feather), either rate or final size attained, with the assumption that growth rates reflect feeding rates at least in part; and mortality risk before fledging, with the assumption that mortality rates reflect feeding rates at least in part. Nestlings typically died of starvation. Predation risk was excluded as much as possible by considering only partial brood losses); the type of long-term condition variable (five-level factor: health, rank, weight, condition and long-term changes to food intake); whether the offspring contrast was dichotomous (bigger versus smaller) or continuous (all offspring included); whether the female, male, both sexes combined or a helper was the responder (four-level factor); and whether the data were experimental or observational (two-level factor). Not all study methodology variables were relevant for all aspects of this communication system. Analyses of potential confounding factors were only run if at least two factor levels had at least 10 effect sizes.

No methodological factors had an impact on any of the five relationships tested in this communication system (MCMCglmm phylogenetically controlled and weighted regression: $p_{MCMC} > 0.05$). The 95% credible intervals of the correlation coefficients

for each methodological factor are presented in Supplementary Tables 2.1, 2.2, 2.3, 2.4 and 2.5.

Because measures of feeding preference such as mortality and growth rate may be partially confounded by how we classified environmental predictability, we ran models excluding all effect sizes generated using these measures. There was no change in the significance of results for any parental responsiveness model, despite a reduction in sample size of 50 species. In the model of how much parents feed their offspring in response to size cues, the slope for environmental quality changed from -0.14 ($pMCMC < 0.0002$) to -0.25 ($pMCMC = 0.005$), and the difference between brood reducing and whole-brood survival changed from -0.30 ($pMCMC = 0.006$) to -0.26 ($pMCMC = 0.018$). In the model of how much parents feed their offspring in response to begging, the slope for environmental quality changed from 0.35 ($pMCMC = 0.01$) to 0.34 ($pMCMC = 0.01$). In the model of how much parents feed their offspring in response to structural signals, the slope for environmental quality did not change, the difference between brood reducing and whole-brood survival changed from -0.45 ($pMCMC = 0.09$) to -0.46 ($pMCMC = 0.06$), and the interaction from 0.61 ($pMCMC = 0.09$) to 0.58 ($pMCMC = 0.10$).

Heterogeneity

We measured the heterogeneity in our data set with I^2 , the proportion of observed variance due to true differences in effect sizes, rather than measurement errors (Supplementary Table 2.6) (Higgins *et al.* 2003; Borenstein *et al.* 2011; Nakagawa & Santos 2012). Total I^2 was calculated by dividing the summed variance attributed to phylogeny, species, study and units by the overall variance observed in the data

(variance attributed to measurement error, phylogeny, species, study and units). Higher values of I^2 indicate that more of the observed variance is true rather than due to measurement error, with 25%, 50% and 75% as low, moderate and high benchmarks, respectively (Borenstein *et al.* 2011; Nakagawa & Santos 2012).

I^2 describes the amount of true heterogeneity seen, but these results should be interpreted with caution. I^2 is independent of the absolute value of the variance observed, which is good because it does not vary based on the scale or number of studies included in the meta-analysis (Borenstein *et al.* 2011). However, this measure does not take into account the dispersion of effect sizes, only the precision with which effect sizes were measured (Borenstein *et al.* 2011). Thus, identical I^2 values could be obtained even if the between-species variance differed by an order of magnitude (Borenstein *et al.* 2011). If the true effect size for each species or study is spread over a wide range, I^2 cannot capture this dispersion.

Supplementary Information

Supplementary Methods

Example R code: MCMCglmm

```
prior=list(R=list(V=1, nu=0.002), G=list(G1=list(V=1,nu=0.002),
G2=list(V=1,nu=0.002), G3=list(V=1,nu=0.002)))

model <- MCMCglmm(Z_condition_beg ~ reduction_y_n*environment -1,      #1
  random=~ animal + common_name + study,                             #2
  prior=prior,                                                         #3
  pedigree=full_tree[[i]],                                           #4
  mev=CB_data_beh$variance,                                          #5
  data=CB_data_beh, family="gaussian", verbose=F, pr=T, slice=T,    #6
  nitt=8000000, burnin=2000000, thin=1000)                          #7

#1 Z-transformed correlation coefficient ~ Brood reduction strategy * Environment –
Intercept

#2 Controlling for phylogeny, repeated measures on each species, repeated measures on
each study

#3 Uninformative prior probability

#4 The phylogenetic tree

#5 Weighted by variance:  $(n-3)^{-1}$ , where n=number of broods for that effect size

#6 Data set, distribution of Y variable, and model output arguments

#7 8,000,000 iterations, excluding the first 2,000,000 iterations, and thinning every 1000
```

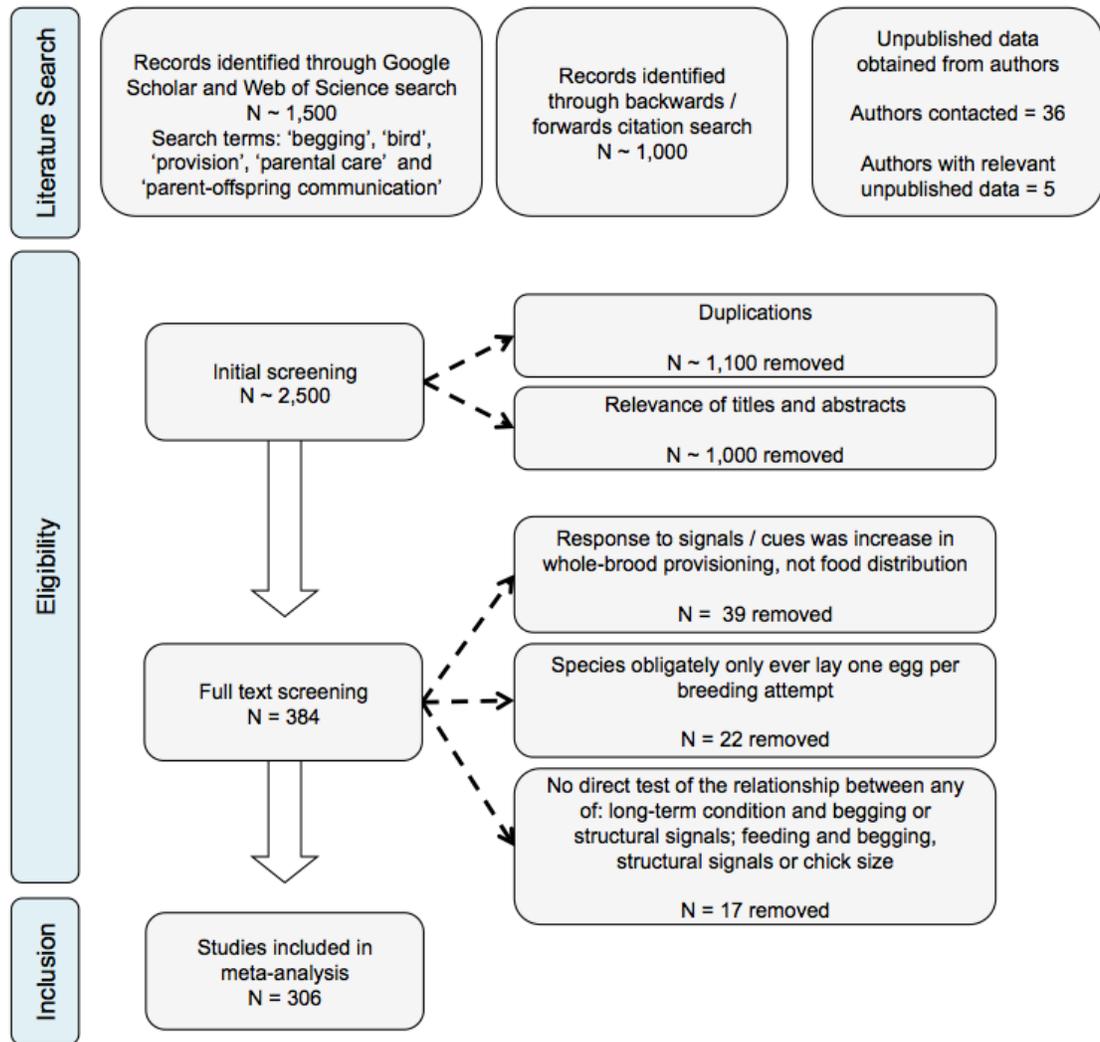
ASReml Analyses

To confirm the MCMCglmm results, we analysed the data using ASReml-R (Butler *et al.* 2009; R Core Team 2013). MCMCglmm is a Bayesian analysis that moves through parameter space through repeated iterations until the model converges on the best posterior estimate of confidence intervals, which allows the detection of effects with smaller sample sizes than traditional, maximum likelihood statistical tests, which assume larger sample sizes (Lee & Song 2004; Hadfield 2010; Hadfield *et al.* 2014).

However, *a priori* assumptions about the prior probability distributions of random effects must be made. Those assumptions could potentially bias results. ASReml makes no such assumptions, but gives less accurate confidence intervals for variance components, which could bias estimates of fixed effects' coefficients (Hadfield 2010; Hadfield *et al.* 2014). Employing both techniques allows us to determine whether our results are robust or statistical artefacts. Linear mixed models were run with 250 random trees with an Erickson backbone and 250 with a Hackett backbone (Jetz *et al.* 2014). The 500 models were averaged to determine the significance of fixed effects using the Wald test, a pseudo-analysis of variance (Supplementary Table 8).

The only difference between the results of our ASReml and MCMCglmm analyses is that the effect of the environment on the correlation between structural signals and feeding changes from significant ($p_{\text{MCMC}}=0.007$) to non-significant ($p=0.098$). This may be due to low sample size for this analysis ($n=4$ effect sizes in poor environments and $n=6$ in good environments), which influences maximum likelihood statistical analyses (such as ASReml) more than Bayesian analyses (such as MCMCglmm) (Lee & Song 2004). Bayesian analyses can accommodate a lower sample size to parameters ratio than maximum likelihood models (Lee & Song 2004).

Supplementary Figures



Supplementary Figure 2.1. PRISMA flow chart of search results and the study selection process. See Supplementary Table 2.9 for a list of papers excluded from the analysis.

Supplementary Tables

Supplementary Table 2.1. Condition and begging: tests for confounding methodological factors

		n	95% CI
Study design	Experimental	155	-0.29 to 0.00
	Observational	92	-0.36 to -0.05
Long-term condition measure	Long term change to food intake	47	-0.37 to -0.05
	Condition	31	-0.44 to -0.14
	Health	17	-0.47 to 0.08
	Size rank	117	-0.21 to 0.07
	Weight	35	-0.23 to 0.12
How chick comparisons were made	Continuous	180	-0.31 to -0.03
	Dichotomous	64	-0.36 to 0.02
	Whole brood	3	-0.55 to 0.14
Beg variable type	Continuous	226	-0.30 to -0.04
	Probability	21	-0.40 to 0.12
Beg mode	Audio	82	-0.32 to -0.01
	Posture	113	-0.41 to 0.00
	Combination	52	-0.31 to 0.01

n=number of effect sizes

Supplementary Table 2.2. Condition and structural signals: tests for confounding methodological factors

		n	95% CI
Study design	Experimental	100	-0.12 to 0.69
	Observational	40	-0.13 to 0.02
Long-term condition measure	Long term change to food intake	8	0.09 to 0.60
	Condition	48	-0.11 to 0.34
	Health	15	0.05 to 0.57
	Size rank	32	-0.04 to 0.44
	Weight	37	-0.08 to 0.39

n=number of effect sizes. Analyses not run: How chick comparisons were made: continuous (n=133) vs dichotomous (n=7)

Supplementary Table 2.3. Feeding and begging: tests for confounding methodological factors

		n	95% CI
Study design	Experimental	193	0.43 to 0.75
	Observational	108	0.47 to 0.84
Feeding measurement type	Food amount	113	0.36 to 0.73
	Chick growth	9	-0.11 to 0.78
	Probability	179	0.50 to 0.84
How chick comparisons were made	Continuous	237	0.48 to 0.78
	Dichotomous	4	-0.49 to 1.24
	High quality chicks	33	0.28 to 0.84
	Low quality chicks	27	0.27 to 0.86
Beg variable type	Continuous	240	0.49 to 0.79
	Hunger*	31	0.26 to 0.81
	Probability	30	0.17 to 0.82
Beg mode	Audio	51	0.24 to 0.73
	Posture	147	0.53 to 0.89
	Combination	103	0.38 to 0.74
	Both	235	0.46 to 0.76
Which parent was tested	Female only	36	0.33 to 0.82
	Male only	26	0.48 to 1.03
	Helper	4	-0.22 to 1.19

n=number of effect sizes

*Chicks were food deprived, and authors presumed this increased their behavioural begging intensity. Feeding rates were typically compared pre- and post-deprivation

Supplementary Table 2.4. Food allocation and structural signals: tests for confounding methodological factors

		n	95% CI
Feeding measurement type	Food amount	38	0.08 to 0.69
	Chick growth	10	-0.05 to 0.73
	Mortality	3	-0.21 to 0.90
	Probability	9	-0.14 to 0.86
How chick comparisons were made	Continuous	44	0.07 to 0.60
	High quality chicks	9	0.09 to 0.83
	Low quality chicks	7	0.07 to 0.83

n=number of effect sizes. Analyses not run: Study design: experimental (n=59) vs observational (n=1). (b) Which parent tested: both (n=54), female only (n=3) or male only (n=3).

Supplementary Table 2.5. Food allocation and body size: tests for confounding methodological factors

		n	95% CI
Study design	Experimental	384	0.25 to 0.55
	Observational	430	0.31 to 0.60
Feeding measurement type	Food amount	282	0.22 to 0.53
	Chick growth	288	0.32 to 0.62
	Mortality	140	0.29 to 0.60
	Probability	104	0.24 to 0.61
How chick comparisons were made	Continuous	449	0.25 to 0.51
	Dichotomous	361	0.35 to 0.63
	Whole brood	4	0.15 to 1.65
Which parent was tested	Both	670	0.31 to 0.59
	Female only	70	-0.07 to 0.30
	Male only	66	0.18 to 0.55
	Helper	8	0.04 to 0.86

n=number of effect sizes.

Supplementary Table 2.6. Random effects and heterogeneity in the analyses

a. Long-term condition and signals

	Random effect	Posterior mean	95% CI	I ²
Begging: Null model	Phylogeny	0.0145	0.0001 to 0.0590	1.2%
	Species	0.0151	0.0002 to 0.0566	1.3%
	Study	0.1245	0.0621 to 0.1977	10.4%
	Units	0.0424	0.0141 to 0.0725	3.5%
	<i>Total</i>			
Begging: Full model	Phylogeny	0.0136	0.0002 to 0.0543	1.1%
	Species	0.0132	0.0002 to 0.0504	1.1%
	Study	0.1220	0.0543 to 0.1902	10.3%
	Units	0.0411	0.0131 to 0.0718	3.5%
	<i>Total</i>			
Structural signals: Null model	Phylogeny	0.0226	0.0002 to 0.0753	2.1%
	Species	0.0229	0.0002 to 0.0647	2.1%
	Study	0.0149	0.0002 to 0.0384	1.4%
	Units	0.0169	0.0047 to 0.0307	1.6%
	<i>Total</i>			
Structural signals: Full model	Phylogeny	0.0328	0.0002 to 0.1060	3.0%
	Species	0.0325	0.0002 to 0.0910	3.0%
	Study	0.0163	0.0003 to 0.0399	1.5%
	Units	0.0087	0.0007 to 0.0183	0.8%
	<i>Total</i>			

b. Feeding and chick information

	Random effect	Posterior mean	95% CI	I ²
Begging: Null model	Phylogeny	0.0108	0.0001 to 0.0400	0.8%
	Species	0.0143	0.0002 to 0.0472	1.1%
	Study	0.0929	0.0326 to 0.1621	7.1%
	Units	0.1840	0.1329 to 0.2371	14.1%
	<i>Total</i>			<i>23.2%</i>
Begging: Full model	Phylogeny	0.0104	0.0002 to 0.0380	0.8%
	Species	0.0138	0.0002 to 0.0472	1.1%
	Study	0.0762	0.0149 to 0.1404	5.9%
	Units	0.1888	0.1379 to 0.243	14.6%
	<i>Total</i>			<i>22.4%</i>
Structural signals: Null model	Phylogeny	0.0283	0.0002 to 0.1163	2.4%
	Species	0.0211	0.0002 to 0.0863	1.8%
	Study	0.1288	0.0030 to 0.2735	10.7%
	Units	0.0248	0.0003 to 0.0687	2.1%
	<i>Total</i>			<i>16.9%</i>
Structural signals: Full model	Phylogeny	0.0282	0.0002 to 0.1190	2.2%
	Species	0.0222	0.0001 to 0.0920	1.8%
	Study	0.1897	0.0132 to 0.2105	15.1%
	Units	0.0157	0.0002 to 0.0477	1.3%
	<i>Total</i>			<i>20.4%</i>
Body size: Null model	Phylogeny	0.0163	0.0003 to 0.0402	1.4%
	Species	0.0072	0.0002 to 0.0223	0.6%
	Study	0.0690	0.0421 to 0.0996	5.8%
	Units	0.0893	0.0726 to 0.1081	7.6%
	<i>Total</i>			<i>15.4%</i>
Body size: Full model	Phylogeny	0.0085	0.0002 to 0.0233	0.7%
	Species	0.0044	0.0002 to 0.0130	0.4%
	Study	0.0620	0.0380 to 0.0869	5.3%
	Units	0.0875	0.0694 to 0.1055	7.5%
	<i>Total</i>			<i>14.0%</i>

Full models correspond to Tables 1 and 2. Models were weighted by study sample size (the number of broods used to calculate the original test statistic). Sample error variance was constrained to 1.

Supplementary Table 2.7. Heritability of communication strategies

Signal and response strategies	Heritability
Long-term condition and begging	7.16%
Long-term condition and structural signals	36.32%
Feeding and begging	3.60%
Feeding and body size	5.23%
Feeding and structural signals	11.06%

Table reports the percentage of variance in signalling or response strategy that is due to shared phylogeny, from 200 MCMCglmm linear mixed models, including environmental predictability and quality as fixed effects, controlling for repeated measures on studies and species, and weighted by study sample size (the number of broods used to calculate the original test statistic).

Supplementary Table 2.8. Results of ASReml analyses on environmental and life history influences on parent-offspring communication

Correlation between...	Fixed effects	Mean Wald Statistic	Mean Pr (Chisq)
condition and begging	Reduction strategy	7.40	0.007**
	Environmental quality	7.87	0.02*
	Reduction * Environment	0.52	0.5
condition and structural signal	Reduction strategy	1.02	0.3
	Environmental quality	15.28	0.0005***
	Reduction * Environment	7.48	0.02*
begging and feeding	Reduction strategy	0.05	0.8
	Environmental quality	6.89	0.03*
	Reduction * Environment	1.02	0.6
structural signals and feeding	Reduction strategy	0.72	0.4
	Environmental quality	4.64	0.1
	<i>Reduction * Environment</i>	<i>5.53</i>	<i>0.06.</i>
body size and feeding	Reduction strategy	40.71	2e-10***
	Environmental quality	15.81	0.0004***
	Reduction * Environment	0.32	0.9

. $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$

Supplementary Table 2.9. Studies excluded from the meta-analysis

This table was published online: <http://www.nature.com/articles/ncomms10985>. It has been omitted from the hard copy of this dissertation due to space considerations.

3. ENVIRONMENTAL CONDITIONS AND FACULTATIVE ADJUSTMENT OF PARENT-OFFSPRING COMMUNICATION

Abstract

Parents rely on signals and cues of offspring condition to guide how they distribute food amongst their brood. Whether parents benefit more from feeding the offspring in the worst or the best condition depends on how likely offspring starvation is: when all offspring are likely to survive, parents should preferentially feed offspring in the worst condition, but when partial brood starvation is likely, parents should preferentially feed the highest quality offspring. Different signalling systems have evolved to facilitate this distribution of resources. Across species, birds respond more to begging signals when the whole brood is likely to survive, but more to size cues when brood reduction is likely. Here, we test whether we can observe the same variation in responsiveness to begging and size cues within bird species. We use a combination of detailed field data on great tits, *Parus major*, and comparative data from 57 species to assess whether parents change how they respond to begging signals and size cues based on the likelihood of brood reduction. We show that: (i) individual great tits change how they respond to begging and size cues depending on how variable in size offspring within their brood vary are, how big their brood is, how intensely their whole brood is begging, and how old their brood is; and (ii) across 57 species, birds show consistent within-species patterns of responding more to begging and less to size cues when the environment is better. These findings indicate that parents can facultatively adjust how they respond to offspring signals based on local conditions.

Introduction

Parents must decide how to distribute food amongst their offspring. Those who choose incorrectly risk allowing the starvation of offspring that could have survived, or wasting resources on offspring that have no chance of survival. Parents can base their decisions on cues of offspring quality, such as body size, or on signals of condition, such as begging calls. Evolutionary theory predicts that the way in which parents should respond to and feed their offspring will depend upon the local environmental conditions (Davis *et al.* 1999; Mock *et al.* 2011; Grodzinski & Johnstone 2012). If parents are likely to find enough food to raise their whole brood, theory predicts parents should distribute food based on honest signals of need, feeding the offspring with greater need (Godfray 1995b; Davis *et al.* 1999; Godfray & Johnstone 2000). Conversely, when some of their offspring will probably starve, theory predicts parents should distribute food based on offspring cues or signals of high quality, feeding the highest-quality offspring (Lack 1947; 1954; Grafen 1990; Davis *et al.* 1999; Royle *et al.* 2002; Mock *et al.* 2011; Caro *et al.* 2016a).

Empirical data from 143 species of birds support the prediction that when food is relatively plentiful, parents preferentially feed offspring in the worst condition (a whole-brood survival strategy), but when food is relatively scarce, parents preferentially feed offspring in the best condition (a brood-reduction strategy) (Caro *et al.* 2016a). Species achieve these preferred food distribution patterns by responding differently to offspring signals and cues based on environmental conditions (Caro *et al.* 2016a). For example, in the Rufous-tailed scrub robin, the whole brood almost always survives, and parents preferentially feed offspring in the worst condition by distributing food based on begging (Moreno-Rueda *et al.* 2009). In contrast, brood reduction is common in the

hoopoe, and parents preferentially feed offspring in the best condition by distributing food based on size cues (Martin-Vivaldi *et al.* 1999). It is clear that species have evolved different rules for allocating food based on the likelihood that parents will not be able to rear their whole brood (Caro *et al.* 2016a).

In contrast, it is less clear whether facultative parental responsiveness to offspring begging and body size cues can be observed within species, with parents adjusting their behaviour conditionally in response to the local conditions (Kilner 2002; Figure 3.1). We might expect flexibility to evolve in species that experience variable ecological conditions within or between breeding bouts. There is some evidence that parents modulate how they respond to signals of quality based on environmental conditions. For example, hihi (Thorogood *et al.* 2011), alpine swift and European starling (Bize *et al.* 2006) parents respond differently to offspring colouration as environmental conditions change. American coot parents completely reverse their preference for larger offspring after the critical period of brood reduction has passed (Shizuka & Lyon 2012). It is not known, however, whether we can observe the combined pattern of parents relying more on size cues of quality and less on begging signals as brood reduction becomes more likely within species.

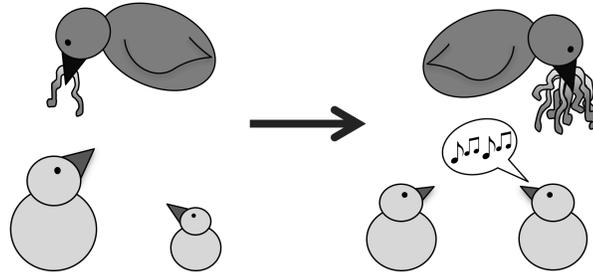


Figure 3.1. Facultative adjustment of parental responsiveness to begging and size cues. As local environmental conditions improve, parents should shift from preferentially feeding offspring in the best condition to feeding offspring in the worst condition. We predict that parents will do this by responding less to size cues and more to begging when food is plentiful enough to support the survival of the whole brood. Figure adapted from Caro *et al.* 2016a.

We examined this question using a combination of field data on parental provisioning in great tits (*Parus major*) and a comparative study across 57 species of birds. We asked whether parents varied their sensitivity to postural begging signals and size rank cues under different conditions, when brood reduction was more or less likely. For our great tit study, we used several proxies for the risk of brood reduction, including hatching date, weight spread within the brood, brood size, and overall begging intensity of the brood. Broods that hatch later in the breeding season may experience worse conditions, with a higher risk of brood reduction (Perrins 1970; Nager & van Noordwijk 1995; Van Noordwijk *et al.* 1995; Verhulst *et al.* 1995a, b). Broods with a large weight spread contain runts, marginal offspring that may be close to starvation (Magrath 1990; Forbes *et al.* 1997). Parents of larger broods may be less able to rescue needy offspring that are close to starvation. Finally, broods with a higher overall begging intensity may be hungrier, indicating a greater risk of offspring starvation (reviewed in Wright & Leonard 2002). We also tested for any differences between years, as well as for any interactions between these variables which could amplify the risk of brood reduction (Nager & van Noordwijk 1995). For example, parents with only 3 hungry offspring may

be more likely to be able to rescue a small runt from starvation than parents with 11 hungry offspring to feed. We predicted that great tit parents would respond less to begging and more to size cues when the risk of brood reduction is greater.

For our comparative study, we assessed how widespread flexibility in parental responsiveness is in a phylogenetic meta-analysis on 57 species. Following our previous meta-analysis, we categorised species' current environmental quality as poor (high risk of brood reduction), normal, and good (low risk of brood reduction) (Caro *et al.* 2016a). We measured parental responsiveness using the correlation coefficients between feeding and begging, and feeding and size cues. We assessed facultative adjustment by looking at the slope of responsiveness as environmental conditions vary. We predicted a consistent within-species pattern where parents respond less to begging but more to size cues when environmental conditions are worse.

Methods

Great tit study

Data on great tits were collected by Camilla Hinde as part of long-term field studies on wild great tits living in mixed deciduous woodland in Cambridgeshire, UK. Study sites, data collection procedures and brood size manipulations have been described in detail elsewhere (Hinde 2006; Hinde & Kilner 2007; Stoddard *et al.* 2012; Johnstone *et al.* 2013). We standardised brood size to 7 in 2000, 2001 and 2002 using age-matched offspring as in Brinkhof *et al.* 1999, and brood size varied between 3 and 11 offspring in other years (mean brood size in this population=6.7, Hinde 2006). Video data on responsiveness to postural begging were available for years 1999, 2000 and 2001.

Growth data on responsiveness to size cues were available for years 2002, 2004 and 2009.

Parental response to offspring postural begging

We videotaped feeding visits and recorded both parent and chick behaviour at 52 nests over three years (n=1534 feeding visits). Broods were filmed approximately midway through the nestling period (approximately 9 days after hatching) for one hour. Nests had an average of 29 feeding visits each recording (range 6 to 36). We ranked all chicks' begging posture intensity on a scale of 0-3, where 0=mouth closed, 1=mouth open with neck bent, 2=mouth open with neck outstretched, and 3=mouth open with body raised. Analyses of offspring behaviour are included in Supplementary Figure 3.1 and Supplementary Table 3.1.

To determine how much parents respond to begging, we divided the begging posture of the fed chick by the mean posture of all begging chicks on that feeding visit. Values greater than 1 indicate that parents preferentially feed chicks having a higher posture score than their siblings (that is, begging relatively more than their siblings). Values less than 1 indicate that parents preferentially feed offspring begging less than the mean begging posture of all begging offspring (that is, begging relatively less than their siblings). Calculating this measure for each feeding visit and including the mean posture of all siblings as a control variable in models, rather than only calculating the mean begging posture of fed chicks, controls for differences in overall brood begging intensity. Some broods may beg less intensely than others, which could confound measures of food distribution based on absolute begging intensity.

We analysed responsiveness to begging in four ways to account for potential issues with our ability to detect parental preferences (Supplementary Table 3.2). In the first model, reported in the main text, we included all feeding visits, and our measure of the mean begging posture of offspring excluded nestlings that were not begging at all. This response variable captured parents' response to begging behaviour from nestlings that they could see begging. In the second model, we used the same parental response variable, but we excluded 491 feeding visits where there was no variation in begging posture (Supplementary Table 3.3). In such cases, parents may have been unable to respond to begging posture, decreasing the potential effectiveness of begging. In the third model and fourth models, we used a slightly different measure of parental responsiveness. Here, our parental response variable was relative to the mean begging posture of the entire brood, including nestlings that were not begging during that feeding visit (Supplementary Tables 3.4 and 3.5). The third model used all feeding visit data, and the fourth excluded data where there was no variation in begging. Differences between models are considered in the Discussion and Supplementary Information.

Parental response to offspring size

We quantified how much parents respond to offspring body size by examining the slope of the amount of weight gained over the next two days over size rank, within broods (n=99 nests over 3 years, approximately 7 measurements per nest). Using the slope of this relationship within each brood circumvents the issue of non-independence of data on chicks from the same brood. Negative slopes between size rank and subsequent weight gain imply that parents preferentially fed relatively smaller chicks. Positive slopes imply parents preferentially fed larger chicks, or that larger chicks receive more food through scramble competition. If parents exert even partial control over resource

distribution, this measure should capture their size preferences. Three nests were excluded from analyses because males deserted during the nestling period.

Brood reduction risk

We estimated the risk of brood reduction using a combination of hatching date, weight spread within the brood, brood size, and overall begging intensity of the brood. Great tit broods that hatch later in the breeding season may experience worse environmental conditions (Nager & van Noordwijk 1995; Van Noordwijk *et al.* 1995; Verhulst *et al.* 1995b). A wide weight spread within the brood midway through the nestling period indicates the smallest chicks are marginal runts who are at a significant competitive disadvantage and face a high risk of starvation (Magrath 1990; Forbes *et al.* 1997). The size difference between the largest and smallest chick in the nest is likely obvious to parents, and therefore may be used by parents to determine how likely the smallest chick's survival is. This size difference represents the combined effect of hatching asynchrony and feeding history. Larger broods may also face a higher risk of brood reduction, especially in combination with other risk factors. Finally, the overall mean postural begging intensity of the brood is a marker of how demanding the brood is overall: hungrier broods may be at a greater risk of starvation (Kilner 2002).

Statistical analysis

We analysed data using the lme4 package for linear mixed models in R (R Core Team 2013; Bates *et al.* 2015). We standardised and centred all predictor variables within years, and we log-transformed relative begging intensity to account for skew (Cohen *et al.* 2003). We included year as a fixed effect. We selected the final models using backwards elimination: we ran a maximum model with all possible three-way

interactions, and sequentially removed higher-order interactions if the likelihood ratio test was not significant based on reductions to AIC (Akaike 2011). We conservatively used $p < 0.01$ as the significance criterion for interaction terms because we ran multiple models. If an interaction was significant, we treated all lower-order terms as significant. We did not remove any main effects from the final model because they were planned *a priori*. We controlled for nest ID in all models, and for parent ID in begging models.

Comparative study

Data collection for the meta-analysis

To determine whether birds show a consistent adjustment of feeding rules based on local conditions across species, we collected data on within-species changes in the strength of the relationship (correlation coefficient) between feeding and begging in 17 species, and feeding and size cues in 52 species. This data was collected as part of a previous meta-analysis (Caro *et al.* 2016a). We conducted a literature search on Web of Science and Google Scholar using the keywords ‘beg’, ‘parent-offspring’, ‘bird’, ‘begging’, ‘communication’ and ‘provision’ (see Supplementary Figure 3.2 for PRISMA flowchart detailing data collection). We performed backwards and forwards citation searches on all studies. We included studies published before August 2014. We included all papers with any measure relating to the relationship between parental food allocation and offspring behavioural begging or size cues. We excluded species that did not have data on these relationships in more than one environment condition, since we were interested in the change in the strength of these relationships over different ecological conditions. We excluded effect sizes if it was impossible to determine whether parents were responding to begging or to size cues. We excluded studies where offspring signals were structural (such as mouth colour), rather than behavioural (such

as begging postures), as these may represent different signalling systems. We only included effect sizes for the relationship of begging on within-brood food allocation, rather than on increases in overall parental feeding effort, as these represent fundamentally different aspects of parental care. We excluded data on species that lay only one egg per brood, as selective pressures on these species are likely to differ from species laying multiple eggs per brood. If relevant data were given in papers without statistical tests, such as raw means and standard errors, we estimated effect sizes (Borenstein *et al.* 2011). This resulted in a dataset of 719 effect sizes from 145 studies on 57 species (Appendix, Tables A1 and A2).

Environmental conditions

We categorized populations as experiencing normal, better than normal, or worse than normal environments, based on experimental manipulations (parents were fed reduced or supplemented diets, or chick demand was artificially increased or decreased), ecological measures (such as prey density, date or rainfall), or average mortality across different years in long-term observational studies (Caro *et al.* 2016a). Only long-term manipulations of food availability over multiple days were included, to ensure offspring long-term condition, and not simply normal differences in hunger level, was affected by the ecological variation. If no information on environmental quality was available, data were conservatively classified as normal conditions.

Measures of feeding, begging and size cues

Many aspects of the behavioural and structural signalling suite were reported in the literature, such as begging amplitude, duration, latency, likelihood, call structure, and begging postures. Different measures of food allocation were also presented, such as

weight gain over a short time period, actual food intake, number of food items received, likelihood of being fed, growth rate, and mortality. We assumed all measures of begging intensity and feeding preferences were functionally equivalent, and so included all reported statistics in our analyses. Because test statistics were converted to a standardized scale, differences between the various measures of begging intensity or feeding preferences should not influence the overall trends seen. Our previous comparative analysis, using a more comprehensive dataset, found no impact of study methodology, such as which measure of feeding preference was used or whether studies were experimental or observational, on the effect size of begging or size cues on feeding preferences (Caro *et al.* 2016a).

Statistical analyses

We transformed any test statistic measuring either an effect of begging or size cues on feeding into a standardized effect size (Fisher's *Z*-transformed correlation coefficient) (Borenstein *et al.* 2011; Grissom & Kim 2011; Koricheva *et al.* 2013). These correlation coefficients follow a normal distribution, account for different scales in their original measurements, are well suited to the ordered nature of the data, and are more straightforward to interpret than standardized difference in means (Borenstein *et al.* 2011; Grissom & Kim 2011; Koricheva *et al.* 2013). Fisher's *Z*-transformed correlation coefficients were analysed using the MCMCglmm package in R, which implements Bayesian generalized linear mixed models with Markov chain Monte Carlo methods (Hadfield 2010; R Core Team 2013). We ran bivariate response models so we could measure phylogenetic covariance between responsiveness to begging and responsiveness to size cues. We weighted models by sample size, and controlled for phylogeny and repeated measures on the same study and species. Our measure of

sample size was the number of broods used to generate the original test statistic, because this is a standard measure across studies, and conservatively avoids pseudoreplication if chick number or number of observations were used as the sample size. We treated environmental quality as a three-level ordered categorical variable. We obtained phylogenies from Birdtree.org, ran models on 4 random phylogenetic trees with Ericson and Hackett backbones, and then averaged model results (Jetz *et al.* 2014).

Results

Great tits study

Parental responsiveness to postural begging

Great tit parents respond less to their offspring's postural begging when brood reduction is more likely based on a combination of having a larger brood, indicating greater overall provisioning needs; having a larger weight spread within the brood, indicating the presence of runty offspring; and having the whole brood begging at higher intensities, indicating a greater overall need for food (3-way interaction: 95% CI -0.06 to -0.02, $p=0.0003^{***}$; Table 3.1; Figure 3.2). When mean begging intensity is high, parents of large, but not small, broods respond less to begging when there is a greater weight spread in the brood. When the overall demand for food is low, a different pattern is seen: parents of both large and small broods respond more to begging as weight spread increases.

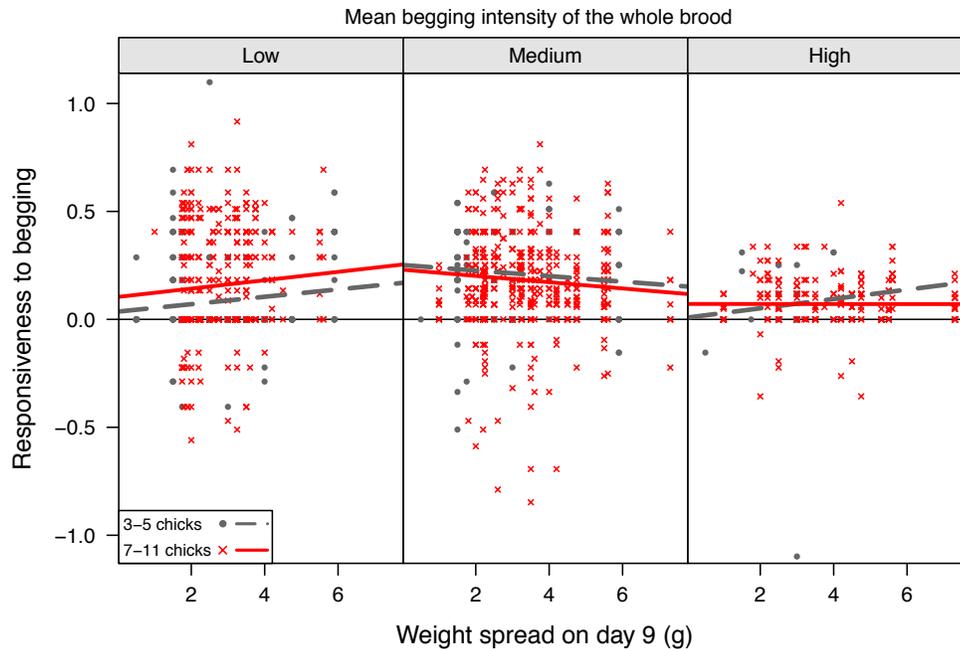


Figure 3.2. Parents adjust how they respond to individual offspring begging based on brood size, weight spread and the brood's begging intensity. Each data point represents a parent's responsiveness to begging on a feeding visit. Response to begging was calculated as the posture of the fed chick divided by the average begging intensity of all begging chicks on that feeding visit. Larger values indicate that parents preferentially fed chicks begging at a relatively high intensity, and values below zero indicate parents fed a chick begging less intensely than its siblings. For graphical simplicity, broods were classified as small (grey, closed circles and dashed line) or large (red, crosses and solid line), and feeding visits were classified as having relatively low (>1), medium (1-2), or high (>2) mean begging intensity of the whole brood. Statistical analyses were done on brood size and mean brood posture as continuous variables. Weight spread within the brood midway through the nestling period is used as a proxy for offspring starvation risk: larger spreads indicate greater competitive asymmetry among chicks. The greater this asymmetry, the less parents respond to an individual chick's begging posture, especially in large broods when the whole brood is begging more intensely. n=1534 feeding visits, 104 birds in 52 nests over 3 years.

Parents in different years behaved differently (Table 3.1; Figure 3.3). Parents in 2000 were more responsive to the begging of individual chicks when the overall demand for food was greater, but this pattern flipped in 2001 and 2002 (2001: 95% CI -0.12 to -

0.04, 2002: 95% CI -0.12 to -0.06, $p < 0.0001^{***}$; Table 3.1; Figure 3.3). We did not find an effect of hatch date (95% CI -0.01 to 0.02, $p=0.71$; Table 3.1).

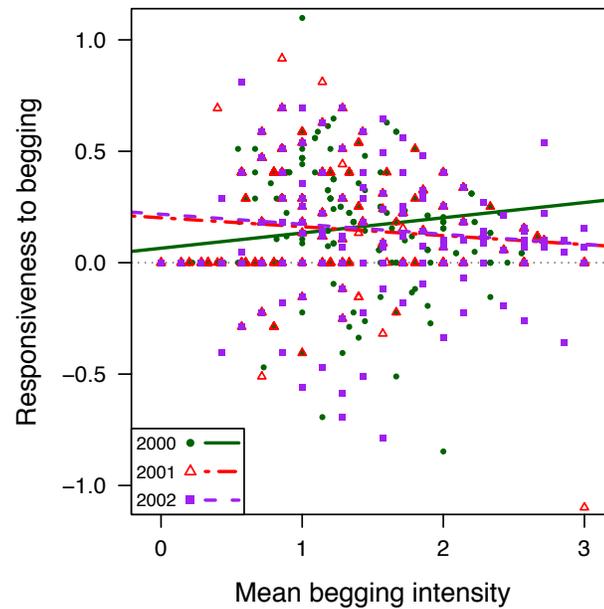


Figure 3.3. As overall demand for food increases, parents responded less to postural begging in 2001 and 2002, but not in 2000. Each data point represents an individual's responsiveness to begging on a feeding visit. Response to begging was calculated as the posture of the fed chick divided by the average begging intensity of all begging chicks on that feeding visit. Larger values indicate that parents preferentially fed chicks begging at a relatively high intensity, and values below zero indicate parents fed a chick begging less intensely than its siblings. The mean begging intensity of the whole brood is used as a measure of the overall demand for food. Parents were less responsive to begging as overall demand increased only in some years. $n=1534$ feeding visits, 104 birds in 52 nests over 3 years.

Table 3.1. Parental responsiveness to postural begging

	Estimate ± SE	95% CI	Δ AIC	Pr(Chi)
<i>Intercept</i>	0.15 ± 0.02	0.12 to 0.18		
Year				
2001	0.00 ± 0.03	-0.05 to 0.05		
2002	0.01 ± 0.02	-0.03 to 0.05		
Weight spread of brood on day 9	0.01 ± 0.01	-0.01 to 0.03		<i>significant</i>
Brood size	0.02 ± 0.01	0.00 to 0.05		<i>significant</i>
Hatchdate	0.00 ± 0.01	-0.01 to 0.02	+1.76	0.71
Mean posture of begging chicks	0.07 ± 0.01	0.04 to 0.09		<i>significant</i>
Brood's mean posture * Year			-31.81	>0.0001***
2001	-0.08 ± 0.02	-0.12 to -0.04		
2002	-0.09 ± 0.02	-0.12 to -0.06		
Weight spread * Brood size	-0.01 ± 0.01	-0.03 to 0.02		<i>significant</i>
Weight spread * Mean posture of begging chicks	-0.02 ± 0.01	-0.04 to -0.01		<i>significant</i>
Brood size * Mean posture of begging chicks	0.00 ± 0.01	-0.02 to 0.01		<i>significant</i>
Weight spread * Brood's mean posture * Brood size	-0.04 ± 0.01	-0.06 to -0.02	-11.40	0.0003***

Response to begging was calculated as the posture of fed chick divided by the average begging posture of all begging offspring on that visit. Relative begging posture was log-transformed to correct skew. All predictor variables were scaled and centred. We included all possible three-way interactions in the original model, and then simplified the model using backwards elimination based on likelihood-ratio tests. We included interactions only when $p < 0.01$. If a higher-order interaction was significant, all lower-order terms included in it were considered significant, and Δ AIC was only reported for the highest order interaction. No main effects were eliminated from the final model. Nest ID and parent ID were included as random effects. $n=1534$ feeding visits, 52 nests, 3 years.

Parental responsiveness to offspring size

Parents are more likely to preferentially feed larger offspring when there is a larger weight spread within the brood (95% CI 0.004 to 0.176, $p=0.040^*$; Table 3.2; Figure 3.4). Brood size had no impact on the relationship between offspring size rank and weight gain (95% CI -0.10 to 0.13, $p=0.9$; Table 3.2). As their offspring aged, parents across all broods shifted to preferring smaller chicks or to ignoring size cues (95% CI -0.48 to -0.20, $p < 0.0001^{***}$; Table 3.2; Figure 3.5). Parents were more responsive to chick size in 2002 than in 2004 or 2009 ($p=0.00025^{***}$; Table 3.2).

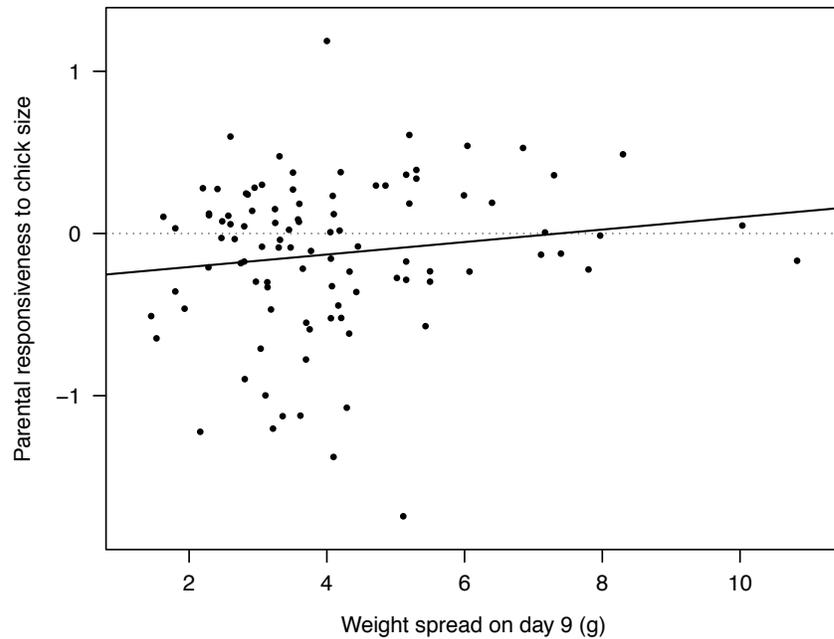


Figure 3.4. Parents respond more to chick size when there is a greater weight spread within the brood. Each data point represents the mean responsiveness to offspring size rank within a brood: the slope of each measurement day's relationship between chick weight rank and subsequent weight gain rank over the next two days. Positive values indicate that larger chicks gained relatively more weight. Negative values indicate that smaller chicks gained relatively more weight. Weight spread within the brood nine days after hatching is used as a proxy for offspring starvation risk: larger spreads indicate greater competitive asymmetry among chicks. The greater the risk of brood reduction, the more parents prefer to feed larger chicks. n=515 nest-dates combinations in 99 nests over 3 years.

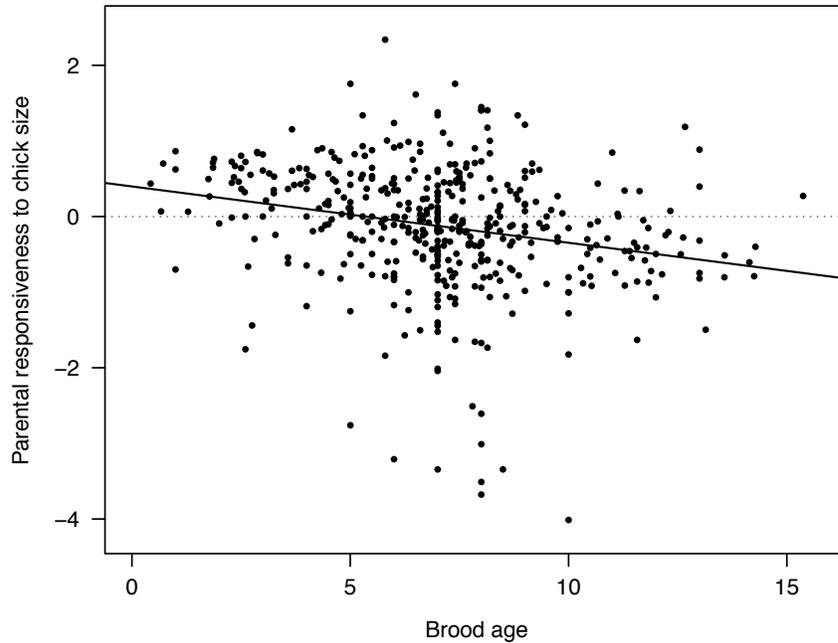


Figure 3.5. Parents respond less to chick size as their brood ages. Each data point represents the responsiveness to offspring size rank of a brood on a measurement day. Brood age is the mean age of all nestlings in the brood, and takes estimated hatching asynchrony into account. Response to size was calculated as the slope of each measurement day’s relationship between chick weight rank and subsequent weight gain rank over the next two days. Positive values indicate that larger chicks gained relatively more weight. Negative values indicate that smaller chicks gained relatively more weight. As chicks approached fledging age, parents responded less to chick size. n=515 nest-dates combinations in 99 nests over 3 years.

Table 3.2. Parental response to chick size in great tits

	Estimate ± SE	95% CI	Δ AIC	Pr(Chi)
<i>Intercept</i>	<i>0.04 ± 0.10</i>	<i>-0.14 to 0.23</i>		<i>0.65</i>
Weight spread on day 9	0.09 ± 0.04	0.004 to 0.18	-2.2	0.040*
Brood age	-0.34 ± 0.07	-0.48 to -0.20	-20.2	<0.0001***
Brood size	0.01 ± 0.06	-0.10 to 0.13	+2.0	0.86
Hatchdate	0.01 ± 0.06	-0.10 to 0.12	+2.0	0.81
Year			-12.6	0.00025***
2004	-0.16 ± 0.13	-0.42 to 0.10		
2009	-0.46 ± 0.11	-0.68 to -0.23		

Response to size was calculated as the slope of the relationship between chick weight rank and subsequent weight gain rank over the next two days. All interactions were dropped after backwards elimination of non-significant interactions. n=515 nest-dates combinations, 99 nests, 3 years.

Comparative Study

As predicted, we found that parents responded more to begging calls and postures in better environmental conditions (95% CI of the slope=0.13 to 0.67, pMCMC=0.0037; Figure 3.6a). Across the 17 species with data on responsiveness to begging in more than one environmental condition, 14 species showed the predicted positive slope (82%), and 3 had negative slopes (18%). Also as predicted, we found the opposite pattern with regard to size cues. Parents responded less to offspring size cues in worse environmental conditions (95% CI of the slope=-0.23 to -0.05, pMCMC=0.0016; Figure 3.6b). Across the 52 species with data on responsiveness to size cues in more than one environmental condition, 32 species showed the predicted negative slope (62%), and 20 had positive slopes (38%). We could not quantitatively compare slopes across species, because the magnitude of the difference between poor and good environmental categories may differ across species. There was no phylogenetic correlation between how responsive parents are to begging and how responsive they are to size cues (95% CI -0.54 to 0.52).

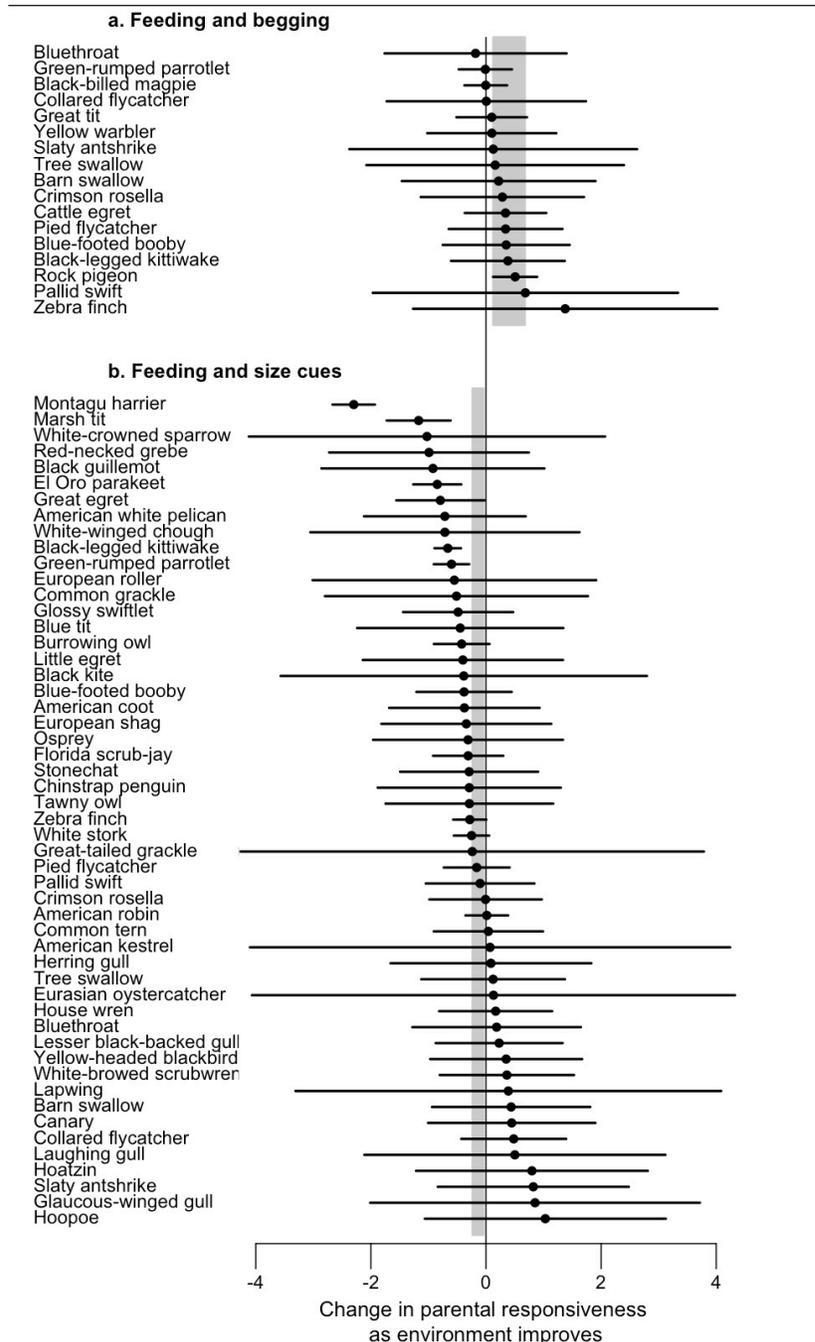


Figure 3.6. Environmental conditions and parental response to offspring begging and size. Circles represent each species' slope for the correlation coefficient between feeding and (a) begging, and (b) size cues, over environmental quality. Positive values indicate that parents respond more in better environments. Negative values indicate parents respond less in better environments. Lines represent the 95% CI of the slope within each species. The shaded region shows the 95% CI across all species, controlling for phylogeny and weighted by sample size. Species respond more to begging (n=17 species), and less to size cues (n=52 species), in better environments.

Discussion

The empirical and comparative evidence presented here suggests that parental response to offspring signals and cues is not fixed within species, but can vary depending on local conditions in a predictable way. Overall, we found that when the quality of the environment deteriorates, parents responded less to begging but more to size cues. This observation is consistent with the prediction that parents should switch to a brood reducing strategy when times are hard, and consistent with the previously observed between-species variation (Chapter 2, Caro *et al.* 2016a). We showed that great tits parents responded less to begging but more to size cues when their risk of brood reduction increased (Figures 3.2 and 3.3). Essentially, great tit parents shifted from preferentially feeding offspring in the worst condition to preferentially feeding offspring in the best condition to maximise the number and/or quality of their surviving offspring. Our meta-analysis suggests that the switch in strategy observed in great tits is typical across species: we found that parents adjust their response to signals or cues of offspring condition, in response to local environmental conditions (Figure 3.6a,b).

We found that great tit parents do not follow a simple rule for how to respond to begging and size cues, but instead integrate information from multiple sources as they gradually shift between strategies. As we had predicted, we found they responded to less to begging and more to size cues when there is a larger weight spread within the brood. However, this adjustment in responsiveness differed for parents of small and large broods, for parents with broods begging at different mean intensities, and for parents breeding in different years (Table 3.1; Figures 3.2 and 3.3). This indicates that parents combine multiple sources of information as they determine their food allocation rules, which is logical because multiple factors determine just how great the risk of starvation

will be for a particular brood. For example, the impacts of brood size and weight spread on brood reduction likelihood may be greater when the whole brood is demanding food at maximum intensity, because more demanding broods may be needier and closer to starvation. External environmental factors may also mediate parental responsiveness to begging, since parents behaved differently in different years (Kilner 2002; Table 3.1; Figure 3.3). In 2001 and 2002, parents were less responsive to individual level begging on feeding trips when all offspring were begging intensely, but they showed the opposite pattern in 2000 (Tables 3.1 and 3.3; Figure 3.3). This is likely because local conditions were better in 2000 than in 2001 and 2002: overall, offspring begged less intensely in 2000 than in 2001 or 2002, suggesting that offspring were less needy throughout the nestling period in 2000 (Supplementary Table 3.1; Supplementary Figure 3.1). Given that offspring behaviour shifts along with external environmental factors, correlational studies alone will be unable to determine what exactly causes shifts in signalling systems, and so experimental manipulations will be required to tease apart how parental attention is influenced by the interplay of the different factors.

A complicating factor is that it can be hard to determine whether parents actively ignore begging signals, or whether begging signals simply become less informative. It may be that if all offspring are begging at the maximum level, parents are forced to rely on size cues to determine which offspring to feed. Similarly, if all offspring are the same size, parents may be forced to rely on begging even if their preferred strategy would have been to feed according to size cues. Changes in offspring behaviour may also complicate parents' ability to actively choose how they respond to signals and cues: as weight spread increases within broods, so does the mean begging posture of the whole brood (Supplementary Table 3.1). This may mean that parents of broods containing

runts respond less to begging not through an active shift in strategy, but simply because it is more likely that all their offspring are begging at maximum intensity. However, when we excluded feeding visits where there was no variation in begging, we found similar results to the model containing all feeding visits (Supplementary Tables 3.2, 3.3, 3.4 and 3.5). This suggests that shifts in parental strategies are not completely determined by a lack of variation in signals.

We found that great tit parents show a dynamic response to size cues over the course of the nestling period, similar to the patterns seen in American coots (Shizuka & Lyon 2012). As nestling age increases, smaller chicks begin receiving relatively more food (Table 3.2; Figure 3.5). This pattern is consistent with a logical shift in parental strategies: the older nestlings are, the more likely they all are to survive to fledging, and the more parents benefit from feeding needier offspring. This finding also implies that resource distribution is controlled at least in part by parents, rather than solely by scramble competition amongst chicks. It is reasonable to assume that if offspring alone control resource distribution, larger chicks would increasingly be able to outcompete their smaller siblings as they gain mobility, vision and sharp beaks. This would have led to a stronger correlation between size and weight gain as nestlings age, rather than the weaker correlation we observed. Parents' responsiveness to begging may also be dynamic as the brood ages, and future studies could see whether this shift complements the shift in responsiveness to chick size.

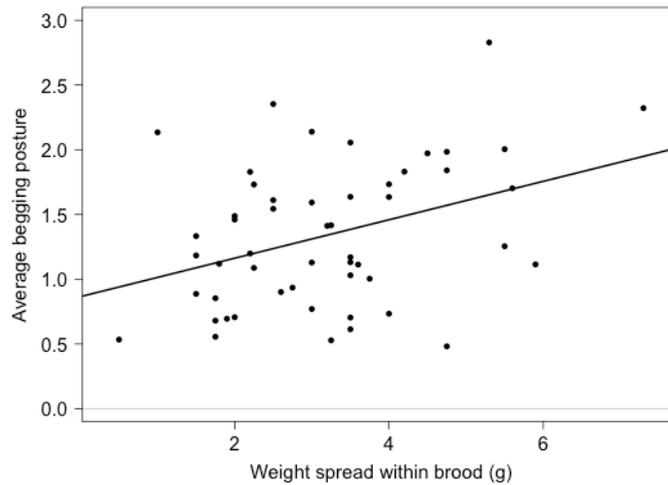
Taken together, the findings of our within-species comparative study and our great tits field study suggest that birds facultatively adjust how they respond to information about offspring condition. There is a consistent, general pattern that parents respond more to

begging signals and less to offspring size cues when local conditions are better. This change in food allocation rules is indicative of a dynamic shift in parental investment strategies: parents shift from preferentially feeding offspring in the best condition when brood reduction through starvation is likely, to preferentially feeding offspring in the worst condition when whole brood survival is likely. We even observed changes in food allocation rules within a single breeding bout. This flexibility highlights the need for new theory on parent-offspring communication that allows for dynamic changes in strategies, and that incorporates the iterative nature of parent-offspring interactions (Godfray 1995a; McNamara *et al.* 1999; Royle *et al.* 2002; Kilner & Hinde 2008).

Supplementary Information

Offspring postural begging and the risk of brood reduction

Great tit chicks beg more intensely when there is likely to be a greater risk of brood reduction. Mean begging intensity across broods was positively correlated with weight spread within the brood (95% CI 0.03 to 0.30, $p=0.014^*$; Supplementary Table 3.1; Supplementary Figure 3.1). Neither brood size (95% CI -0.09 to 0.23, $p=0.37$) nor hatch date (95% CI -0.11 to 0.15, $p=0.78$; Supplementary Table 3.1) impact the overall begging intensity of the brood.



Supplementary Figure 3.1. Begging intensity is higher when there is a greater weight spread within the brood. Each data point represents a brood's mean begging posture ($n=52$ nests). We ranked all chicks' postural begging intensity on a scale of 0-3, where 0=mouth closed, 1=mouth open with neck bent, 2=mouth open with neck outstretched, and 3=mouth open with body raised. Larger weight spreads midway through the nestling period indicate greater competitive asymmetry among chicks and higher risk that the smallest chick will starve.

Supplementary Table 3.1. Determinants of begging intensity across broods

	Estimate ± SE	95% CI	Δ AIC	Pr(Chi)
<i>Intercept</i>	<i>1.06 ± 0.10</i>	<i>0.376 to 1.25</i>		
Year			-9.2	0.0014**
2001	0.29 ± 0.19	-0.07 to 0.65		
2002	0.55 ± 0.15	0.26 to 0.83		
Weight spread on day 9	0.17 ± 0.07	0.03 to 0.30	-4.1	0.014*
Brood size	0.07 ± 0.08	-0.09 to 0.23	+1.2	0.37
Hatchdate	0.02 ± 0.07	-0.11 to 0.15	+1.9	0.78

Begging intensity was calculated as the average begging posture of the whole brood on each feeding visit. Non-significant interactions were dropped from the final model. Analyses controlled for nest ID. n=1534 feeding visits, 52 nests, 3 years.

Comparisons of models containing different measures of parental responsiveness to begging

Supplementary Table 3.2. Model comparisons

	All feeding visits (n=1534)	Only feeding visits with variation in begging (n=1043)
Posture of fed chick relative to only begging siblings	Model 1 (in main text)	Model 2
Posture of fed chick relative to all siblings	Model 3	Model 4

Model 1, the model reported in the main text had two significant 3-way interactions and one additional 2-way interaction. The results below compare the results of each final model for all possible interactions. The final model for each of the four models were determined using backwards elimination of non-significant interactions, with the cut-off value of $p < 0.01$.

- 3-way interaction between **weight spread, brood size, and mean brood posture**
 - Model 1: Kept in
 - $\Delta AIC -11.40$, $p=0.00025$
 - Model 2: Dropped out because of the stringent interaction cut-off of $p < 0.01$
 - $\Delta AIC -3.6$, $p=0.018$
 - Lower order interaction between brood size and mean brood posture ($p=0.0005$)
 - Model 3: Dropped out because of the stringent interaction cut-off of $p < 0.01$
 - $\Delta AIC -4.26$, $p=0.064$
 - Lower order interaction between brood size and mean brood posture ($p < 0.0001$)
 - Model 4: Dropped out because of the stringent interaction cut-off of $p < 0.01$
 - $\Delta AIC -1.164$, $p=0.075$
- 3-way interaction between **year, mean brood posture and hatch date**
 - Model 1: Dropped out
 - $\Delta AIC +3.74$, $p=0.88$
 - Model 2: Dropped out
 - $\Delta AIC +3.16$, $p=0.66$
 - Model 3: Dropped out because of the stringent interaction cut-off of $p < 0.01$
 - $\Delta AIC -4.27$, $p=0.016$
 - Model 4: Kept in
 - $\Delta AIC -9.25$, $p=0.0013$
- 2-way interaction between **year and brood posture**
 - Model 1: Kept in
 - $\Delta AIC -31.81$, $p < 0.0001$
 - Model 2: Kept in
 - $\Delta AIC -8.46$, $p=0.002$
 - Model 3: Dropped out because of the stringent interaction cut-off of $p < 0.01$
 - $\Delta AIC -4.20$, $p=0.017$
 - Model 4: Kept in as part of higher-order interaction

Supplementary Table 3.3. Parental responsiveness to postural begging: Model 2

	Estimate ± SE	95% CI	Δ AIC	Pr(Chi)
<i>Intercept</i>	<i>0.21 ± 0.02</i>	<i>0.18 to 0.24</i>		
Year				<i>significant</i>
2001	0.02 ± 0.03	-0.03 to 0.07		
2002	-0.02 ± 0.02	-0.06 to 0.02		
Weight spread of brood on day 9	0.01 ± 0.01	-0.01 to 0.03	+1.56	0.51
Brood size	0.02 ± 0.01	0.00 to 0.05		<i>significant</i>
Hatchdate	0.01 ± 0.01	-0.01 to 0.02	+1.62	0.54
Mean posture of begging chicks	0.01 ± 0.01	-0.02 to 0.04		<i>significant</i>
Brood's mean posture * Year			-8.46	0.002**
2001	-0.03 ± 0.02	-0.08 to 0.01		
2002	-0.06 ± 0.02	-0.10 to -0.03		
Brood size * Mean posture of begging chicks	-0.05 ± 0.01	-0.07 to -0.03	-16.47	>0.0001***

Response to begging was calculated as the posture of fed chick divided by the average begging posture of all begging offspring on that visit. Relative begging posture was log-transformed to correct skew. All predictor variables were scaled and centred. We included all possible three-way interactions in the original model, and then simplified the model using backwards elimination based on likelihood-ratio tests. We included interactions only when $p < 0.01$. If a higher-order interaction was significant, all lower-order terms included in it were considered significant, and Δ AIC was only reported for the highest order interaction. No main effects were eliminated from the final model. Nest ID and parent ID were included as random effects. $n=1534$ feeding visits, 52 nests, 3 years.

Supplementary Table 3.4. Parental responsiveness to postural begging: Model 3

	Estimate ± SE	95% CI	Δ AIC	Pr(Chi)
<i>Intercept</i>	<i>0.69 ± 0.02</i>	<i>0.65 to 0.73</i>		
Year			-12.33	0.0003***
2001	-0.04 ± 0.04	-0.11 to 0.03		
2002	-0.13 ± 0.03	-0.19 to -0.07		
Weight spread of brood on day 9	0.02 ± 0.01	-0.01 to 0.05	-0.58	0.12
Brood size	0.11 ± 0.02	0.08 to 0.15		<i>significant</i>
Hatchdate	-0.01 ± 0.01	-0.03 to 0.02	+1.69	0.58
Mean posture of begging chicks	-0.30 ± 0.01	-0.31 to -0.28		<i>significant</i>
Brood size * Mean posture of begging chicks	-0.04 ± 0.01	-0.06 to -0.02	-10.12	0.0005***

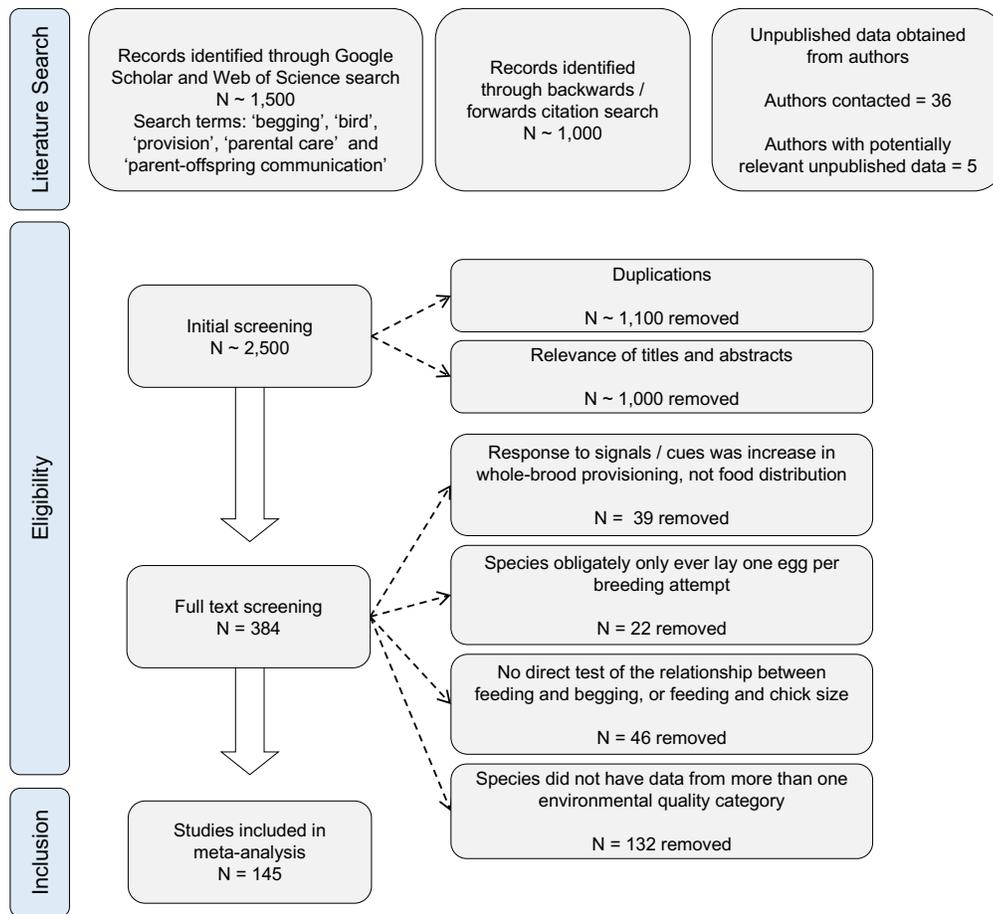
$n=1534$ feeding visits, 52 nests, 3 years.

Supplementary Table 3.5. Parental responsiveness to postural begging: Model 4

	Estimate ± SE	95% CI	Δ AIC	Pr(Chi)
<i>Intercept</i>	<i>0.85 ± 0.02</i>	<i>0.82 to 0.88</i>		
Year				<i>significant</i>
2001	-0.13 ± 0.03	-0.19 to -0.08		
2002	-0.26 ± 0.02	-0.30 to -0.21		
<i>Weight spread of brood on day 9</i>	<i>0.02 ± 0.01</i>	<i>0.00 to 0.05</i>	<i>-1.26</i>	<i>0.07.</i>
Brood size	0.06 ± 0.02	0.03 to 0.08	-12.40	0.0002***
Hatch date	0.01 ± 0.02	-0.03 to 0.04		<i>significant</i>
Mean posture of begging chicks	-0.40 ± 0.02	-0.43 to -0.37		<i>significant</i>
Hatch date * Brood's mean posture	-0.07 ± 0.02	-0.09 to -0.03		<i>significant</i>
Brood's mean posture * Year				<i>significant</i>
2001	0.01 ± 0.03	-0.04 to 0.06		
2002	0.02 ± 0.02	-0.02 to 0.06		
Hatch date * Year				<i>significant</i>
2001	0.00 ± 0.04	-0.06 to 0.06		
2002	-0.02 ± 0.03	-0.07 to 0.03		
Year * Brood's mean posture *			-9.26	0.0003**
Hatch date				
2001	0.03 ± 0.03	-0.03 to 0.09		
2002	0.08 ± 0.02	0.03 to 0.12		

n=1534 feeding visits, 52 nests, 3 years.

Comparative study



Supplementary Figure 3.2. PRISMA flowchart detailing data collection and exclusion criteria. Data and studies included in the meta-analysis are appended.

4. SIBLING CONFLICT AND DISHONEST SIGNALLING IN BIRDS^{‡§**}

Abstract

Offspring survival can often depend on successful communication with parents about their state of need. Theory suggests that offspring will be less likely to honestly signal their need when they experience greater competition from either a greater number of nestmates or less-related nestmates. We found support for this hypothesis with a comparative analysis, examining data from across 60 species of birds. We found that offspring are less honest about their level of need when (i) they face competition from current siblings; (ii) their parents are likely to breed again, and so they are in competition with future siblings; and (iii) parental divorce or death means that they are likely to be less related to future siblings. More generally, these patterns highlight the sensitivity of communication systems to conflict between signaller and receiver while also suggesting that when there is little conflict, natural selection favours the honest.

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[§] This chapter is presented in the narrative format of *PNAS*, with detailed methods following the main text.

^{**} One section of this chapter did not appear in the published article: *Additional considerations about divorce*

Introduction

In almost every species where offspring live with their parents in family groups, they beg or signal to their parents for food (Wright & Leonard 2002; Bradbury & Vehrencamp 2011). Evolutionary theory suggests that signalling between offspring and their parents will evolve in response to the environment. At one extreme, if parents have enough resources to rear all their offspring, then offspring can be selected to honestly signal their need for food, so the offspring in the worst condition is fed (Godfray 1991; 1995b; Wright & Leonard 2002; Moreno-Rueda *et al.* 2009; Bradbury & Vehrencamp 2011; Mock *et al.* 2011; Grodzinski & Johnstone 2012). At the other extreme, if parents only have enough resources to rear one offspring, then offspring can be selected to competitively signal their quality or scramble for food, so the offspring in the best condition is fed (Grafen 1990; Mock & Parker 1997; Davis *et al.* 1999; Royle *et al.* 2002; Parker *et al.* 2002a; Moreno-Rueda *et al.* 2009; Mock *et al.* 2011). Empirical data support these predictions: offspring appear more likely to signal need when resources are relatively plentiful and quality when resources are scarce (Caro *et al.* 2016a).

Theory also provides an understanding of when signals of need between offspring and parents are expected to break down or become distorted. If the self-interest of an offspring conflicts sufficiently with the interests of its parents, then it can be selected to exaggerate its need (Godfray 1991; Johnstone & Grafen 1993; Godfray 1995b; Rodríguez-Gironés *et al.* 1996; Royle *et al.* 2002; Parker *et al.* 2002a; Johnstone 2004; Mock *et al.* 2011; Akçay 2012; Grodzinski & Johnstone 2012; Bossan *et al.* 2013). Increased competition between siblings can disrupt the alignment of interests between parents and their offspring. Competition between siblings can reduce the benefit of allowing needier siblings to be fed, selecting for each offspring to try to maximize its

own share of parental resources, such that honest signalling of need is not stable. Both increased numbers of siblings and lower relatedness between those siblings could lead to greater sibling competition (Parker *et al.* 1989; Godfray 1991; Johnstone & Grafen 1993; Godfray 1995b; Rodríguez-Gironés *et al.* 1996; Royle *et al.* 2002; Parker *et al.* 2002a; Johnstone 2004; Akçay 2012; Grodzinski & Johnstone 2012; Bossan *et al.* 2013). Competition between siblings could also lead to exaggerated and dishonest signals of need, rather than the complete collapse of honest signalling (Johnstone & Grafen 1993). However, there is a lack of consistent empirical evidence demonstrating that sibling competition leads to either the breakdown of honest signalling or less honest signals (Smith & Montgomerie 1991; Briskie *et al.* 1994; Kacelnik *et al.* 1995; Price & Ydenberg 1995; Cotton *et al.* 1996; Price 1996; Leonard & Horn 1998; Leonard *et al.* 2000; Neuenschwander *et al.* 2003; Mathevon & Charrier 2004; Marques *et al.* 2006; 2011; Mock *et al.* 2011; Romano *et al.* 2012). One problem is that these hypotheses can be hard to test within a single species, where there may not be sufficient variation in offspring number and relatedness.

We utilized the variation in breeding behaviour across birds to test whether offspring beg less honestly in species where there is greater competition between siblings. We estimated the honesty of offspring signals by calculating the strength of the relationship (correlation coefficient) between signals and long-term condition (Supplementary Figure 4.1) (Borenstein *et al.* 2011; Grissom & Kim 2011; Koricheva *et al.* 2013; Carazo & Font 2014). “Condition,” “need,” and “quality” refer to the ultimate fitness effects of receiving additional food; our measures of long-term condition (body condition, health, rank within the brood and long-term food intake) therefore reflect the total requirement for food to improve overall quality before fledging and are likely to

reflect both cryptic and public aspects of condition (Supplementary Methods) (Grafen 1990; Godfray 1991; 1995b; Price 1996; Wells 2003; Hinde & Godfray 2011). An advantage of focusing on the correlation between signalling and condition is that correlation coefficients are less likely to be influenced by non-social differences between species, such as body size, which can affect absolute measures of begging intensity, such as call volume (Borenstein *et al.* 2011). Our hypotheses were based on signal-of-need models (Parker *et al.* 1989; Godfray 1991; 1995b; Rodríguez-Gironés *et al.* 1996; Godfray & Johnstone 2000; Royle *et al.* 2002; Parker *et al.* 2002a; Johnstone 2004; Akçay 2012; Grodzinski & Johnstone 2012; Bossan *et al.* 2013), and so we first analysed behavioural signals, such as begging calls and postures, which are more likely to be signals of need (Caro *et al.* 2016a). We then analysed structural signals, such as mouth colour, which are more likely to be signals of quality (Caro *et al.* 2016a; but see Kilner 1997 and Kilner and Davies 1998, which found that nestling mouth colour can be a signal of need or improve conspicuousness).

Results and Discussion

We compared the strength of species' correlation coefficients (effect sizes) between begging intensity and long-term need using phylogeny-based, linear mixed models, which were weighted by study sample size (Butler *et al.* 2009; Borenstein *et al.* 2011; Nakagawa & Santos 2012). A positive effect size indicates that offspring in worse condition beg more and therefore are more honestly signalling their need (Carazo & Font 2014). Larger positive effect sizes suggest a clearer, more honest signal of need. In contrast, an effect size of zero indicates no correlation with begging intensity, such that begging provides no honest information about long-term need. A negative correlation indicates that offspring with less need beg more intensely.

Honesty and sibling rivalry

We first tested whether sibling conflict leads to less honest signalling. We estimated the effect of competition by dividing species into two categories: ‘siblings present’ and ‘siblings always absent’ (Quillfeldt 2002). This categorization represents a true biological distinction, because some species of birds obligately lay only one egg per breeding attempt (Quillfeldt 2002). Theory suggests that the difference between brood sizes of one and two will be substantially large, going from no to appreciable sibling competition (Godfray 1991; 1995b). Consistent with this, we found that the presence of siblings is correlated with less honest offspring: the relationship between need and begging is weaker in species with multiple offspring per brood (mean Wald statistic=6.69, $p=0.0097$, $n=60$ species; Figure 4.1; Table 4.1, model 1). Offspring in worse condition beg more intensely in species where offspring never interact with siblings (95% CI of the correlation coefficient=0.13–0.56, $p=0.0055$) than in species where siblings compete for food (95% CI=–0.02 to 0.22, $p=0.075$). Phylogeny did not influence how honest offspring are (Supplementary Table 4.1).

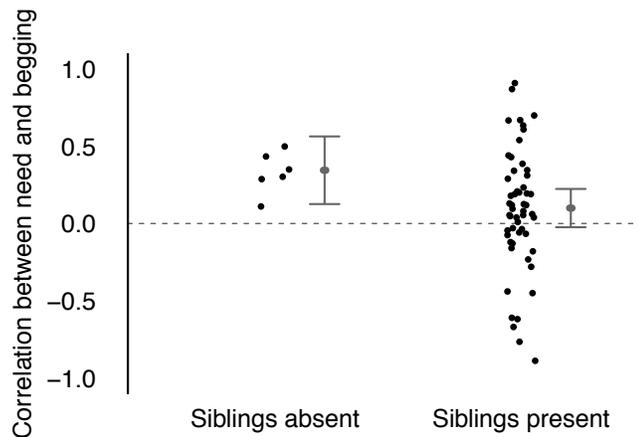


Figure 4.1. The presence of siblings is associated with a reduction in offspring honesty. Data points represent species’ mean correlation coefficients of long-term need and begging

intensity for species where parents rear only one (n=6 species), or more than one offspring per brood (n=54 species). Positive correlations indicate that offspring in worse condition beg more intensely, providing honest information about need. Grey lines represent the 95% confidence intervals from the model, run on the full dataset, controlling for phylogeny and repeated measures. Species with siblings present have a weaker correlation between need and begging, suggesting less honest signalling of need (Wald=6.69, p=0.0097).

Table 4.1. Results for all models: fixed effects.

Model	Fixed effects	Results	N species	N study	N obs
1	Siblings present y/n	$F_{1,71.8}=6.69, p=0.0097$	60	108	336
2	Brood size	$F_{1,31.0}=4.57, p=0.033$			
3	Siblings present y/n <i># of future broods possible</i>	$F_{1,67.0}=8.45, p=0.0050$ <i>$F_{1,87.9}=3.13, p=0.080$</i>	51	98	317
4	Brood size # of future broods possible	$F_{1,82.2}=11.87, p=0.0009$ $F_{1,83.5}=7.22, p=0.0087$			
5	Siblings present y/n # of future broods possible Full vs half sibs likelihood	$F_{1,84.2}=0.42, p=0.42$ $F_{1,95.4}=9.39, p=0.0028$ $F_{1,112.5}=6.94, p=0.0096$	49	96	314
6	<i>Brood size</i> # of future broods possible Full vs half sibs likelihood	$F_{1,87.1}=3.07, p=0.083$ $F_{1,86.4}=13.09, p=0.0005$ $F_{1,89.6}=5.98, p=0.016$			
7	Siblings present y/n <i># of future broods possible</i> <i>Full vs half sibs likelihood</i> EPP	$F_{1,60.5}=0, p=1$ $F_{1,58.4}=3.10, p=0.083$ $F_{1,76.0}=3.77, p=0.056$ $F_{1,58.5}=0.04, p=0.84$	31	68	230
8	<i>Brood size</i> # of future broods possible Full vs half sibs likelihood EPP	$F_{1,66.2}=3.87, p=0.053$ $F_{1,58.3}=4.94, p=0.038$ $F_{1,67.1}=1.00, p=0.32$ $F_{1,58.5}=0.27, p=0.61$			

Table reports the mean results (conditional Wald statistics) of 500 ASReml linear mixed models. Models controlled for phylogeny, repeated measures on studies and species, and were weighted by study sample size (the number of broods used to calculate the original test statistic). Fixed effects in bold are significant at the p<0.05 level, and in italics at the p<0.10 level. Models are grouped by the dataset used for analysis, as sample size decreased in later analyses due to unavailable life history data.

We then examined whether increasing intensity of sibling competition led to a corresponding decrease in honesty using data on average brood size. The intensity of within-family conflict may increase as more offspring compete for food in bigger

broods, and this conflict could favour exaggerated signals of need (Rodríguez-Gironés *et al.* 1996; Parker *et al.* 2002a; Johnstone 2004). For instance, offspring sharing a nest with ten siblings may experience more intense competition than those with only one sibling. It has also been suggested that parent-offspring communication can be affected in more complicated ways in larger broods, with only offspring in the most need selected to invest in costly signalling (Johnstone 1999; Johnstone & Roulin 2003; Johnstone 2004). We found that the strength of the correlation between need and begging was lower in species with larger brood sizes: offspring with more siblings are less honest with their parents about their level of need (mean Wald statistic=4.57, $p=0.033$; Table 4.1, model 2).

We might expect to see similar patterns within species that exhibit consistent variation in the intensity of sibling competition if individuals can assess the relative intensity of competition from siblings in their environment. Consistent with this, offspring of several species have been found to adjust their level of begging facultatively: American robins (Smith & Montgomerie 1991), great tits (Neuenschwander *et al.* 2003), tree swallows (Leonard & Horn 1998; Leonard *et al.* 2000; Marques *et al.* 2011), and yellow-headed blackbirds (Price 1996; Price *et al.* 1996) all escalate their begging intensity when competing against more or needier nestmates. In contrast, barn swallows (Romano *et al.* 2012) and black-headed gulls (Mathevon & Charrier 2004) show the opposite pattern, reducing their begging intensity when faced with more or needier nestmates, and European starling offspring do not change how they beg at all based on the begging of their nestmates (Kacelnik *et al.* 1995; Cotton *et al.* 1996). These discrepancies may be due to biological differences between species, particularly whether parents or offspring control offspring food distribution (Kacelnik *et al.* 1995;

Johnstone 2004). For instance, in black-headed gulls, parents regurgitate food to the nest floor, rather than distributing it, and so offspring completely determine food distribution (Mathevon & Charrier 2004). Because offspring control food distribution, they do not fit the assumptions of standard signal-of-need models; instead, theory predicts that offspring in better condition are selected to decrease, rather than increase, begging when their needier siblings beg more (Johnstone 2004).

Honesty and future siblings

Parental investment is not only shared within a brood, but also between broods produced throughout a parent's lifetime. Therefore, unborn siblings, which may potentially exist in the future, could potentially impact the honesty of signalling between current offspring and their parents. If parents are saving resources for future breeding attempts, then this could make them less responsive to their current brood's begging, and hence select for their offspring to exaggerate their signals (Godfray 1991; Parker *et al.* 2002b; Grodzinski & Johnstone 2012; Griffin *et al.* 2013). We estimated conflict with future siblings from the relative number of potential future breeding attempts: adult life expectancy multiplied by the maximum number of successful broods parents can raise each year. These data were available for 51 of the 60 species in our dataset, and we controlled for current sibling competition (brood size) in these analyses.

As we predicted, offspring were less honest with parents in species where offspring compete against more future siblings. The correlation between begging and need was significantly lower in species where parents can rear more broods over their lifetime (mean Wald statistic=7.22, $p=0.0087$; Figure 4.2; Table 4.1, model 4), and species with larger broods (mean Wald statistic=11.87, $p=0.0009$). Offspring compete with both

their current and future siblings for resources by manipulating parental behaviour through their begging. Overall, our analysis suggests that the honesty of offspring signalling varies in response to how parental investment is distributed over the parents' lifetime.

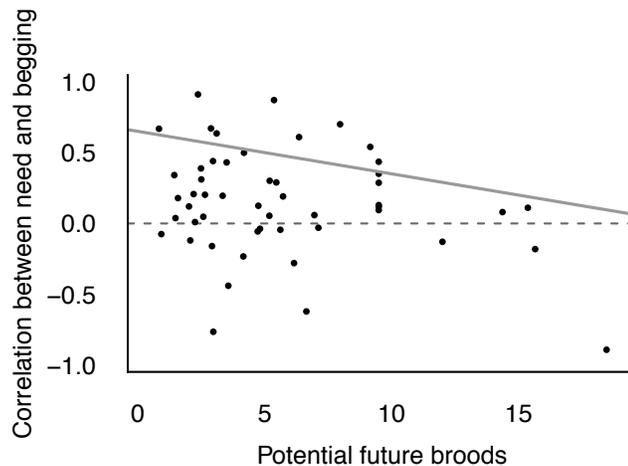


Figure 4.2. Conflict with future siblings is associated with a reduction in offspring honesty. Data points show species' mean correlation coefficient of long-term need and begging intensity. The number of potential future broods is the adult life expectancy multiplied by the number of successful broods that can be reared each breeding season ($n=51$ species). The grey line is the regression coefficient from the model, run on the full dataset, controlling for phylogeny and repeated measures. Positive correlations indicate that offspring in worse condition beg more intensely, providing honest information about need. The dashed line at zero indicates no relationship between condition and begging. The correlation between need and begging is weaker in species where parents can potentially produce more broods over their lifetimes (Wald=7.22, $p=0.0087$), suggesting that future reproduction selects for less honest signalling of need.

We might also expect to see individuals adjusting their behaviour conditionally in response to variation in the likelihood of competition with future siblings. For example, offspring born to younger parents, with greater reproductive potential, might make less reliable signals than offspring that represent a parents' terminal investment (Stearns 1992). Previous studies within species that produce multiple broods in a season have

found such patterns. For example, European starlings can lay two broods per year, and offspring only signal need honestly if they are in the second brood, when parents cannot lay another brood (Bize *et al.* 2006). Hihi bird parents' response to offspring signals in their first brood decreases if their likelihood of breeding again is experimentally increased (Thorogood *et al.* 2011).

Honesty and relatedness to siblings

When relatedness is lower between offspring sharing the same parent or parents, there will be stronger selection to monopolize parental investment and weaker selection on higher-quality offspring to show restraint in begging for food (Godfray 1991; 1995b; Godfray & Johnstone 2000; Parker *et al.* 2002a, b; Johnstone 2004; Mock *et al.* 2011; Akçay 2012; Grodzinski & Johnstone 2012; Bossan *et al.* 2013). The survival of unrelated nestmates or broods fails to enhance the inclusive fitness of a focal offspring. Consequently, we predict that decreased relatedness between offspring will lead to less honest signalling of need. We examined the consequences of two factors that can reduce relatedness within families: (i) parents breeding with different partners, such that all future broods can only contain half (genetic relatedness, $r=0.25$), rather than full ($r=0.50$), siblings; and (ii) parents being promiscuous, such that some brood-mates are only half siblings.

We determined the likelihood of parents changing breeding partners by combining the rates of mortality and divorce. Divorce is the rate at which pairs mate with different partners when both original partners are still present in the population (Culina *et al.* 2014). In nine species where data on divorce rates were unavailable, we used mating system (lifetime vs. seasonal monogamy) to estimate the likelihood that parents will

breed together again. Because the divorce rate was estimated in some cases, we binned species according to whether pairs had a higher or lower than 50% chance of breeding together again. Data on the likelihood of breeding together again were available for 49 of the 60 species in our original data set, and so we carried out analyses on this subset, controlling for the number of current and future siblings.

Offspring whose parents are unlikely to breed together again, through either death or divorce, are significantly less honest with their parents (mean Wald statistic=5.98, $p=0.016$; Figure 4.3; Table 4.1, model 6). The number of potential future siblings predicts species' honesty in this model as well (Wald statistic=13.09, $p=0.0005$), but brood size was no longer significant, perhaps due to the reduction in sample size (Wald statistic=3.07, $p=0.083$). Overall, this suggests that an increased conflict of interest, due to lower relatedness between siblings, favours less honest signalling.

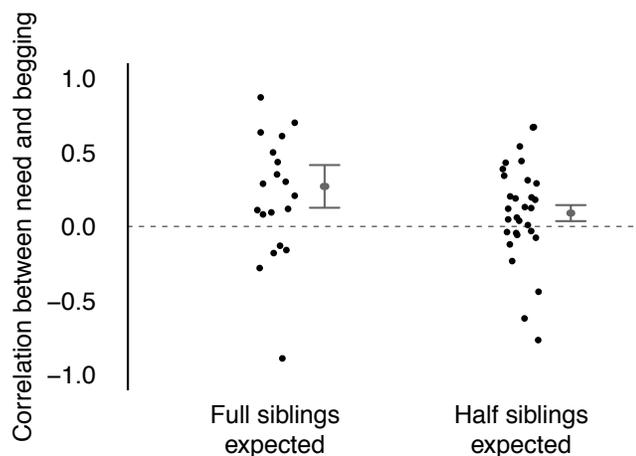


Figure 4.3. Parental divorce and death is associated with a reduction in offspring honesty. Data points represent species' mean correlation coefficients of long-term need and begging intensity for species. We divided species by whether there is a higher or lower than 50% chance that parents will breed together again in the next year, based on survival and divorce rates ($n=19$ species where full siblings are expected; $n=30$ species where half siblings are expected). Positive correlations indicate that offspring in worse condition beg more intensely, providing

honest information about need. Grey lines represent the 95% confidence intervals from our analyses. The correlation between need and begging is weaker in species with higher rates of divorce and lower rates of survival, where half siblings are expected (Wald=5.98, $p=0.016$), suggesting less honest signalling of need.

We next looked at whether variation in within-brood relatedness due to promiscuity also impacts offspring honesty (Godfray 1991; 1995b; Johnstone 2004; Akçay 2012; Grodzinski & Johnstone 2012; Bossan *et al.* 2013). We used the percentage of broods with at least one extrapair offspring as our measure of promiscuity. These data were available for only 31 of the species in our dataset, and so we ran our analyses on this subset, controlling for the number of current and future siblings and the likelihood that parents will breed together again. We did not find an effect of extrapair paternity (mean Wald statistic=0.27, $p=0.61$; Table 4.1, model 8). Of the control variables, only the number of future broods remained significant in this model, again potentially because we are examining a much smaller data set (mean Wald statistic=4.94, $p=0.038$).

A possible explanation for a lack of a significant influence of promiscuity is that it selects relatively weakly on honesty. The likelihood that parents will breed together again could be a more consistent and reliable predictor of relatedness: although extrapair paternity may reduce relatedness to a proportion of nestmates, divorce or death means that all future offspring produced by a mother or a father must be half siblings ($r \leq 0.25$). However, an experimental study on barn swallows found that offspring were less honest about their hunger when their nestmates were nonrelatives (Boncoraglio & Saino 2008), and a previous comparative study on 11 species found that absolute begging intensity was significantly correlated with promiscuity, as would be expected if lower relatedness led to escalation in begging (Briskie *et al.* 1994). This discrepancy may be because we assessed changes in honesty, rather than changes in absolute

begging levels. Another possible reason we did not see an effect of promiscuity is that the influence of sibling number could obscure the influence of relatedness to those siblings. Specifically, species with larger broods may be less honest, irrespective of how many of those nestmates are half siblings (Supplementary Figure 4.2). This effect of brood size is a specific case of the more general point that local competition can reduce the importance of relatedness between interacting individuals (West *et al.* 2002a).

Additional considerations about divorce

The effects of divorce may be complicated. We reasoned that offspring should be selected to exaggerate their signals if their parents are likely to divorce, since they gain half as much inclusive fitness benefit from half siblings receiving parental investment. This argument assumes that, for example, divorce causes an offspring to go from having 10 full siblings to having 10 half siblings. Yet if both parents manage to successfully breed again with new partners, then an offspring could go from having 10 full siblings to 20 half siblings. These are equivalent in an inclusive-fitness sense, and we would not expect divorce to affect signalling if this were the case. Crucially, this depends on the probability that parents have equal breeding success regardless of divorce, which may not be the case in all species or in both sexes (Culina *et al.* 2014). For example, if mothers can breed equally well after divorce but males only have a 50% chance of finding a new partner, divorce would cause an offspring to go from having 10 full siblings to 15 half siblings, on average. Consequently, divorce's impact on selection for offspring honesty may be mediated by other factors, such as adult sex ratio and sex differences in the effects of divorce or costs of parental care, in a way that we do not yet have the data to test.

Ecology and life history

Our above analyses explored the link between life history variables and signal honesty. Previous analyses (Chapter 2) have suggested that environmental quality and environmental predictability can also influence the extent to which offspring signal need (Caro *et al.* 2016a). If these environmental variables co-vary with sibling number or relatedness, our results could have been driven purely by environmental variation. We tested whether environmental quality and predictability confounded our results in two ways: by assessing their relationship with life history traits (Supplementary Table 4.2) and by comparing models with and without these variables (Supplementary Table 4.3). We found no relationships between life history traits and environmental quality/predictability in our dataset, except for the presence/absence of siblings (Supplementary Table 4.2). The obligate absence of siblings was nested within the ‘predictable’ level of environmental predictability, and so this relationship was unavoidable. Models that included both environmental predictability and the presence/absence of siblings had somewhat variable results, as expected if these factors are partially collinear (Supplementary Table 4.3, models 1, 3, 5 and 7). However, when we used brood size, rather than the presence/absence of siblings, the coefficients of fixed effects were equivalent across models, and both environmental factors and life history traits generally remained significant (Supplementary Table 4.3, models 2, 4, 6 and 8). This result suggests that both life history and ecology influence parent-offspring communication.

Signalling theory and empirical data

The hypotheses tested here are based on existing theory that examines the conditions required for the evolutionary stability of honest signalling of need (Godfray 1991;

Johnstone & Grafen 1993; Godfray 1995b; Rodríguez-Gironés *et al.* 1996; Godfray & Johnstone 2000; Royle *et al.* 2002; Parker *et al.* 2002a; Johnstone 2004; Akçay 2012; Grodzinski & Johnstone 2012). These previous models tend to predict that honest signalling is either stable or not, rather than a continuum of more gradual shifts between these extremes (Johnstone 1999). In contrast, the empirical data show much more gradual variation, with a wide range of correlation coefficients between condition and signalling (Figures 4.1, 4.2 and 4.3). Our extrapolation is to take predictions for when stable signalling is or is not favoured (extremes) and use them to make predictions about how honest signalling should be (variation across intermediates). This mismatch between the predictions of theoretical models (extremes), and the patterns observed empirically (intermediates) has previously been analysed in the context of sex allocation. Sex allocation represents a much simpler game theoretic case, where it was found that by increasing biological complexity, models were able to move from the prediction of extremes (all or nothing) to the prediction of more gradual and realistic variation (Wild & West 2007; West 2009). We suggest that increased biological complexity could similarly lead to the prediction of more gradual shifts in signalling models, and further theory is clearly required to examine the evolutionary stability of intermediate levels of honesty (Johnstone & Grafen 1993). Another complication is that many signalling models predict multiple possible equilibria (Lachmann & Bergstrom 1998) without distinguishing which of the possible equilibria natural selection will lead to (Maynard Smith & Harper 2003). There is clearly also a need for signalling theory that can be better linked to the kind of variation in signalling systems that is observed in empirical studies.

Another complication with linking to data to theory is that empirical estimates of need could be unreliable or fail to capture character states in a way that is relevant to theory (Mock *et al.* 2011). These errors would, however, be most likely to obscure any underlying biological pattern, and it is unlikely that such error would have produced the patterns we observe. Indeed, by finding patterns in the predicted direction, our results suggest that empirical researchers have successfully managed to capture biologically relevant aspects of condition.

Signals of quality

Offspring can solicit food using either signals of need or quality, and the same life history traits may influence the evolution of both kinds of signals (Wright & Leonard 2002; Bradbury & Vehrencamp 2011). Our predictions were derived from signal-of-need models, where parents are assumed to have enough food to feed all their offspring and are selected to feed the offspring with the greatest need (Godfray 1991; 1995b; Wright & Leonard 2002; Moreno-Rueda *et al.* 2009; Bradbury & Vehrencamp 2011; Mock *et al.* 2011; Grodzinski & Johnstone 2012). In contrast, when parents do not have enough food to feed all their offspring, they are expected to pay attention to signals of quality and to feed the highest quality offspring (Grafen 1990; Mock & Parker 1997; Davis *et al.* 1999; Royle *et al.* 2002; Parker *et al.* 2002a; Moreno-Rueda *et al.* 2009; Mock *et al.* 2011). Consequently, we predict the opposite patterns with signals of quality as those we observed with signals of need. For example, when relatedness is higher, chicks in better condition should reduce their signalling to allow related nestmates in worse condition to be fed. This restraint could create a situation where chicks in worse condition give more intense signals—increasing the correlation between need and signals but decreasing the correlation between quality and signals.

To determine whether signals of quality respond to life history traits, we repeated our above analyses, but examining structural signals, such as mouth size or colour, which are more likely to represent measures of quality (Caro *et al.* 2016a; but see Kilner 1997 and Kilner and Davies 1998, which found that nestling mouth colour can be a signal of need or improve conspicuousness). We could not find an effect of any of our life history traits on structural signals, whether or not environmental factors were included as covariates (Supplementary Tables 4.4 and 4.5). Our null result could be because the evolution of structural signalling is influenced by other factors or because our sample size was too low to identify true effects: we only had data on 18 species and had no data on species without siblings present. More empirical studies on structural signals could help reveal the selection pressures on such signals. Furthermore, theory that explicitly models offspring signals of quality, without the assumption that all offspring will survive, is necessary to generate testable predictions about which life history traits could influence the evolution of signals of quality.

Conclusions

We found support for the prediction that increased conflict between siblings disfavors honest signalling of need from offspring to their parents (Figure 4.4). Specifically, offspring are less likely to honestly signal their need when they have more siblings, when their parents are more likely to breed again, and when they are less related to their future siblings, due to parental divorce or death. These results suggest that siblings that are not even born yet, and, indeed, may never be born, cast a competitive shadow back in time, which selects for exaggerating need to parents. The logical next step would be to explore how parents' response to begging is affected by the same life history factors

(Bize *et al.* 2006; Thorogood *et al.* 2011; Grodzinski & Johnstone 2012; Stucki & Kölliker 2013). Longevity and lifetime fecundity have already been shown to influence other aspects of parental care, such as how parents respond to nest predators, with species that have less potential for future reproduction engaging in riskier defence behaviour (Ghalambor & Martin 2001). The results of this study suggest that parents within a stable pair bond may be selected to be the most responsive parents, especially if they produce few offspring.

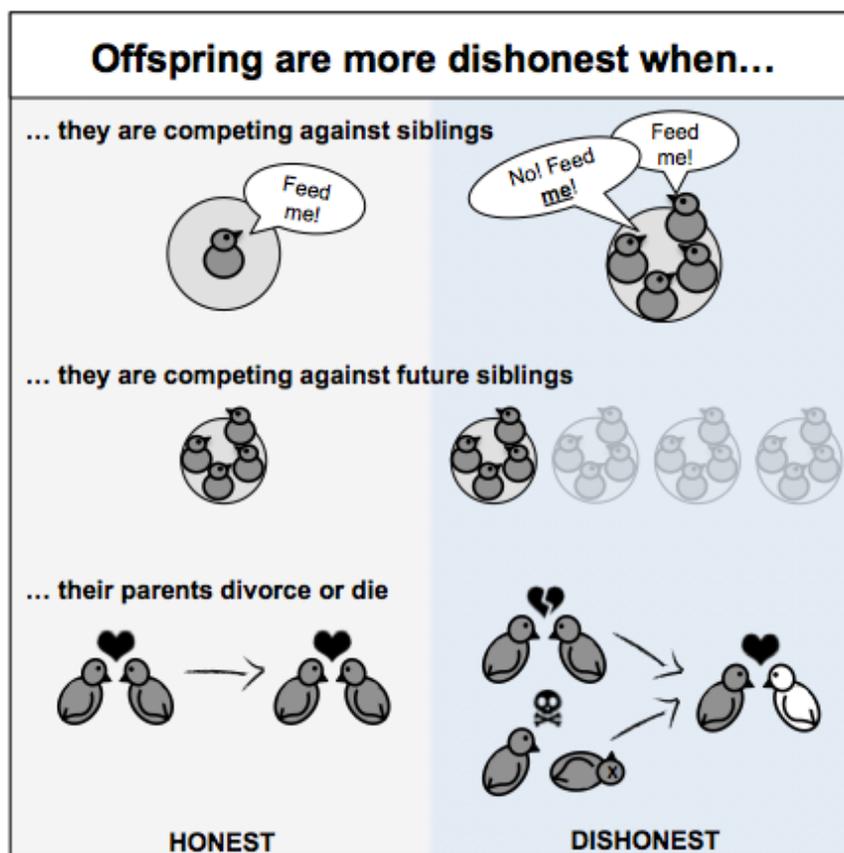


Figure 4.4. Family conflict is associated with a reduction in the honesty of offspring signals of need. Offspring in species with siblings present are less honest when signalling need (Wald statistic=6.69, $p=0.0097$). The probability that parents will breed again is also associated with more dishonest offspring, as the current brood competes against future broods for parental investment (Wald=7.22, $p=0.0087$). Finally, offspring are less honest in species where parents are likely to divorce or die before breeding again, and all future siblings will be half siblings (Wald=5.98, $p=0.016$).

Methods

We searched the literature for data relating to the effect of offspring condition on begging intensity, leading to a dataset of 336 test statistics from 108 studies on 60 species of birds (see Supplementary Figure 4.3 for PRISMA flowchart of study selection; the data included in the meta-analysis, life history references and a list of excluded studies were published online: www.pnas.org/content/113/48/13803.full). We included any reported measures of behavioural begging, such as vocalizations and postures. We also collected data on the effect of condition on structural signals, leading to a dataset of 140 effect sizes from 33 studies on 18 species. We included any reported measures of structural signals, such as mouth colour or UV reflectance. We calculated the correlation coefficient between condition and signals to generate a standardized effect size across studies and species (Borenstein *et al.* 2011; Grissom & Kim 2011; Koricheva *et al.* 2013; Carazo & Font 2014). This coefficient varies between ± 1 , with positive values indicating that offspring in worse condition signal more, and negative values indicating that offspring in better condition signal more. We assumed offspring were dishonest if there was no correlation between condition and signal intensity. We used health, body condition, rank within the brood, and experimental manipulations that affected food intake over multiple days as proxies for long-term condition (Supplementary Information).

We analysed differences in honesty across species using ASReml linear mixed models in R that were weighted by sample size and controlled for phylogeny and repeated measures on studies and species (Butler *et al.* 2009; R Core Team 2013). We averaged the results of 500 models using different trees to account for uncertainty in the

phylogeny, which we obtained from www.Bird.tree.org, with both Ericson and Hackett backbones (Jetz *et al.* 2014). Results relating to random effects can be found in Supplementary Table 4.1. We compared honesty to a variety of relevant life history traits related to sibling completion and relatedness. We estimated current sibling competition in two ways: (i) presence or obligate absence of siblings and (ii) mean brood size of the study population, or species if population data were unavailable. We estimated species-level competition against potential future siblings by multiplying annual adult survival and the maximum number of broods parents can raise each year. We estimated species-level relatedness to siblings in two ways: (i) whether parents have a better than 50–50 chance of mating together again based on mortality and divorce rates, leading to half siblings; and (ii) the percentage of broods with extrapair paternity. We classified environmental predictability and quality following our previous comparative study, Chapter 2 (Caro *et al.* 2016a).

Supplementary Information

Supplementary Methods

Data extraction and effect sizes

All relevant statistical tests of the effect of offspring long-term need on begging intensity were included in the meta-analysis. We converted these test statistics to Pearson's correlation coefficients, a standardized effect size that allows comparisons across studies (Borenstein *et al.* 2011; Koricheva *et al.* 2013). Almost any test statistic (such as an F or χ^2 value) or effect size (such as a risk ratio) can be transformed to a correlation coefficient. Sixteen papers also contained information such as raw means and standard deviations that could be used to calculate effect sizes. Correlation coefficients range from ± 1 and describe the relationship between two variables. They account for different scales in their original measurements, are well suited to the ordered nature of the data, and are more straightforward to interpret than standardized difference in means (Borenstein *et al.* 2011). We transformed the data extracted from the literature to correlation coefficients following Borenstein *et al.* (2011), Grissom and Kim (2011), Koricheva *et al.* (2013), and Nakagawa and Schielzeth (2013).

Correlation coefficients were transformed to Fisher's Z before analysis: $Z_r = \frac{1}{2} \ln\left(\frac{1+r}{1-r}\right)$, so that the data could be weighted by the inverse variance: $1/(n-3)$, which approximates the variance on Fisher's z and is not dependent on the strength of the correlation (Borenstein *et al.* 2011). We used the number of broods used to generate the original test statistic for sample size, because this is a standard measure across studies and avoids the issue of pseudoreplication of having multiple non-independent offspring from the same nest as the sample size. All analyses were conducted on the transformed

values, and results were converted back into correlation coefficients for figures and discussion.

Tests for publication bias and study methodology bias

Although we did not expect to find one true effect size across all studies and species (Borenstein *et al.* 2011), we tested our meta-analysis for publication bias using the regression test for funnel plot asymmetry (Egger's test) in the 'metafor' package in R (Viechtbauer 2010; R Core Team 2013). We calculated the mean effect size per study and compared it to its variance to determine whether studies with smaller sample sizes were more likely to show biased effects. We found no evidence of publication bias ($z=0.90$, $p=0.37$).

We also tested whether study methodology biased the strength or direction of the correlation coefficient. We recorded additional information on study methodology for each coefficient, including: whether the data were experimental or observational (two-level factor); whether the correlation coefficient was estimated or derived from a test statistic provided by the original study (2-level factor); the type of begging variable (2-level factor: continuous intensity measure, likelihood of signalling); the measure of long-term need (5-level factor: health, rank, weight, condition, brood-level effects); and whether the offspring contrast was dichotomous (bigger vs. smaller) or continuous (all offspring included). Analyses were run on the full dataset (Null (a)). Presence/absence of siblings was included as a control factor, because some methodological factors, such as size rank within the brood and offspring contrast, were only available for species with siblings, and the presence/absence of siblings influences the effect size (Table 4.1).

We found no evidence that study methodology influences the correlation coefficient ($p > 0.20$ for all factors: experimental/observational Wald=0.30, $p=0.58$; estimated correlation coefficient Wald=0.09, $p=0.77$; begging variable type Wald=0.00, $p=0.95$; long-term need measure Wald=1.53, $p=0.20$; offspring contrast type Wald=1.09, $p=0.36$).

Detailed explanation of offspring long-term need

Many aspects of offspring need were reported in the literature, such as hunger, body mass to skeletal size ratio, dominance rank, experimentally reduced or enlarged broods, and experimental immune challenges. We excluded correlation coefficients that examined only the effect of short-term food deprivation, i.e. hunger. While hunger and condition may be intertwined, they represent very different selection pressures (Price *et al.* 1996; Wright *et al.* 2002; Wells 2003; Hinde & Godfray 2011; Johnstone & Kilner 2011). Each piece of food eaten increases the likelihood that an offspring will fledge, but the fitness benefit of food to fatally diseased offspring is zero, because they will not live to breed (Price *et al.* 1996; Wells 2003). Furthermore, the influence of hunger on begging is already well established (Wright & Leonard 2002; Mock *et al.* 2011). Consequently, we focused on the influence of long-term need, and so data on the relationship between hunger and signal intensity were not included in analyses of offspring strategies.

According to traditional theory, though see Chapter 5, costly signals of need must contain information about a cryptic, rather than public, aspect of offspring need (e.g. Grafen 1990; Godfray 1991; Kilner & Johnstone 1997; Bergstrom *et al.* 2002; Johnstone 2004). Our estimate of honesty uses proxies of long-term need that may be

obvious to parents without a signal, such as body condition. It is possible that all species are equally honest, but that public and cryptic condition are more tightly linked in species with less sibling competition and lower relatedness. While we know of no reason this should be the case, the connection between cryptic and public condition is opaque. Given the strength of the effect of sibling competition in the predicted direction, it seems reasonable to assume that researchers in the field have captured a relevant aspect of offspring need.

We assumed all measures of long-term need were driving towards the same biological phenomenon, and so included all reported statistics in our analyses. Because test statistics were converted to a standardized scale, differences between the various measures of long-term should not influence the overall trends seen. The kind of measure of long-term need used to generate the original test statistic had no impact on effect size ($p=0.20$).

- Rank: Relative condition within brood (e.g. body mass rank, hatching rank, dominance rank)
- Weight: Absolute measures of offspring size (e.g. body mass or skeletal size)
- Health: Offspring health indicators (e.g. experimental immune challenge, parasite load, carotenoid supplementation)
- Body condition: Measures such as body mass to skeletal size ratio and blood glucose levels
- Long-term changes to food intake: Changes in condition that are expected to affect all offspring within the brood over a period of at least 2 days (e.g. experimentally reduced or enlarged broods, with the assumption that offspring in

larger broods receive less food per capita; or neck-taping which restricts food intake over multiple days)

Measures of begging intensity included in analyses

Many aspects of behavioural begging were reported in the literature, such as begging amplitude, duration, latency, likelihood, call structure and posture. We assumed all measures were driving towards the same biological phenomenon, and so included all reported statistics in our analyses. No measures including offspring height or proximity to parents or nest entrance were used, since these combine both motivation and size factors (larger offspring can reach higher and may be better able to compete for access to feeding sites). Because test statistics were converted to a standardized scale, differences between the various measures of begging intensity should not influence the overall trends seen. The type of begging variable used to generate the original test statistic had no impact on effect size ($p=0.95$).

- Probability: Whether or not begging occurred
- Continuous intensity: Any continuous measure of begging vocalization (duration, amplitude, rate, frequency, latency, playback) or posture (including gaping).

Measures of sibling competition

Current siblings

- **Siblings present or absent**: 2-level factor indicating whether or not species obligately lay only one egg per brood
- **Brood size**: Continuous variable with the mean brood size for the study population, or the species if population-level data was unavailable

Future siblings

- **Number of future broods possible:** Continuous variable calculated by multiplying adult life expectancy by the maximum number of broods parents can successfully rear each breeding season (species-level)

Relatedness to nestmates or future broods

- **Full vs half sibs likelihood:** 2-level factor indicating whether or not there is a better than 50% chance that parents will breed together again in the following year. We calculated this by multiplying annual adult mortality and divorce rate, and subtracting that value from 1 to generate the remarriage rate. The majority of divorce rate data were collected from the recent meta-analysis, which generated species-level mean divorce rates (Culina *et al.* 2014). Some species did not have exact divorce rate data available but did have qualitative descriptions of mating system (lifetime vs seasonal monogamy). The 50% likelihood cut-off allowed us to increase our sample size by 9 species: *Casmerodius albus*, *Larus michahellis*, *Larus ridibundus*, *Luscinia svecica*, *Phoenicurus phoenicurus*, *Riparia riparia*, *Strix aluco*, *Sula neboxii*, *Toxostoma rufum*. Divorce rates for these species were conservatively estimated as 0.05 for lifetime monogamy, 0.25 for multiple-season pair bonds, and 0.9 for no indication of pair bond persistence for calculations
- **EPP:** Extra-pair paternity: the percentage of broods containing at least one offspring sired by a different male. The percentage of EPP broods, rather than the percentage of EPP offspring, was used as the measure of promiscuity so we could include species that only lay one egg per breeding attempt.

Data analysis: Life history traits used in various analyses

Not all species had data on all life history traits. We ran separate models for each additional life history traits to take advantage of the greater sample size possible with fewer parameters (see Table 4.1 for sample size reduction with each model). Subsequent models controlled for life history traits analysed using the larger dataset. We used brood size, rather than the presence or absence of siblings, as the measure of current sibling competition in later models to allow our models to converge properly for models reported in the text. The six species that never experience sibling competition directly are also long-lived and have the potential to reproduce many times over their lives. This strong overlap between predictor variables makes it less likely that models will be able to detect the effect of the presence or absence of siblings when other terms are added to the model. The results of models using presence/absence as the measure of current sibling competition were qualitatively similar and can be found in Table 4.1.

Data analysis: Example R code

```
IA <- inverseA(full_tree[[1]], nodes="TIPS") #1
IAasreml <- sm2asreml(IA$Ainv, IA$node.names) #2

Modell <- asreml(fixed=Z_condition_beg ~ #3
  sib_present + max_expt_lifetime_broods + half_sibs_likelihood, #4
  random=~giv(animal) + common_name + study + units, #5
  ginverse=list(animal=IAasreml), #6
  weights=weights, #7
  family=asreml.gaussian(dispersion=1.0), #8
  data=my_data, na.method.X="omit", na.method.Y="omit") #9

anova(Modell, denDF="numeric", ssType="conditional") #10
```

#1-2 Phylogeny put in format usable by ASReml

#3 Response variable=Z-transformed correlated coefficient (effect size)

#4 Fixed effects depend on model

#5 Random effects to control for phylogeny, species and study. Units term allow residual variance to vary, as assumed by random effects meta-analysis

#6 Phylogeny

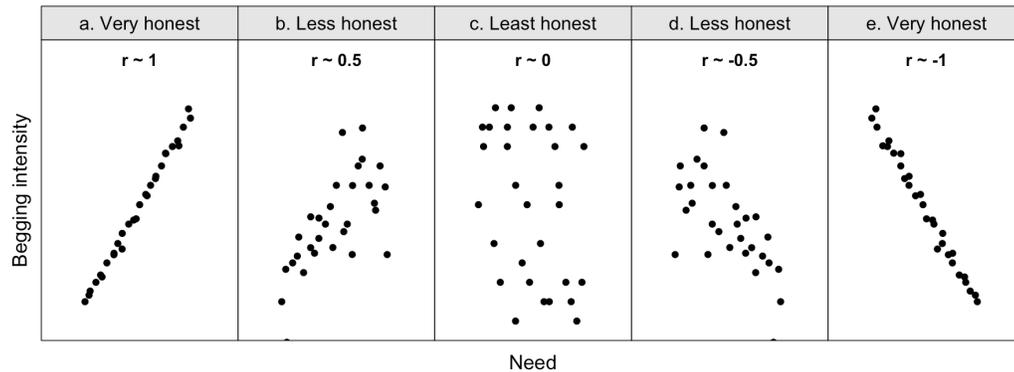
#7 Weighted by inverse of the variance

#8 Units variance constrained to 1 because weights are absolute

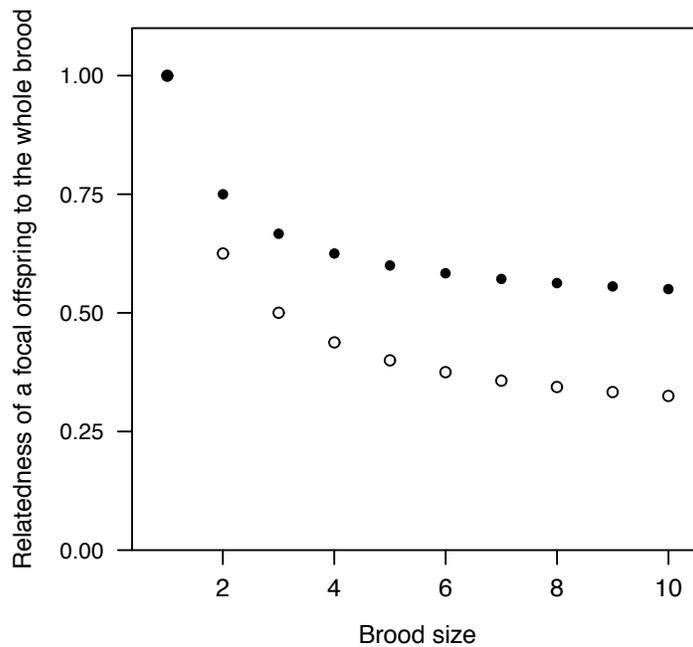
#9 Missing values discarded rather than imputed (ASReml treats missing values as zeros)

#10 Conditional Wald tests (which adjust sum of squares based on other fixed effects, rather than adding them sequentially) used to assess significance of life history traits

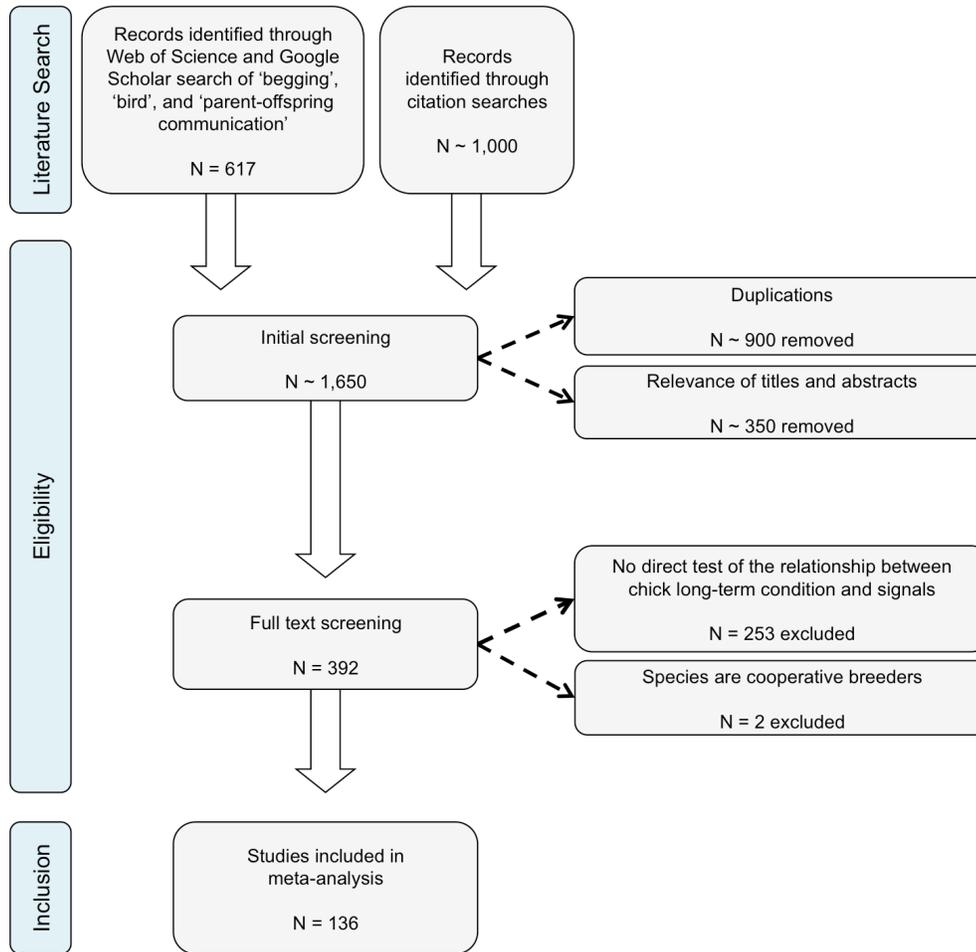
Supplementary Figures



Supplementary Figure 4.1. What is honesty? Species were considered honest if there was a strong relationship between offspring need and begging intensity, as measured by the correlation coefficient (Carazo & Font 2014). **(a)** When the correlation coefficient approaches 1, begging is considered honest because it is almost perfectly informative. **(b)** When the correlation is weaker (e.g. $r=0.5$), begging may provide some information about need, but it is less reliable. **(c)** When the correlation coefficient approaches 0, begging is considered dishonest because it provides no information about need. **(d,e)** Begging could also function as an honest signal of quality, rather than need, in which case the correlation coefficient would be negative rather than positive. Our analyses looked at whether differences in the relative strength of the correlation between need and begging across species can be explained by increases in within-family conflict as predicted by Hamilton's rule.



Supplementary Figure 4.2. Relatedness to the whole brood decreases as brood size increases. The average relatedness of a focal offspring to the whole brood decreases with each additional sibling, until reaching an asymptote $r=0.5$ for full siblings (closed circles), and $r=0.25$ for half siblings (open circles). Whole brood relatedness is calculated by averaging a focal offspring's relatedness to itself and each of its siblings. For example, $r=0.75$ for two full siblings: $(1+0.5)/2$, and $r=0.5$ for three half siblings: $(1+0.25+0.25)/3$. Even without any extra-pair paternity, the relatedness of a focal chick to the whole brood decreases rapidly as brood size increases: average relatedness to the whole brood is 75% with one full sibling, drops to 67% with two full siblings, and to 55% with ten full siblings.



Supplementary Figure 4.3. PRISMA flow chart of search results and the study selection process. See <http://www.pnas.org/content/113/48/13803.full> for a list of papers excluded from the analysis.

Supplementary Table 4.1. Results for all models: random effects.

#	Total I ²	Random effects	Component	SE	N species	N study	N obs	Notes
Null (a)	12.8%	Phylogeny	0.0086	0.0182	60	108	336	Full dataset
		Species	0.0005	0.0254				
		Study	0.1059	0.0265				
		Residual	0.0320	0.0077				
1	12.0%	Phylogeny	0.0000	NA				
		Species	0.0000	NA				
		Study	0.1039	0.0224				
		Residual	0.0321	0.0077				
2	12.0%	Phylogeny	0.0000	NA				
		Species	0.0056	0.0187				
		Study	0.0990	0.0277				
		Residual	0.0324	0.0078				
Null (b)	12.7%	Phylogeny	0.0060	0.0214	51	98	317	Excluding 9 species missing data on adult mortality or the broods possible each breeding season
		Species	0.0048	0.0266				
		Study	0.1014	0.0294				
		Residual	0.0330	0.0080				
3	11.6%	Phylogeny	0.0000	NA				
		Species	0.0000	NA				
		Study	0.0986	0.0227				
		Residual	0.0330	0.0080				
4	11.0%	Phylogeny	0.0000	NA				
		Species	0.0000	NA				
		Study	0.0896	0.0213				
		Residual	0.0335	0.0080				
Null (c)	12.4%	Phylogeny	0.0104	0.0189	49	96	314	Excluding 11 species missing data on adult mortality, the broods possible each breeding season, or mating system
		Species	0.0001	0.0245				
		Study	0.0984	0.0255				
		Residual	0.0328	0.0079				
5	10.5%	Phylogeny	0.0000	NA				
		Species	0.0000	NA				
		Study	0.0850	0.0205				
		Residual	0.0329	0.0079				
6	10.1%	Phylogeny	0.0000	NA				
		Species	0.0000	NA				
		Study	0.0787	0.0196				
		Residual	0.0333	0.0080				
Null (d)	12.9%	Phylogeny	0.0241	0.0274	31	68	230	Excluding 29 species missing data on adult mortality, the broods possible each breeding season, mating system, or extra pair paternity
		Species	0.0000	NA				
		Study	0.0955	0.0283				
		Residual	0.0288	0.0079				
7	11.3%	Phylogeny	0.0000	NA				
		Species	0.0000	NA				
		Study	0.0985	0.0262				
		Residual	0.0285	0.0079				
8	10.6%	Phylogeny	0.0000	NA				
		Species	0.0000	NA				
		Study	0.0900	0.0244				
		Residual	0.0289	0.0079				

Table reports the mean results of 500 ASReml linear mixed models. Models were weighted by study sample size (the number of broods used to calculate the original test statistic). Models are

grouped by the dataset used for analysis, and the notes column describes the loss in sample size due to missing life history data. Sample error variance was constrained to 1. Total heterogeneity (I^2) is a measure of the proportion of observed variance due to true differences in effect sizes in the null model. I^2 values of 25%, 50% and 75% indicate low, moderate and high levels ratios of signal to noise. This measure does not take effect size dispersion into account. Model numbers correspond to Table 4.1.

Supplementary Table 4.2. Relationships between environmental and life history variables.

		Environmental variables		N species
		Predictability	Quality	
Life history variables	Siblings y/n	-33.07 to -2.56	-4.24 to 23.28	60
	Brood size	-0.76 to 0.47	-0.28 to 0.59	
	Siblings y/n	-19.37 to -9.42	-2.18 to 9.03	51
	Brood size	-0.72 to 0.56	-0.31 to 0.52	
	# future broods possible	-0.02 to 0.02	-0.01 to 0.01	
	Siblings y/n	-33.19 to -13.06	-3.69 to 8.12	49
	Brood size	-0.89 to 0.41	-0.30 to 0.53	
	# future broods possible	-0.02 to 0.02	-0.01 to 0.01	
	Full vs. half siblings likelihood	-5.50 to 2.81	-3.54 to 2.22	
	Siblings y/n	-61.65 to -5.45	-6.66 to 25.08	33
	Brood size	-0.91 to 0.74	-0.64 to 0.43	
	# Future broods possible	-0.03 to 0.03	-0.01 to 0.01	
	Full vs. half siblings likelihood	-9.01 to 37.59	-80.76 to 7.21	
	Promiscuity	-0.03 to 0.03	-0.01 to 0.01	

Table reports the 95% CI for the relationship of environmental variables on each of the life history variables used with each subset of the overall dataset (n=60 species corresponds to Models 1 and 2; n=51 species corresponds to Models 3 and 4; n=49 species corresponds to Models 5 and 6; n=33 species corresponds to Models 8 and 7). Results are from MCMCglmm models, controlling for phylogeny. MCMCglmm was used instead of ASReml because ASReml models did not converge properly when accounting for phylogenetic variance in some models with smaller sample sizes. Cells in bold indicate the relationship is significant (the 95% CI does not include 0).

Supplementary Table 4.3. Effect of adding environmental variables to models.

		Only		All		N
		Life History	Environmental	Variables		
Model 1	Intercept	Coef=0.10 ± 0.04 F _{1,89,9} =13.57, p=0.0005	Coef=-0.09 ± 0.09 F _{1,91,6} =13.23, p=0.0002	Coef=-0.09 ± 0.09 F _{1,88,9} =13.57, p=0.0005	60 species, 108 studies, 336 effect sizes	
	Environmental predictability		Coef=0.20 ± 0.08 F _{1,91,7} =6.73, p=0.011*	Coef=0.14 ± 0.09 F _{1,92,7} =2.66, p=0.11		
	Environmental quality		Coef=0.32 ± 0.09 F _{2,191,8} =7.13, p=0.0010**	Coef=0.32 ± 0.09 F _{2,192,2} =7.14, p=0.0010**		
Siblings present y/n	Coef=-0.28 ± 0.11 F _{1,71,8} =6.69, p=0.0097**		Coef=-0.20 ± 0.12 F _{1,73,7} =2.86, p=0.095.			
<hr/>						
Model 2	Intercept	Coef=0.31 ± 0.09 F _{1,34,1} =12.61, p=0.0002	Coef=-0.09 ± 0.09 F _{1,91,6} =13.23, p=0.0002	Coef=0.05 ± 0.12 F _{1,89,6} =13.45, p=0.0004		
	Environmental predictability		Coef=0.20 ± 0.08 F _{1,91,7} =6.73, p=0.011*	Coef=0.18 ± 0.08 F _{1,92,6} =4.86, p=0.03*		
	Environmental quality		Coef=0.32 ± 0.09 F _{2,191,8} =7.13, p=0.0010**	Coef=0.32 ± 0.09 F _{2,192,2} =7.18, p=0.0010**		
	Brood size	Coef=-0.04 ± 0.02 F _{1,31,0} =4.57, p=0.033*		Coef=-0.04 ± 0.02 F _{1,96,1} =3.07, p=0.083.		

Variables included in the model

	Only Life History	Only Environmental	All Variables	N
Model 3	Intercept	Coef=0.21 ± 0.07 F _{1,79} = 9.14, p=0.0034	Coef=-0.06 ± 0.09 F _{1,81} = 15.70, p=0.0002	Coef=0.03 ± 0.11 F _{1,78} = 9.04, p=0.0036
	Environmental predictability		Coef=0.19 ± 0.08 F _{1,81} = 5.26, p=0.024*	Coef=0.09 ± 0.09 F _{1,81} = 0.92, p=0.34
	Environmental quality		Coef=0.32 ± 0.09 F _{2,183} = 6.93, p=0.0013**	Coef=0.32 ± 0.09 F _{2,182} = 6.86, p=0.0013**
	Siblings present y/n	Coef=-0.33 ± 0.11 F _{1,67} = 8.45, p=0.0050**		Coef=-0.27 ± 0.13 F _{1,69} = 4.14, p=0.046*
# Future broods possible			Coef=-0.02 ± 0.01 F _{1,99} = 2.03, p=0.16	
Model 4	Intercept	Coef=0.65 ± 0.14 F _{1,78} = 20.21, p=0.0000	Coef=-0.06 ± 0.09 F _{1,81} = 15.70, p=0.0002	Coef=0.39 ± 0.18 F _{1,80} = 19.77, p=0.0000
	Environmental predictability		Coef=0.19 ± 0.08 F _{1,81} = 5.26, p=0.024*	Coef=0.12 ± 0.08 F _{1,80} = 2.02, p=0.16
	Environmental quality		Coef=0.32 ± 0.09 F _{2,183} = 6.93, p=0.0013**	Coef=0.32 ± 0.09 F _{2,184} = 6.86, p=0.0013**
	Brood size	Coef=-0.08 ± 0.02 F _{1,82} = 11.87, p=0.0009***		Coef=-0.07 ± 0.03 F _{1,85} = 8.2, p=0.005**
# Future broods possible	Coef=-0.03 ± 0.01 F _{1,83} = 7.22, p=0.0087**		Coef=-0.03 ± 0.01 F _{1,85} = 5.13, p=0.026*	

51 species,
98 studies,
317 effect
sizes

Variables included in the model

	Only Life History	Only Environmental	All Variables	N
Model 5	Intercept	Coef=0.64 ± 0.18 F _{1,76,5} =8.58, p=0.0045	Coef=-0.06 ± 0.09 F _{1,80,7} =14.47, p=0.0003	Coef=0.46 ± 0.20 F _{1,76,1} =8.42, p=0.0049
	Environmental predictability		Coef=0.17 ± 0.08 F _{1,81,0} =4.44, p=0.038*	Coef=0.07 ± 0.09 F _{1,79,1} =0.63, p=0.43
	Environmental quality		Coef=0.32 ± 0.09 F _{2,184,5} =6.94, p=0.0012**	Coef=0.32 ± 0.09 F _{2,185,3} =6.79, p=0.0014**
	Siblings present y/n	Coef=-0.11 ± 0.14 F _{1,84,2} =0.42, p=0.42		Coef=-0.07 ± 0.15 F _{1,83,7} =0.19, p=0.67
Model 6	# Future broods possible	Coef=-0.05 ± 0.01 F _{1,95,4} =9.39, p=0.0028**		Coef=-0.04 ± 0.02 F _{1,96,4} =7.87, p=0.0061**
	Full vs. half sibs likelihood	Coef=-0.39 ± 0.15 F _{1,112,2} =6.94, p=0.0096**		Coef=-0.39 ± 0.15 F _{1,111,5} =6.76, p=0.011*
	Intercept	Coef=0.83 ± 0.16 F _{1,76,5} =21.95, p=0.0000	Coef=-0.06 ± 0.09 F _{1,80,7} =14.47, p=0.0003	Coef=0.62 ± 0.20 F _{1,77,7} =21.23, p=0.0000
	Environmental predictability		Coef=0.17 ± 0.08 F _{1,81,0} =4.44, p=0.038*	Coef=0.06 ± 0.08 F _{1,78,9} =0.62, p=0.43
Model 6	Environmental quality		Coef=0.32 ± 0.09 F _{2,184,5} =6.94, p=0.0012**	Coef=0.32 ± 0.09 F _{2,186,8} =6.78, p=0.0014**
	Brood size	Coef=-0.05 ± 0.03 F _{1,87,1} =3.07, p=0.083.		Coef=0.04 ± 0.03 F _{1,87,1} =2.51, p=0.12
	# Future broods possible	Coef=-0.05 ± 0.01 F _{1,86,4} =13.09, p=0.00050***		Coef=-0.05 ± 0.01 F _{1,89,7} =10.15, p=0.0020**
	Full vs. half sibs likelihood	Coef=-0.33 ± 0.14 F _{1,89,6} =5.98, p=0.016*		Coef=-0.31 ± 0.14 F _{1,90,3} =5.14, p=0.026*

49 species,
96 studies,
314 effect
sizes

Variables included in the model

	Only Life History	Only Environmental	All Variables	N			
Model 7	Intercept	Coef=0.65 ± 0.23 $F_{1,55.6}=4.93, p=0.030$	Coef=0.08 ± 0.11 $F_{1,2.7}=9.24, p=0.0000$	Coef=0.56 ± 0.25 $F_{1,54.8}=4.32, p=0.045$	31 species, 68 studies, 230 effect sizes		
	Environmental predictability		Coef=0.13 ± 0.10 $F_{1,33.1}=1.43, p=0.24$	Coef=0.07 ± 0.11 $F_{1,58.1}=4.73, p=0.036^*$			
	Environmental quality		Coef=0.22 ± 0.09 $F_{2,128.2}=2.95, p=0.056.$	Coef=0.22 ± 0.09 $F_{2,127.4}=3.09, p=0.049^*$			
	Siblings present y/n	Coef=0.00 ± 0.22 $F_{1,60.5}=0, p=1$		Coef=0.06 ± 0.24 $F_{1,60.2}=1.11, p=0.30$			
	# Future broods possible	Coef=-0.03 ± 0.02 $F_{1,58.4}=3.10, p=0.083.$		Coef=-0.03 ± 0.02 $F_{1,60.0}=0.08, p=0.79$			
	Full vs. half sibs likelihood	Coef=-0.43 ± 0.22 $F_{1,76.0}=3.77, p=0.056.$		Coef=-0.44 ± 0.22 $F_{1,74.9}=1.07, p=0.31$			
	Promiscuity (% EPPbr)	Coef=0.00 ± 0.01 $F_{1,58.5}=0.04, p=0.84$		Coef=0.00 ± 0.01 $F_{1,57.9}=1.22, p=0.28$			
	Model 8	Intercept	Coef=0.81 ± 0.19 $F_{1,55.9}=17.26, p=0.0001$	Coef=0.08 ± 0.11 $F_{1,2.7}=9.24, p=0.0000$		Coef=0.68 ± 0.23 $F_{1,55.4}=18.95, p=0.0001$	31 species, 68 studies, 230 effect sizes
		Environmental predictability		Coef=0.13 ± 0.10 $F_{1,33.1}=1.43, p=0.24$		Coef=0.05 ± 0.10 $F_{1,57.5}=4.73, p=0.035^*$	
Environmental quality			Coef=0.22 ± 0.09 $F_{2,128.2}=2.95, p=0.056.$	Coef=0.22 ± 0.09 $F_{2,128.0}=2.94, p=0.057.$			
Brood size		Coef=-0.07 ± 0.03 $F_{1,66.2}=3.87, p=0.053.$		Coef= -0.06 ± 0.03 $F_{1,64.6}=3.29, p=0.076.$			
# Future broods possible		Coef=-0.04 ± 0.02 $F_{1,58.3}=4.94, p=0.038^*$		Coef=-0.04 ± 0.02 $F_{1,60.5}=0.03, p=0.87$			
Full vs. half sibs likelihood		Coef=-0.19 ± 0.18 $F_{1,67.1}=1.00, p=0.32$		Coef=-0.18 ± 0.19 $F_{1,67.8}=2.45, p=0.12$			
Promiscuity (% EPPbr)		Coef=0.00 ± 0.01 $F_{1,58.5}=0.27, p=0.61$		Coef=0.00 ± 0.01 $F_{1,57.5}=1.24, p=0.27$			

Table reports the coefficient, Wald statistic and p-value for fixed effects for three sets of models: 1) a model with life history variables only (Model numbers correspond to Table 4.1); 2) a model with environmental variables only; and 3) a model with all fixed effects included. Results are the mean from 500 ASReml linear mixed models. Models controlled for phylogeny, repeated measures, and were weighted by study sample size (the number of broods used to calculate the original test statistic). Fixed effects in bold are significant at the $p < 0.05$ level, and in italics at the $p < 0.10$ level.

Supplementary Table 4.4. Results for all signal-of-quality models: fixed effects.

#	Fixed effects	df	Wald stat	p-value	N species	N study	N obs	Notes
9	Intercept	1, 16.8	4.23	<i>0.056</i>				
	Brood size	1, 18.8	1.06	0.32				
10	Intercept	1, 13.9	2.67	0.12	18	33	140	Full dataset
	Brood size	1, 17.0	0.18	0.68				
	Predictability	1, 11.3	0.69	0.42				
	Quality	2, 133.0	7.61	0.00075				
	Predictability * Quality	2, 133.0	3.74	0.026				
11	Intercept	1, 12.4	2.24	0.16				Excluding 2 species missing data on adult mortality or the broods possible each breeding season
	Brood size	1, 14.7	0.88	0.36				
	# of future broods possible	1, 10.1	0.11	0.75				
12	Intercept	1, 10.5	1.83	0.20	16	30	115	Excluding 8 species missing data on adult mortality, the broods possible each breeding season, or mating system
	Brood size	1, 12.1	0.38	0.55				
	# of future broods possible	1, 11.4	0.21	0.66				
	Predictability	1, 9.6	0.03	0.88				
	Quality	2, 107.0	10.18	0.00009				
13	Intercept	1, 5.2	0.78	0.42				Excluding 8 species missing data on adult mortality, the broods possible each breeding season, or mating system
	<i>Brood size</i>	1, 5.7	0.00	0.97				
	# of future broods possible	1, 4.3	0.24	0.65				
	Full vs half sibs likelihood	1, 4.3	0.46	0.53				
14	Intercept	1, 4.0	0.99	0.38	10	20	80	Excluding 8 species missing data on adult mortality, the broods possible each breeding season, or mating system
	<i>Brood size</i>	1, 4.3	0.10	0.77				
	# of future broods possible	1, 3.7	0.13	0.74				
	Full vs half sibs likelihood	1, 3.4	0.06	0.82				
	Predictability	1, 3.6	0.16	0.72				
	Quality	1, 73.0	4.83	0.011				

Table reports the mean results of 500 ASReml linear mixed models. Models controlled for phylogeny, repeated measures on studies and species, and were weighted by study sample size (the number of broods used to calculate the original test statistic). Fixed effects in bold are significant at the $p < 0.05$ level, and in italics at the $p < 0.10$ level. Models are grouped by the dataset used for analysis, and the notes column describes the loss in sample size due to missing life history data. Models did not converge when promiscuity was included as a fixed effect.

Supplementary Table 4.5. Results for all signal-of-quality models: random effects.

#	Total I ²	Random effects	Component	SE	N species	N study	N obs	Notes
Null (a)	5.87%	Phylogeny	0.0143	0.0329	18	33	140	Full dataset
		Species	0.0197	0.0259				
		Study	0.0118	0.0105				
		Residual	0.0166	0.0068				
9	5.79%	Phylogeny	0.0149	0.0267	18	33	140	Full dataset
		Species	0.0147	0.0215				
		Study	0.0146	0.0116				
		Residual	0.0162	0.0067				
Null (b)	13.1%	Phylogeny	0.0980	0.0354	16	30	115	Excluding 2 species missing data on adult mortality or the broods possible each breeding season
		Species	0.0222	0.0285				
		Study	0.0106	0.0108				
		Residual	0.0197	0.0078				
11	6.04%	Phylogeny	0.0110	0.0320	16	30	115	Excluding 2 species missing data on adult mortality or the broods possible each breeding season
		Species	0.0213	0.0259				
		Study	0.0128	0.0118				
		Residual	0.0192	0.0077				
Null (c)	4.74%	Phylogeny	0.0046	0.1095	10	20	80	Excluding 8 species missing data on adult mortality, the broods possible each breeding season, or mating system
		Species	0.0450	0.0460				
		Study	0.0002	0.0035				
		Residual	0.0000	NA				
13	9.07%	Phylogeny	0.0988	0.0769	10	20	80	Excluding 8 species missing data on adult mortality, the broods possible each breeding season, or mating system
		Species	0.0000	NA				
		Study	0.0009	0.0044				
		Residual	0.0000	NA				

Table reports the mean results of 500 ASReml linear mixed models. Models were weighted by study sample size (the number of broods used to calculate the original test statistic). Models are grouped by the dataset used for analysis, and the notes column describes the loss in sample size due to missing life history data. Sample error variance was constrained to 1. Total heterogeneity (I²) is a measure of the proportion of observed variance due to true differences in effect sizes in the null model (Borenstein *et al.* 2011). I² values of 25%, 50% and 75% indicate low, moderate and high levels ratios of signal to noise (Borenstein *et al.* 2011). This measure does not take effect size dispersion into account (Borenstein *et al.* 2011). Model numbers correspond to Table 4.1.

5. SIGNALLING OF INFORMATION THAT IS NEITHER CRYPTIC NOR PRIVATE^{††}

Abstract

It is commonly assumed that in order for animal signals to be advantageous, the information being signalled could not have been obtained otherwise, and is therefore ‘cryptic’ or ‘private’. Here, we suggest a scenario in which individuals can gain an advantage by signalling ‘public’ information that is neither cryptic nor private. In that scenario signalling increases the efficiency with which that ‘public’ information is transmitted. We formalize our idea with a game in which offspring can signal their condition to their parents. Specifically, we consider a resource-strapped parent who can only invest in one of its two offspring, and we allow offspring the chance to influence parental investment through a signal. A parent in the game seeks to invest in the higher-quality offspring, which it could identify either through a publicly available cue, such as body size, or by relying on a signal provided by the offspring. We find that if the signal can convey information about offspring quality more efficiently than cues, then signalling of condition between offspring and parents can be favoured by selection, even though parents could potentially have acquired the same information from the cue. Our results suggest that the biological function of signals may be broader than currently considered, and provide a scenario where low cost signalling can be favoured. More generally, efficiency benefits could explain signalling across a range of biological and economic scenarios.

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Introduction

Animals use signals to communicate information, ranging from their quality as a potential mate to their need for food (Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). Signalling systems are vulnerable to collapse because individuals could potentially signal dishonestly to coerce others in ways that benefit the signaller (Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). Evolutionary theory has provided solutions to this problem by showing that individuals can be selected to signal honestly for a number of reasons, such as if the signaller and receiver share a common interest, or if dishonest signals are too costly to produce (Zahavi 1975; Grafen 1990; Godfray 1991; Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). In these cases, signalling can be an evolutionary stable outcome when any potential benefits of signalling dishonestly are outweighed by the costs.

A prevailing explicit assumption in the signalling literature is that in order for signalling to be favoured, the information being signalled could not be obtained otherwise, and is therefore 'cryptic' or 'private' (e.g. Grafen 1990; Godfray 1991; Kilner & Johnstone 1997; Bergstrom *et al.* 2002; Johnstone 2004). We challenge this assumption here. Our hypothesis is that individuals can be favoured to signal information that is not cryptic or private, if signalling increases the efficiency with which that information can be transmitted. In order for this hypothesis to hold, it would require that the increase in efficiency outweighs the cost of signalling, and that honest (or at least meaningful) signalling is favoured. Our aim is to investigate the theoretical plausibility of this hypothesis.

It is useful to consider our hypothesis in a specific scenario, and so we examine the case of offspring signalling their condition to their parents. We pick this scenario because it has been explicitly stated, on numerous occasions, that offspring must be signalling cryptic information (e.g. Godfray 1991; Kilner & Johnstone 1997; Royle *et al.* 2002; Johnstone 2004). We focus on a scenario in which a parent has only enough food to feed one of its two offspring. Parents in this scenario will be favoured to invest in the higher-quality offspring, which they could identify via publicly available cues, such as body size (Lack 1954; Mock & Parker 1997; Davis *et al.* 1999). This kind of scenario is reflected in the biology of bird species like the hoopoe (*Upupa epops*) and blue-footed booby (*Sula nebouxii*), as parents in those species tend to experience brood reduction, and preferentially feed larger, higher quality, offspring (Drummond & Garcia Chavelas 1989; Martin-Vivaldi *et al.* 1999; Caro *et al.* 2016a). If parents in species like the hoopoe or the blue-footed booby could obtain information about offspring quality more quickly via offspring signals, then they would have more time to acquire food for the offspring. This efficiency benefit could potentially outweigh the costs of signalling, and make signalling evolutionarily stable (Figure 5.1). We examine the theoretical plausibility of this scenario by proposing and solving a simple game theory model. We specifically want to determine the conditions under which production of the offspring signal will provide the parent with a means for distinguishing offspring on the basis of quality, at evolutionary equilibrium. In this sense, we are looking for an ‘honest’ signalling solution to the game. We then address the biological plausibility and empirical applications of the model in our discussion.

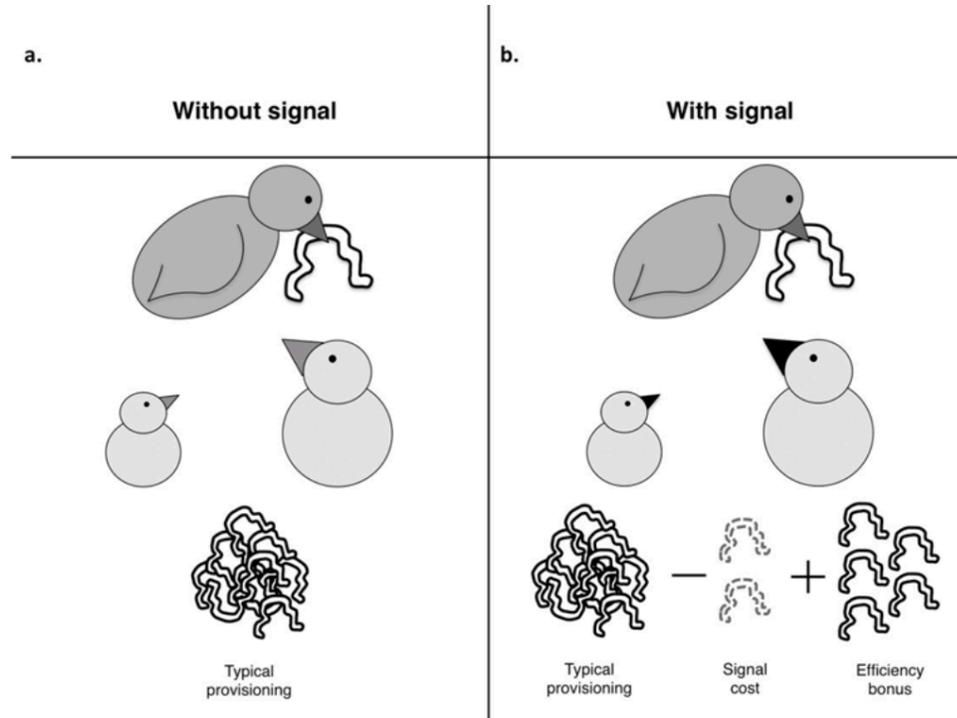


Figure 5.1. Signals of non-cryptic condition are biologically feasible. (a) Parents can distribute food amongst their offspring by relying on a cue of condition, such as body size. **(b)** Alternatively, parents could distribute food amongst their offspring by relying on a signal of non-cryptic condition, such as mouth gape area, begging calls or begging height. If it is much faster for parents to use the signal, they could spend more time foraging for additional caterpillars to feed their brood. As long as the efficiency benefit of using the signal outweighs the cost of producing the signal, this communication system can be advantageous, even if the information encoded in the signal is non-cryptic.

The Model

We consider a parent that has one low-quality offspring and one high-quality offspring. Offspring quality is not cryptic, and the parent can distinguish the low-quality offspring from the high-quality one by investigating some cue (e.g. body size). Our starting point could mirror some natural cases, such as blue-footed boobies, where two eggs hatch asynchronously, leading to a large size disparity (Drummond & Garcia Chavelas 1989).

We assume, first, that a parent can also distinguish offspring from one another through means other than the cue. Specifically, the parent can respond to a signal (possibly) produced by the offspring. We assume further that assessing the signal is more efficient than assessing the cue, saving the parent time that can be spent acquiring more food. Signalling can, however, be costly to the offspring.

We then assume that the parent, after producing two offspring, is experiencing relatively poor environmental conditions. Conditions are so poor, in fact, that the parent can successfully rear only one of its two offspring. Therefore, the parent must decide which offspring it will invest in, and which offspring it will allow to die. Offspring, in turn, must decide on what information (if any) to attempt to convey to the parent via the signal. We assume that a high-quality offspring who receives parental investment has fitness equal to 1, and that a low-quality offspring who receives parental investment has a fitness equal to $0 < v < 1$. An offspring who does not receive investment has fitness equal to zero. We assume parents have complete control over the distribution of resources like food (e.g., Godfray 1991).

We model the decisions made by the parent and offspring as moves in a three-player evolutionary game (Figure 5.2). In this game, the high-quality offspring moves either by producing a signal (strategy H_1), or by not signalling at all (strategy H_2). At exactly the same time, the low-quality offspring also moves either by producing a signal (strategy L_1), or by not signalling at all (strategy L_2). Any offspring that signals reduces its fitness by a fraction c , which reflects the cost of signal production.

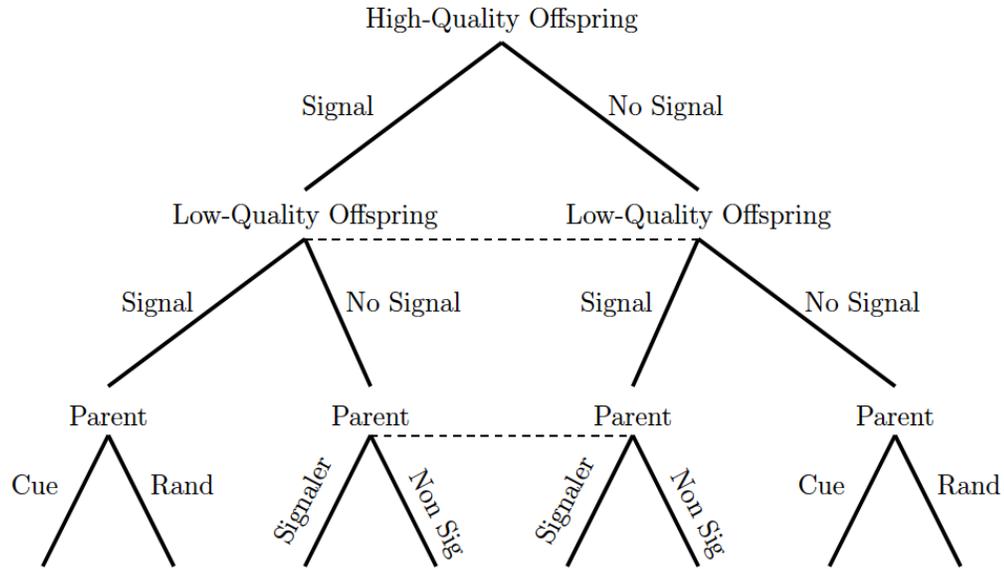


Figure 5.2. Tree depiction of the game proposed in the main text. Individual decision-makers appear at nodes, and solid branches indicate different actions available to individual decision-makers. Nodes linked by dashed lines indicate that the corresponding decisions are made by individuals who have been given the same information (i.e. the parents connected by the dotted line have both seen only one offspring signal). In particular, the fact that offspring decide upon their respective strategies simultaneously means that the nodes depicting the low-quality offspring's decision must be connected by a dashed line.

The parent's move in the game follows those made by the offspring, and its available moves vary depending on the situation. If both offspring signal, or if neither offspring signals, then the parent cannot use the signal to distinguish one offspring from the other. In these two cases, the parent moves either by using the cue to direct investment to the high-quality offspring, or by investing in a randomly chosen offspring. Assessing the cue is assumed to incur some time cost, such that investing at random confers an efficiency benefit, which means that the parent is able to increase the fitness of the offspring who receives investment by an additive amount b . If only one offspring signals, then we assume the parent moves either by investing in the signaller, or by investing in the non-signaller. In this case, the parent also avoids the cost of assessing

the cue, and so gains the multiplicative efficiency benefit b . Because the parent can choose between two moves in each of three different situations, there are eight parental strategies in this game (P_1 to P_8 in Table 5.1).

Table 5.1. Description of the eight possible parental strategies, P_1 to P_8 , in the game.

Strategy	Both offspring signal	One offspring signals	Neither offspring signals
P_1	Feed according to cue	Feed signaller	Feed according to cue
P_2	Feed according to cue	Feed signaller	Feed at random
P_3	Feed according to cue	Feed non-signaller	Feed according to cue
P_4	Feed according to cue	Feed non-signaller	Feed at random
P_5	Feed at random	Feed signaller	Feed according to cue
P_6	Feed at random	Feed signaller	Feed at random
P_7	Feed at random	Feed non-signaller	Feed according to cue
P_8	Feed at random	Feed non-signaller	Feed at random

Each strategy specifies a course of action given the presence or absence of offspring signals.

Method of Analysis

We solve the game proposed in the previous section by identifying strategies that are likely to remain fixed in a population. The solution concept we turn to is the Nash equilibrium. Here, the Nash equilibrium is a strategy profile (H_i, L_j, P_k) that produces a payoff to each player that cannot be improved upon by a unilateral change in strategy. The Nash equilibrium is a necessary condition of Maynard Smith's (1982) evolutionarily stable strategy (ESS, Maynard Smith 1982). The Nash equilibrium has also been the solution concept used in other theoretical treatments of signals between offspring and parents (e.g., Rodríguez-Gironés 1999). We are particularly interested in those equilibria in which one, and only one, offspring signals. The signal would then provide a parent with a clear means of distinguishing offspring based on quality. In those cases the signal conveys meaningful (or, in some sense, 'honest') information to the parent.

To find the Nash equilibrium, we translate the consequences of the various strategies into inclusive-fitness payoffs (Hamilton 1964). The inclusive-fitness payoff awarded to an offspring depends upon the relatedness between it and its sibling, $0 < r < 1$. In contrast, relatedness factors out of any inclusive-fitness payoff the parent receives, because the parent is equally related to both offspring.

Results

The Nash equilibria we obtain vary according to whether investment using the public cue of quality is more or less profitable than investment at random. If the efficiency benefit b falls below a threshold value of $(1 - v)/(1 + v)$, then using the cue is more profitable and we obtain one set of Nash equilibria. If b exceeds the threshold value of $(1 - v)/(1 + v)$, then investing at random is more profitable and we obtain a different set of Nash equilibria. The details surrounding the equilibria are given below.

Case 1: Following the Cue is Better than Investing at Random

We first consider the scenario where the efficiency benefits gained from not investigating the cue are low, $b < (1 - v)/(1 + v)$. In this scenario, following the cue is better than investing at random. Consequently, we are able to examine a reduced game that excludes the parental strategies that rely on random investment (Table 5.2). In that reduced game, there may be two Nash equilibria at which one, and only one, offspring signals.

Table 5.2. Reduced payoff matrix for the case when investing in offspring based on the cue is more profitable than investing at random ($b < (1 - v)/(1 + v)$).

		H_1		H_2	
		L_1	L_2	L_1	L_2
P_1	$(1 - c)$	$(1 - c)(1 + b)$	$v(1 - c)(1 + b)$	1	
	$r(1 - c)$	$r(1 - c)(1 + b)$	$v(1 - c)(1 + b)$	r	
	$(1 - c)$	$(1 - c)(1 + b)$	$rv(1 - c)(1 + b)$	1	
P_3	$(1 - c)$	$v(1 + b)$	$(1 + b)$	1	
	$r(1 - c)$	$v(1 + b)$	$r(1 + b)$	r	
	$(1 - c)$	$rv(1 + b)$	$(1 + b)$	1	

Each cell presents the payoff to the parent (row player), the low-quality offspring (column player), and the high-quality offspring (super-column player), in that order. H_1 and L_1 indicate that high- and low-quality offspring produce the signal, while H_2 and L_2 indicate that offspring do not signal. P_1 and P_3 correspond to parental strategies in Table 5.1. Shaded cells indicate Nash equilibria where signalling can be stable.

The first candidate Nash equilibrium is the triplet (H_1, L_2, P_1) . This triplet corresponds to the situation in which only the high-quality offspring signals, and the parent directs its investment toward that signal in an efficient manner. In keeping with definition of the Nash equilibrium, a unilateral switch from L_2 to L_1 will not increase the low-quality offspring's inclusive-fitness payoff. However, unilateral switches from H_1 to H_2 , or from P_1 to P_3 may be rewarded, and so there is a chance the definition of a Nash equilibrium will not be met. To ensure strategy switches made by the high-quality offspring and the parent, respectively, are not rewarded, we must have $(1 + b)(1 - c) \geq \max\{1, v(1 + b)\}$, or equivalently $c \leq 1 - \max\{1/(1 + b), v\}$. Because we have assumed $b < (1 - v)/(1 + v)$, we can be sure that $v < (1 - b)/(1 + b)$, which implies that $\max\{1/(1 + b), v\} = 1/(1 + b)$. The condition for (H_1, L_2, P_1) to be a Nash equilibrium, therefore, can be stated simply as $c \leq 1 - 1/(1 + b)$. In other words, the cost of signalling cannot be too high. This Nash equilibrium condition is illustrated in Figure 5.3 alongside the constraints imposed by other model assumptions. As the figure shows, the largest permissible cost increases as the efficiency benefit rises, and is independent of the relatedness between siblings.

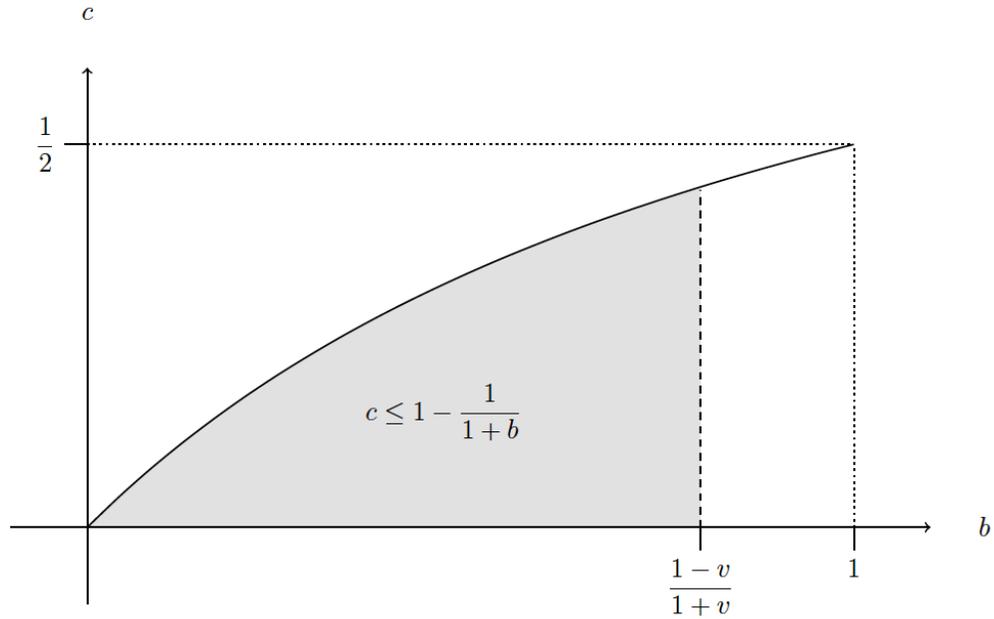


Figure 5.3. If the efficiency benefit is small, meaning ($b < (1 - v)/(1 + v)$), then the strategy profile (H1, L2, P1) is a Nash equilibrium provided b, c parameters remain in the shaded region. The shaded region is bounded by a curve describing maximum permissible cost, $c = 1 - 1/(1+b)$, and the maximum b in this case. One can see that the conditions under which (H1, L2, P1) is a Nash equilibrium become more restrictive either as b decreases or as v increases.

The second Nash equilibrium is the triplet (H_2, L_1, P_3). It corresponds to the situation in which the low-quality offspring signals in order to efficiently guide the parent's investment toward the non-signalling, high-quality offspring. The triplet follows the definition of a Nash equilibrium, because:

- (i) a unilateral switch from H_2 to H_1 penalizes the high-quality offspring by an amount $(1 + b) - (1 - c) = (b + c)$;
- (ii) a unilateral switch from L_1 to L_2 penalizes the low-quality offspring by an amount $r(1 + b) - r = rb$;
- (iii) a unilateral switch from P_3 to P_1 penalizes the parent by an amount $(1 + b) - (1 + b)(1 - c)v = (1 + b)(1 - (1 - c)v)$.

The fact that (H_2, L_1, P_3) is a Nash equilibrium is quite intuitive. Indeed, the effective cost of signalling, here, is actually zero, because the offspring who signals ultimately dies.

Case 2: Investing at Random is better than Following the Cue

We now consider the scenario where the efficiency benefits gained from not assessing the cue are high, $b > (1 - \nu)/(1 + \nu)$. Under this condition, investing at random is better than following the cue, and so we consider a reduced game that excludes the parental strategies that rely on the cue (Table 5.3). As in the previous case, we identify two Nash equilibria, at which only one offspring signals.

Table 5.3. Reduced payoff matrix for the case when investing in offspring randomly is more profitable than investing based on the cue ($b > (1 - \nu)/(1 + \nu)$).

		H_1		H_2	
		L_1	L_2	L_1	L_2
P_6		$(1 - c)(1 + b)(1 + \nu)/2$	$(1 - c)(1 + b)$	$\nu(1 - c)(1 + b)$	$(1 + b)(1 + \nu)/2$
		$(1 - c)(1 + b)(r + \nu)/2$	$r(1 - c)(1 + b)$	$\nu(1 - c)(1 + b)$	$(1 + b)(r + \nu)/2$
		$(1 - c)(1 + b)(1 + r\nu)/2$	$(1 - c)(1 + b)$	$r\nu(1 - c)(1 + b)$	$(1 + b)(1 + r\nu)/2$
P_8		$(1 - c)(1 + b)(1 + \nu)/2$	$\nu(1 + b)$	$(1 + b)$	$(1 + b)(1 + \nu)/2$
		$(1 - c)(1 + b)(r + \nu)/2$	$\nu(1 + b)$	$r(1 + b)$	$(1 + b)(r + \nu)/2$
		$(1 - c)(1 + b)(1 + r\nu)/2$	$r\nu(1 + b)$	$(1 + b)$	$(1 + b)(1 + r\nu)/2$

Each cell presents the payoff to the parent (row player), the low-quality offspring (column player), and the high-quality offspring (super-column player), in that order. H_1 and L_1 indicate that high- and low-quality offspring produce the signal, while H_2 and L_2 indicate that offspring do not signal. P_1 and P_3 correspond to parental strategies in Table 5.1. Shaded cells indicate Nash equilibria where signalling can be stable.

We first consider the triplet (H_1, L_2, P_6) , where only the high-quality offspring signals, and only the high-quality offspring receives parental investment. In this case, (H_1, L_2, P_6) fails to be a Nash equilibrium when either:

- (i) the signal is so costly that it is better, from the parent’s perspective, to

- invest in the offspring whose quality is not diminished by the signal,
- (ii) it is in the high-quality offspring's best interest, in an inclusive-fitness sense, to stop signalling and suffer the possible consequences of its parent's random investment, or
 - (iii) it is in the low-quality offspring's best interests, in an inclusive-fitness sense, to start signalling in order to receive a chance parental investment.

From Table 5.3 we see that (i) and (ii) can be ruled out when $(1 - c) \geq \max\{v, (1 + rv)/2\}$, while (iii) can be ruled out when $r \geq v$. Furthermore, if we do have $r \geq v$, then we can be sure that $v < 1/(2-r)$ so that $\max\{v, (1 + rv)/2\} = (1 + rv)/2$. It follows that (H_1, L_2, P_6) is a Nash equilibrium if and only if $r \geq v$ and $c \leq (1 - rv)/2$. The latter condition sets the largest permissible signalling cost, and it depends on the relatedness between siblings (Figure 5.4). In addition, the largest permissible cost does not depend on the efficiency benefit b beyond the mathematical requirement that defines this case. Of course that mathematical requirement, namely $b > (1 - v)/(1 + v)$, can be rearranged as $v > (1 - b)/(1 + b)$, which puts a lower bound on v (Figure 5.4).

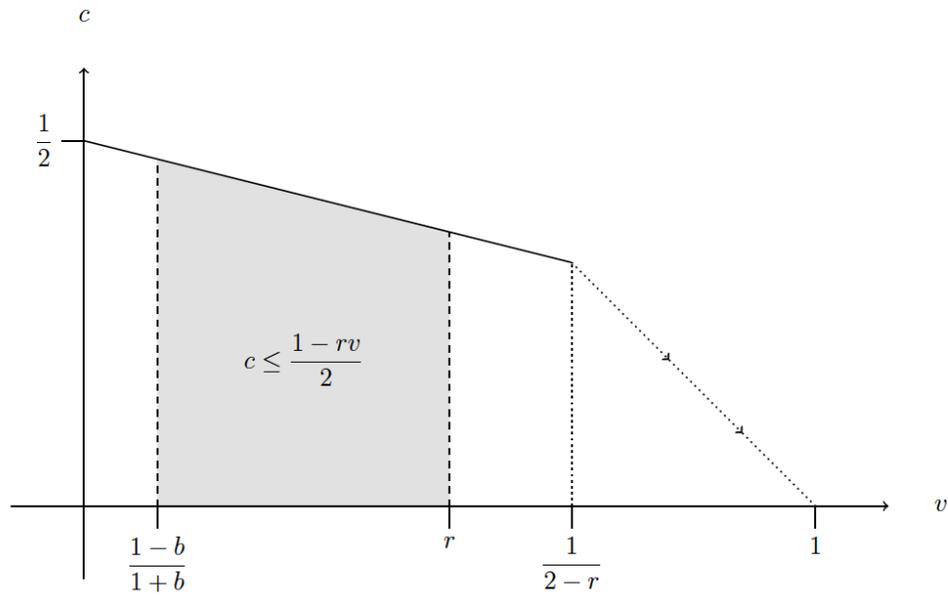


Figure 5.4. If the efficiency benefit is large, meaning $(b > (1 - v)/(1 + v))$, then the strategy profile (H1, L2, P6) is a Nash equilibrium provided v, c parameters remain in the shaded region. The shaded region is bounded by a curve describing maximum permissible cost, $c = (1 - rv)/2$, and the minimum and maximum v , respectively, in this case. One can see that the conditions under which (H1, L2, P6) is a Nash equilibrium become more restrictive as v increases. By contrast, an increase in r has mixed effects, broadening the range of possible v values on one hand, but reducing the maximum permissible cost on the other hand (as indicated by the dotted arrows).

The second candidate Nash equilibrium we consider is (H_2, L_1, P_8) , which corresponds to yet another situation in which only the offspring destined to die provides the signal. However, in contrast to the analogous situation described for the previous case, this triplet is not guaranteed to be an equilibrium. Efficiency gains are now large enough to provide a parent with an incentive to invest at random when there is no signal to guide its behaviour. This means that a low-quality offspring may be able to increase its payoff by switching from L_1 to L_2 , i.e. by turning off its signal. To ensure this kind of gain cannot be made we must have $r \geq v$, so that the low-quality offspring values its high-quality sibling more than it values itself. In contrast to the previous case, examination of

the consequences of other unilateral deviations from (H_2, L_1, P_8) shows that $r \geq v$ is the only condition that needs to be satisfied if the triplet is to be a Nash equilibrium (Table 5.3).

Discussion

Broadly speaking, our game-theoretic model results show that natural selection can lead offspring to signal their quality, even if that quality is not cryptic. This agrees with the hypothesis presented in the introduction, but contradicts the common assumption in the field of parent-offspring communication that offspring signals of need or quality must transmit information that cannot be obtained by parents in any other way (e.g., Grafen 1990; Godfray 1991; Kilner & Johnstone 1997; Bergstrom *et al.* 2002; Johnstone 2004). One implication of our results is that empirical researchers attempting to identify precisely what is encoded in offspring signals should consider the possibility that the biologically relevant aspects of condition may be public. Furthermore, we have focused on the extreme case where cues and signals carry the same information. In reality, signals could have multiple functions, conveying both public information more efficiently, and cryptic information, which could make them even more likely to be favoured (Kilner *et al.* 1999). More generally, while we have modeled signals of non-cryptic quality in the context of parent-offspring communication, similar outcomes could be expected in other honest-signalling scenarios in the fields of biology and economics, such as sexual selection (Grafen 1990), or even competition in the labour market.

Our analysis considered small and large efficiency benefits separately. In both cases we identified two distinct instances in which a signal conveyed meaning at equilibrium

(Table 5.4). In the first instance, only the low-quality offspring produced the signal, and the parent used that signal to direct investment toward the signaller's high-quality counterpart. In the second instance, only the high-quality offspring produced the signal that attracted parental investment away from the low-quality offspring. In both instances, the family group can be understood as using the signal for the purpose of making inclusive-fitness gains. Aligned interests such as these can contribute to the stability of offspring-parent signals (Maynard Smith 1991b; Rodríguez-Gironés 1999), but it has not been previously shown that efficiency benefits are able to bring interests into alignment. That said, our results do rely critically on the assumption that offspring differ in quality. As the variation in offspring quality is diminished (i.e. as v increases) the conditions for one and only one signal at equilibrium become more restrictive, and in the limit as v goes to 1, none of the conditions can be met (Table 5.4).

Table 5.4. Summary of mathematical conditions associated with the two instances of Nash equilibrium solutions at which one, and only one, offspring signals.

Case	Only low-quality offspring signals, high-quality offspring receives parental investment.	Only high-quality offspring signals, and high-quality offspring receives parental investment.
$b < (1 - v)/(1 + v)$	not applicable (always Nash equi)	$c \leq 1 - 1/(1 + b)$
$b > (1 - v)/(1 + v)$	$r \geq v$	$c \leq (1 - rv)/2$ and $r \geq v$

The marginal case $b = (1-v)/(1-v)$ has been neglected.

Signalling models often predict the existence of multiple equilibria (Bergstrom & Lachmann 1997; Lachmann & Bergstrom 1998), and ours is no exception. Indeed, the two distinct instances identified above could *simultaneously* be solutions to the game we proposed. It is important to recognize, though, that the mathematical requirements in the first instance (only the high-quality offspring signals) were more restrictive than those in the second (only the low-quality offspring signals). We found that, if the high-quality

offspring was predicted to signal at equilibrium, then the cost of signalling could not exceed some threshold value. By contrast, no such requirement on cost was made of a low-quality signaller at equilibrium, because, when it signalled at equilibrium, the low-quality offspring did not receive any parental investment, and will therefore die. The actual cost of the signal produced by the low-quality offspring at equilibrium, then, is extremely low. Had we relaxed the assumption that the offspring who does not receive parental investment dies, we would have expected the contrast between equilibrium signalling from the high- and low-quality offspring, respectively, to be weaker. However, it is likely that, in order to be maintained at equilibrium, signals provided by the low-quality offspring would have continued to require the costs of signalling to be sufficiently low. Still, we expect that the threshold condition for the maintenance of the signal from the low-quality offspring only would have continued to be more restrictive.

There are some conceptual similarities between our model and a scenario discussed in Lachmann et al. (2001). Those authors suggest a verbal model for sparrows in which individuals can produce a relatively cheap signal that indicates aggressiveness, fighting ability or other correlates of their resource-holding potential. In their model, individuals who signal dishonestly are punished by conspecifics, which imposes a cost of dishonest signalling. Similarities between our models include: (i) the potential for honest (or meaningful) signalling at equilibrium despite low realised costs of signalling; and (ii) the possibility for individuals to avoid other types of costs, for example agonistic interactions in the sparrow example, by signalling (Lachmann *et al.* 2001). In the case of (ii), the absence of other types of cost parallels the efficiency benefits introduced here, but the two are distinct—the absence of a cost of dishonesty, on one hand, and the presence of an efficiency benefit, on the other hand. Differences between the two

models include: (i) the consideration we give to interactions between relatives; (ii) an explicit efficiency benefit from following signals, relative to using cues (our b term); (iii) our presentation of explicit conditions for stability of honest signalling; and (iv) our examination of stability against invasion by non-signal-based means of achieving efficiency benefits (i.e. investing at random).

Our model also shares some similarities with models of amplifier signals (Hasson 1989; Bogaardt & Johnstone 2016). Amplifiers are traits that magnify differences in cues of quality, and are typically considered in terms of sexual signalling. In both cases, a receiver prefers higher-quality individuals and can use a cue to distinguish between individuals of differing quality, and those cues are linked to a separate trait, which may or may not evolve as a stable signal. The key difference between our models lays in the benefit of the signal: in our model, the benefit is increased efficiency, which increases the amount of parental investment possible, while in amplifier models, the benefit is to reduce perceptual errors in the assessment of male cues. Furthermore, amplifiers increase the total amount of information available to receivers, because signallers can vary their level of amplification. In our model, signalling is stable even though receivers never experience an increase in the amount of information they can gain, whether they respond to the cue, the signal, or both.

Empirical Applications

Under what conditions would our hypothesis be most likely to apply in the real world? We showed that selection can favour signalling of information that is not cryptic or private, to increase the efficiency with which that ‘public’ information can be transmitted. Considering offspring soliciting their parents for food, this is more likely to

be the case when: (i) it would be relatively difficult for parents to make use of public cues or signals of cryptic condition, due to acoustic interference from the environment, limited visibility, or low variability in the public cue, such as in synchronously hatching broods where all nestlings are approximately the same size; (ii) when offspring condition hovers around the viability threshold, so that small increases in the total amount of provisioning could have large impacts on fitness; and/or (iii) when the cost of signalling is relatively low.

How plausible is this set of conditions, where the efficiency benefits from transmitting information with a signal can outweigh the cost of signalling? Consider a common bird species, the great tit (*Parus major*). The efficiency benefit (b) of responding to a low cost signal could be relatively high in birds such as the great tit, because: (i) they nest in dark tree holes, where it may be relatively hard to assess cues such as body size (Wiebe & Slagsvold 2012b); (ii) they frequently experience brood reduction, so slight increases in provisioning rate could have especially large impacts on the fitness of marginal offspring (Bengtsson & Rydén 1983); and (iii) their breeding period is constrained to the relatively short window when caterpillars are abundant, and so efficiency in distributing food could be important (Hinks *et al.* 2015). Great-tit parents can spend an average of 8 hours per day foraging for their brood (Barba *et al.* 2009; García-Navas *et al.* 2013). Over a 15-day nestling period, these parents would have approximately 864,000 seconds of total foraging time. Great-tit parents can make approximately 13 provisioning trips per hour, so a parent can return to the nest with prey, such as caterpillars, approximately every 138 seconds, on average (García-Navas *et al.* 2013). If the smallest offspring are at a high risk of starvation, parents will be selected to feed the offspring in the best condition (Mock & Parker 1997; Davis *et al.* 1999; Caro *et al.*

2016a). Parents could determine condition either by directly assessing body size or by relying on a low cost signal that transmits the same information as body size, such as mouth gape area or begging call volume. For example, assume that parents could realize an efficiency benefit of 5 seconds per caterpillar by using the signal. In this scenario, parents relying on the signal would be able to bring back an additional 218 caterpillars over the 15-day nestling period. Even if producing the signal costs as much as one caterpillar per day per offspring, parents with a brood of seven offspring would experience a net increase of 113 caterpillars per brood. Those 113 extra caterpillars could be enough to tip the scales between the smallest nestling starving or surviving.

Ultimately, the plausibility of our hypothesis can only be determined with empirical work that explicitly measures these kinds of parameters. This would require measuring the efficiency of different parental allocation strategies, which could be done experimentally by varying the information available to parents and comparing the amount of time it takes a parent take to feed its offspring. For instance, previous researchers have removed parents' ability to distribute food based on begging vocalizations by muting individual nestlings (Glasse & Forbes 2002). Empirical work must also exclude the possibility that the biologically relevant aspect of condition being signalled is public and not cryptic, which would require measuring the association between signal intensity and various aspects of condition which are more or less public, such as plasma glucose levels as opposed to body mass (e.g., Quillfeldt *et al.* 2009). Empirical confirmation of our hypothesis would also need to show that parents actively choose which offspring to feed rather than passively allocate food to the most conspicuous signaller (e.g., Heeb *et al.* 2003; Dugas & Rosenthal 2009; Wiebe & Slagsvold 2012b). Comparative studies could test whether signals of public information

with efficiency benefits are more likely to evolve when parents would have more difficulty utilizing cues of condition, such as in species that nest in dark cavities or have more synchronous hatching, or when the period of parental care is shorter. Finally, our model predicts that relatedness plays a key role in the establishment of meaningful signals at equilibrium only when efficiency benefits are large; empirical work could also attempt to verify this prediction. Offspring can also benefit from their siblings directly if their siblings' signals stimulate parents to increase their total investment, and so future work could explore how signals of public condition influence total provisioning as well as food distribution (Kilner *et al.* 2004; Johnstone 2004).

6. CONFLICT WITHIN FAMILIES AND OFFSPRING SIGNALS OF NON-CRYPTIC INFORMATION

Abstract

Families are frequently in conflict over how parents should invest in each offspring, especially when brood reduction is likely. Parent birds may bias investment towards offspring in either better or worse condition by varying their laying, incubating, and feeding patterns. Offspring may attempt to secure more food by signalling their condition. We can extrapolate from signalling theory to predict that these signals are more likely to be honest when within-family conflict is low, and that parents will stop responding if signals are dishonest. Traditionally, theory has also assumed that these signals contain information about cryptic condition, because otherwise parents could directly compare offspring using cues. However, a recent model found that honest signals about non-cryptic condition can be stable. We examine great tits, *Parus major*, to see (i) if parents adjust investment based on the likelihood of brood reduction; (ii) if nestling gape size signals non-cryptic information; and (iii), if gape size is a signal, whether its reliability varies based on within-family conflict. We found that parents adjust clutch size, egg size and incubation patterns to favour fewer, higher-quality offspring when brood reduction is likely. We found that gape size may be a signal of body size, and that it is less reliable when within-family conflict is higher. We also found that parents respond less to gape size when it is less likely to provide reliable information. This study offers a potential biological example of a signal of non-cryptic condition, and supports predictions from signalling theory about dishonesty. It also demonstrates how great tits can combine multiple strategies to optimise parental investment, based on ecological conditions, their current brood size, and how reliably offspring are signalling their condition.

Introduction

Organisms face a number of decisions about parental investment, including how many offspring to produce and how much to invest in each offspring (Clutton-Brock 1991; Stearns 1992; Smiseth *et al.* 2012; Klug *et al.* 2013; Royle *et al.* 2016; Caro *et al.* 2016a). Optimal strategies can depend greatly on food availability. If food availability is low, parents should produce fewer offspring and preferentially invest in the highest-quality offspring who are most likely to survive, to avoid wasting investment on offspring who will eventually starve (Lack 1947; 1954; Stearns 1992; Davis *et al.* 1999; Caro *et al.* 2016a). Conversely, when food is likely to be plentiful, parents should produce more offspring and preferentially invest in the lowest-quality offspring, to ensure all offspring survive (Lack 1947; 1954; Stearns 1992; Davis *et al.* 1999; Caro *et al.* 2016a). Birds have evolved several tactics to achieve their optimal investment strategies, including varying clutch size, varying the size or content of eggs, adjusting incubation to vary the degree of competitive asymmetry within the brood, and distributing food based on offspring condition (Lack 1954; Slagsvold *et al.* 1984; Magrath 1990; Williams 1994; Stoleson & Beissinger 1995; Russell *et al.* 2007; Koenig *et al.* 2009; Merklung *et al.* 2016; Caro *et al.* 2016a).

Offspring, in turn, may attempt to influence parental investment by soliciting their parents for food with vocalizations, postures, and structural ornaments (Kilner & Johnstone 1997; Mock & Parker 1997; Wright & Leonard 2002; Maynard Smith & Harper 2003; Caro *et al.* 2016a). These behaviours and traits may signal cryptic condition, which would give parents additional information about which of their offspring needs food the most (Godfray 1991; Kilner & Johnstone 1997; Wright & Leonard 2002; Maynard Smith & Harper 2003; Hinde & Godfray 2011). Theory and

empirical data have shown that when food is plentiful and conflict within families is low, offspring are likely to honestly signal their need and parents are likely to respond to those signals (Godfray 1995b; Godfray & Johnstone 2000; Caro *et al.* 2016a). When food is limiting and conflict within families is high, however, these signals can break down as offspring exaggerate their need and parents shift to distributing food based on other information, such as cues of body size or signals of condition that cannot be assessed by cues, such as cryptic quality (Grafen 1990; Royle *et al.* 2002; Caro *et al.* 2016a, b).

We propose that offspring may also employ another tactic in their efforts to secure more parental resources: a signal of non-cryptic information. This would violate a widespread assumption that signals must transmit cryptic information, so that receivers gain access to information they could not otherwise obtain (Grafen 1990; Godfray 1991; Kilner & Johnstone 1997; Maynard Smith & Harper 2003; Hinde & Godfray 2011). However, a recent model demonstrated that signals of non-cryptic, or public, information can be stable in situations where signals transfer information more efficiently than cues, perhaps by giving parents more time to forage for their whole brood (Chapter 5, Wild *et al.* 2017).

Here, we investigate the possibility that gape size functions as a signal of body size. In cavity-nesting birds with large broods, parents return to a dark nest and are confronted by a pile of offspring (Figure 6.1). Gapes may be the most conspicuous feature of cavity-nesting offspring, and brood parasites frequently take advantage of parents' responsiveness to gapes (e.g., Kilner *et al.* 1999; Tanaka *et al.* 2005; Dugas & Rosenthal 2009; Wiebe & Slagsvold 2009; 2012a, b). Gape colour is affected by offspring

condition and parents respond to gape colour (reviewed in Caro *et al.* 2016a). Less is known about gape size, which may also influence parental provisioning and which has been shown to vary with local conditions (Table 6.1). However, previous studies have not addressed the possibility that gape size is functioning as a signal of public body size, rather than as a form of scramble competition or as an amplifier of other components of the begging display (Hasson 1989; Kilner *et al.* 1999; Gil *et al.* 2008; Mainwaring *et al.* 2012; Du *et al.* 2015; Bogaardt & Johnstone 2016).



Figure 6.1. Nestling *Parus major*, great tits, present their gapes while begging for food. Gape size may be more readily apparent than body size. © Mikko Karjalinen.

Table 6.1. Gape size varies with local conditions.

Species	Gape variation	Citation
<i>Sturnus unicolor</i> (Spotless starlings)	Gape width was larger in worse conditions and in enlarged broods	(Gil <i>et al.</i> 2008)
<i>Parus caeruleus</i> (Blue tits)	Female nestlings have larger than expected gapes	(Mainwaring <i>et al.</i> 2012)
<i>Eremophila alpestris</i> (Horned larks)	Gape size is larger in 1-chick broods than multiple-chick broods	(Du <i>et al.</i> 2015)
<i>Melospiza lincolni</i> (Lincoln's sparrow)	Bill shape changes with lay order and lay date	(Sockman 2012)

We will use long-term data on a wild population of *Parus major* (great tits) to explore whether offspring are using gape size as a signal to influence parental investment, and to describe parental investment strategies both pre- and post-hatching. This paper has three aims. First, we assess whether gape size can function as signal. To be considered a signal, gape size must: (i) contain information that reliably reflects some aspect of offspring state; (ii) elicit a response that benefits both signallers and receivers by influencing food distribution; and (iii) have evolved because of parents' response to gape size, rather than evolving for some other function or simply scaling with body size (Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). In this correlational study, we use offspring weight gain as a proxy for parental responsiveness, and we assess patterns in gape width and length growth and shrinkage over the nestling period, but we are not able to directly assess this third criterion. In order to show that gape size is a signal of non-cryptic information, we must compare its relationship to the most plausible cryptic and non-cryptic aspects of offspring state: body condition and body size.

Our second and third aims address whether parental investment strategies shift over the breeding season, and whether offspring communication changes when parents follow different strategies. In general, we expect parents to follow a whole-brood survival strategy if they breed early in the season, but a brood-reducing strategy if they breed later in the season, when it is less likely they will be able to provide enough food for all their offspring to survive (Lack 1947; 1954; Perrins 1970; Magrath 1990; Stearns 1992; Stoleson & Beissinger 1995; Verhulst *et al.* 1995b). Our second aim is therefore to investigate pre-hatching investment patterns, so that we can capture parental preferences with less interference from offspring. If parents shift from whole-brood survival to a

brood-reducing strategy, the severity of within-family conflict over food distribution would increase (Lack 1947; 1954; Magrath 1990; Stearns 1992; Stoleson & Beissinger 1995). Our third aim is to assess whether the severity of conflict affects the gape size signalling system. Signalling models typically assesses the conditions under which signalling can be at a stable equilibrium, but signalling in nature need not be at equilibrium. Here, we posit that signalling is not at equilibrium, and that we can predict when honesty and responsiveness will decrease by exploring the conditions under which signalling equilibria become harder to achieve, such as low relatedness and low food availability (Godfray 1991; Johnstone & Grafen 1993; Godfray 1995b; Davis *et al.* 1999; Royle *et al.* 2002; Maynard Smith & Harper 2003; Grodzinski & Johnstone 2012; Caro *et al.* 2016a, b).

Methods

Study site and data collection

Data on great tits were collected by Camilla Hinde as part of long-term field studies on wild great tits living in mixed deciduous woodland in Cambridgeshire, UK. Study sites, data collection procedures and brood size manipulations have been described in detail elsewhere (Hinde 2006; Hinde & Kilner 2007; Stoddard *et al.* 2012; Johnstone *et al.* 2013). Brood size varied between 3 and 11 offspring (mean brood size in this population=6.7, Hinde 2006). Nests were visited daily during laying (in 2004), and visited every other day after hatching. Data on pre-hatching parental investment are available for 2004, and data on the response to and reliability of gape size are available for 2009. In 2004, each egg was numbered on the day it was laid to determine lay order. Whole clutches were transferred to an incubator the day before hatching and hatched in

individual compartments so that lay order was known for each chick. The incubator was checked approximately every two hours.

Measuring gape size and its information content

In 2004, we weighed each chick and recorded its gape area (gape length x width) and lay order as close to hatching as possible, and always before feeding the chick. Chicks were fed and returned to the field on the day of hatching, with half the brood swapped with another nest. Chicks were then weighed every 2 days. In 2009, we measured tarsus length, weight, and gape area for every chick in each nest, approximately every two days over the two-week course of the nestling period. On average, nests had 7.5 observation days each. We calculated body condition—whether a chick was relatively heavy or light for its skeletal size—by extracting its residual weight by tarsus size on every measurement day. To determine whether gape size functions as a signal of overall body size and/or body condition, we extracted the coefficients of the slopes of (i) gape size and tarsus length, and (ii) gape size and body condition for every nest and measurement day separately. This measurement allows us to see the strength of the relationship between the display and its putative information content (Maynard Smith & Harper 2003; Carazo & Font 2014; Caro *et al.* 2016b).

Measuring parental response to gape size

To determine whether parents respond to gape size when allocating food, we quantified how much prior gape size predicts future weight gain. We calculated weight gain as the difference in chick weight after two days. If parents respond to gape size, there will be a positive relationship (slope) between prior gape size and subsequent weight gain. We extracted the coefficient of the slope of weight gain and absolute gape size, controlling

for the effects of overall size and residual gape size. Using coefficients as the response variable in later mixed models overcomes the issue of non-independence of chicks within a brood on a given day. We included only nest-date combinations where more than three chicks were present, to ensure the models creating these coefficients converged.

Measuring pre-hatching parental investment strategies

We measured three aspects of parental investment strategies: clutch size, incubation behaviour, and investment in eggs. The lay date and hatch date of every brood were recorded as the number of days since 1 April. If broods hatched over multiple days, the earliest hatch date was used in analyses. Clutch size is the number of eggs laid, including nonviable eggs. We inferred incubation behaviour from its effect on hatching spread, the number of hours between the hatching of the first and final chick. If eggs hatched between observation points, their hatching time was estimated as the midpoint between the previous and current nest visits. Great tits lay one egg per day, and if mothers delay incubation until all eggs are laid, chicks hatch approximately synchronously (Magrath 1992). If mothers instead begin incubation before the completion of the clutch, chicks will hatch asynchronously, which is associated with brood reduction (Magrath 1990; Stoleson & Beissinger 1995). We recorded the lay order of eggs, where one is the first laid egg within the brood. We used egg mass as a proxy for maternal investment in each egg (Clutton-Brock 1991; Williams 1994; Monaghan & Nager 1997; Krist 2010). Eggs were weighed every 2 days. The last measure where eggs were cold (since eggs lose mass when incubated) was divided by the number of eggs present to give average egg mass.

Measuring conflict within families

Great tit broods that hatch later in the breeding season or that contain more nestlings may experience worse ecological conditions and lower per-capita food availability (Perrins 1970; Nager & van Noordwijk 1995; Van Noordwijk *et al.* 1995; Verhulst *et al.* 1995b). We therefore used hatch date and brood size as proxies for the degree of conflict within families. We used brood age as a covariate to determine whether communication changes more rapidly if families experience greater conflict (Shizuka & Lyon 2012).

Statistical analysis

We ran linear mixed models using `lm` or `lme4` in R (R Core Team 2013; Bates *et al.* 2015). We included nest and observation day as random effects if there were multiple measurements on the same nest or day. We centred and standardised predictor variables (Cohen *et al.* 2003). We determined the significance of fixed effects in mixed models through likelihood ratio tests and 95% confidence intervals. We used backwards elimination to select final models: a maximum model with all possible interactions was run, and higher-order interactions were sequentially removed if a likelihood ratio test was not significant. If an interaction was significant, all lower-order terms were treated as significant. We did not remove any main effects from the final model because they were planned *a priori*. We calculated the overall correlation between gape area and tarsus size, with nest and chick ID as random effects, using the `MuMIn` package in R (R Core Team 2013).

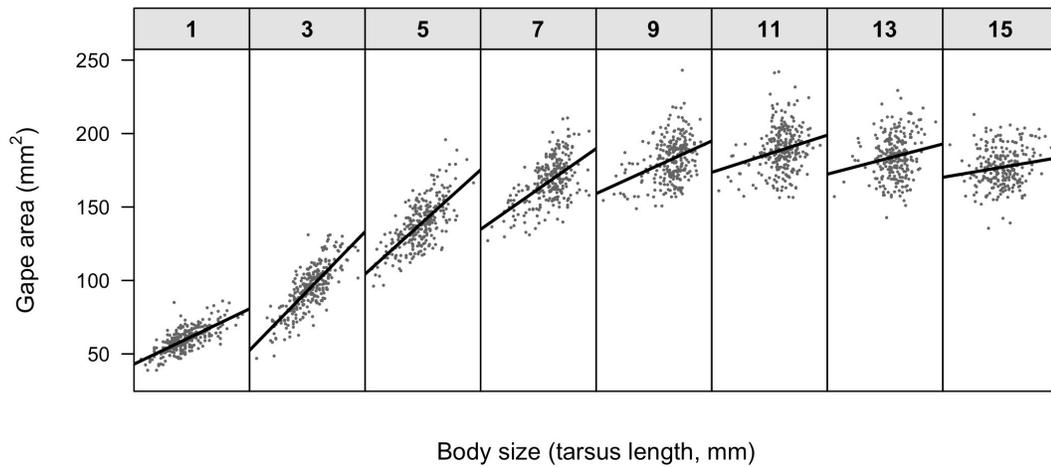
Results

Aim 1: Is gape size a signal?

Does gape size contain information about body size and/or body condition?

Gape area is strongly, but not perfectly, correlated with tarsus size (conditional $r^2=0.89$). Bigger chicks have bigger gapes, but chicks in worse body condition, i.e. that are relatively thin for their skeletal size, have bigger than expected gapes (tarsus size: 95% CI 0.92 to 0.95, $p<0.0001^{***}$; body condition: 95% CI -0.08 to -0.05, $p<0.0001^{***}$; Figure 6.1a,b). Across the whole nestling period, the effect of overall body size on gape area is much stronger than the effect of condition (beta=0.94 compared to beta=-0.06).

a. Relationship between gape area and body size, days after hatching



b. Relationship between gape area and body condition, days after hatching

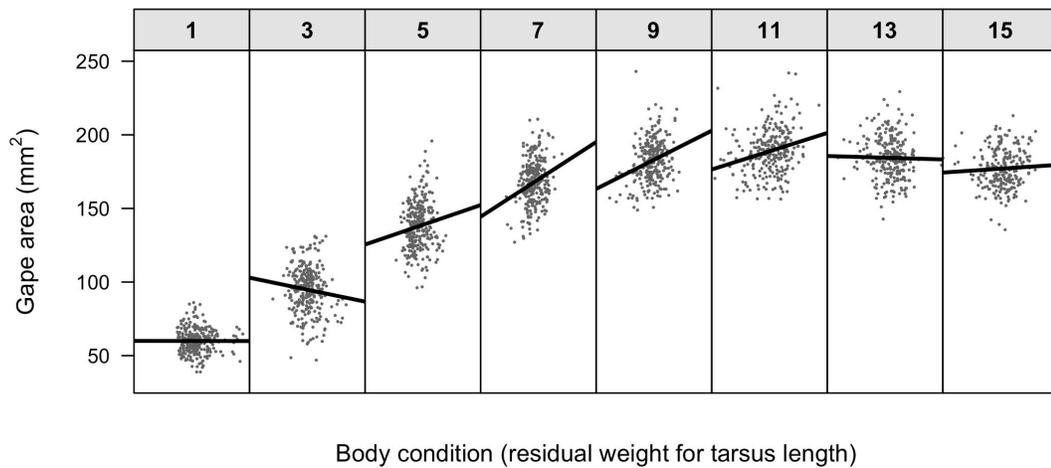


Figure 6.1. Relationships between gape size and body size / condition over the nestling period. Each data point represents one chick on one day (n=306 chicks). Lines are the daily regression of gape area on **(a)** body size, tarsus length, and **(b)** body condition, whether a chick is relatively fat or thin for its skeletal size. Days are the number of days since hatching (hatching=day 0). Most data was collected on odd days, and even days are excluded for graphical simplicity but included in statistical analyses.

Do parents respond to gape size?

Parents respond to gape size: chicks with larger gapes gain more weight (absolute gape size: 95% CI 0.82 to 0.126, $p < 0.0001^{***}$; Table 6.2). Parents also respond to residual gape size: chicks with gapes that are larger than expected for their tarsus size, gain less

weight (residual gape size: 95% CI -0.32 to -0.15, $p < 0.0001$ ***; Table 6.2). Parents do not seem to respond to body size (weight: 95% CI -1.36 to -0.97, $p = 0.5$; Table 6.2). However, absolute gape size and body size are highly collinear, and so any model of parental response that includes both variables will likely only find support for one. It is therefore possible that gape size is an amplifier, rather than a signal, of body size; to distinguish between these possibilities we would need to determine whether the benefit of gape size is reduced perceptual errors in receivers or increased efficiency of information transfer (Hassan 1989; Bogaardt & Johnstone 2016; Wild *et al.* 2017).

Table 6.2. Weight gain by gape size

	Estimate±SE	95% CI	Δ AIC	Pr(Chi)
<i>Intercept</i>	-0.07±0.05	-0.17 to 0.04		
Absolute gape size	1.04±0.11	0.82 to 1.26	-7.3	0.0001***
Residual gape size	-0.24±0.04	-0.32 to -0.15	-28.2	0.0001***
Weight	-1.16±0.10	-1.36 to -0.97	1.6	0.5

N=259 measurement days, 40 nests, 2009 data

Does gape size have a function specific to soliciting food during the nestling period?

Gape area shrinks prior to fledging (Figure 6.2a). Although gape width initially increases with body size, it begins to decrease approximately eight days after hatching ($p < 0.0001$ ***; Figure 6.2b).

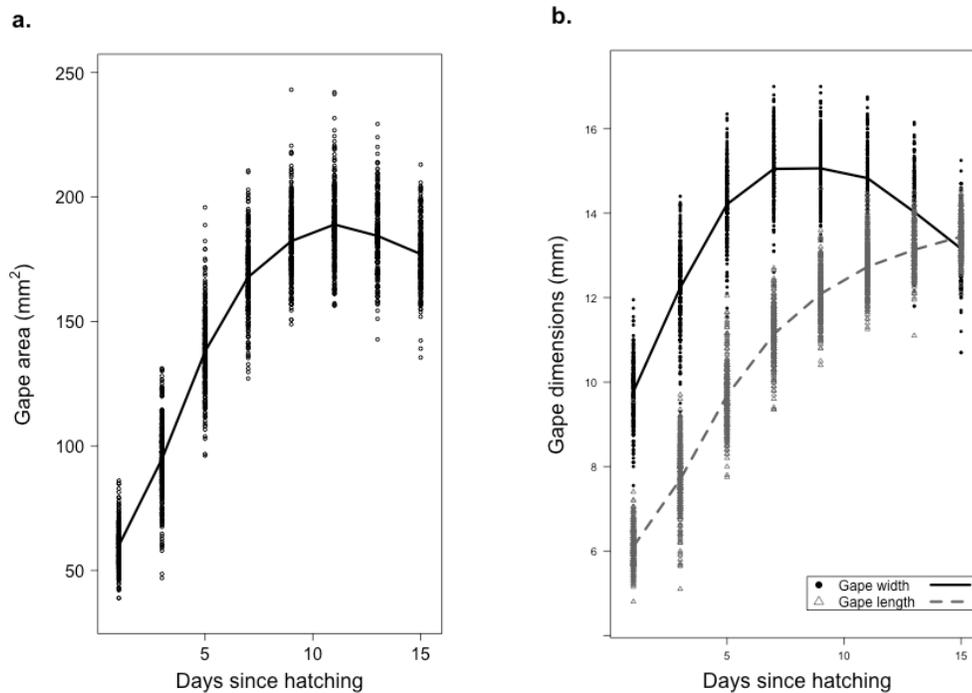


Figure 6.2. Gape area decreases prior to fledging. Each data point represents the gape dimensions of one chick ($n=306$ chicks). Lines pass through the average gape size for all chicks on that day. **(a)** The relationship between chick age and gape area is quadratic, rather than linear, over time. **(b)** This quadratic relationship is due to a decrease specifically in gape width, rather than length.

Aim 2: Do parents invest in offspring differently over the breeding season?

Mothers breeding later in the season, when conditions are likely to be worse, produce smaller clutches that hatch more asynchronously, and they invest less in later-laid offspring. Clutch size decreases by an average of one egg per week after 1 April ($t_{30}=-2.74$, $p=0.01^*$). Later in the breeding season, mothers also begin incubating eggs before the clutch is complete. The time between the hatching of the first and last chick in the brood increases with hatch date, controlling for the effect of clutch size (hatch date: $t_{29}=2.90$, $p=0.007^{**}$; clutch size: $t_{29}=4.06$, $p=0.0003^{***}$). Earlier in the breeding season and in smaller clutches, mothers invested more in later-laid eggs (three-way interaction: 95% CI 0.002 to 0.04, $p=0.03^*$; Table 6.3; Figure 6.3). Egg mass increased with lay

order within a brood, indicating mothers are investing relatively more in later offspring. However, this investment in later eggs within a brood decreased later in the breeding season and in larger clutches. After hatching, chick tarsus growth is slower later in the season ($t_{2,34}=2.73$, $p=0.01^*$) and in larger broods ($t_{2,34}=3.22$, $p=0.003^{**}$).

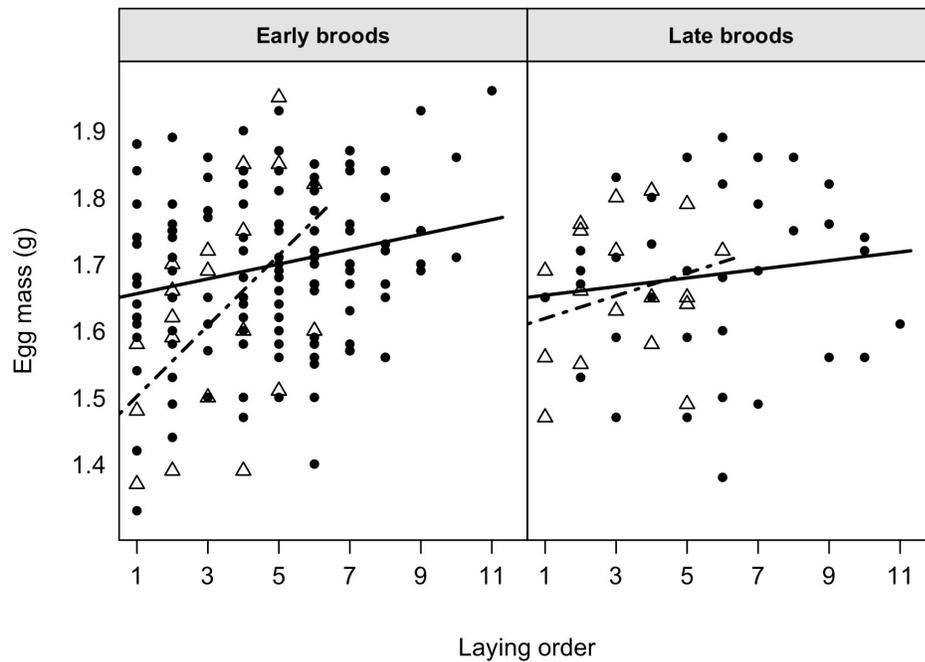


Figure 6.3. Investment in offspring by laying order, clutch size, and hatch date. Each data point represents the mass of each egg in the clutch ($n=207$ eggs, 39 nests), separated by early broods (laid in the first half of the breeding season) and late broods (laid in the second half of the breeding season). Dotted lines and open triangles represent small clutches of 4 to 6 eggs, and solid lines and filled circles represent large clutches of 7 to 11 eggs. This is a graphical simplification, as analyses were run on hatch date and clutch size as continuous variables. Earlier in the breeding season and in smaller clutches, mothers compensate for the disadvantage of being laid later within the clutch by investing more in later-laid eggs.

Table 6.3. Egg mass is correlated with by laying order, clutch size, and hatch date.

	Estimate±SE	95% CI	Δ AIC	Pr(Chi)
<i>Intercept</i>	<i>1.67±0.02</i>	<i>1.63 to 1.71</i>		
Laying order	0.02±0.01	0.01 to 0.03		<i>significant</i>
Clutch size	0.01±0.02	-0.03 to 0.05		<i>significant</i>
Hatch date	0.01±0.02	-0.03 to 0.05		<i>significant</i>
Laying order * clutch size	-0.01±0.01	-0.02 to 0.003		<i>significant</i>
Laying order * hatch date	-0.01±0.01	-0.02 to -0.00		<i>significant</i>
Clutch size * hatch date	0.03±0.03	-0.02 to 0.08		<i>significant</i>
Laying order * clutch size * hatch date	0.02±0.01	0.002 to 0.04	-2.59	0.03*

N=207 eggs, 39 nests, 2004 data

Aim 3: Does conflict affect the gape size signalling system?

Does the reliability of gape size vary based on within-family conflict?

At hatching, bigger chicks have relatively bigger gapes in broods that hatched later in the breeding season (95% CI 0.01 to 0.59, $p=0.04^*$; Table 6.4). Younger siblings, i.e. those laid later within the brood, do not have larger than expected gapes at hatching (95% CI -0.14 to 0.09, $p=0.7$; Table 6.4).

Table 6.4. Gape size at hatching by weight at hatching, laying order and hatch date.

	Estimate±SE	95% CI	Δ AIC	Pr(Chi)
<i>Intercept</i>	<i>0.08±0.18</i>	<i>-0.28 to 0.43</i>		
Hatching weight	0.17±0.10	-0.03 to 0.37		<i>significant</i>
Hatch date	-0.13±0.22	-0.56 to 0.30		<i>significant</i>
Laying order	-0.03±0.06	-0.14 to 0.09	1.92	0.7
Hatching weight * hatch date	0.30±0.15	0.01 to 0.59	-2.01	0.04*

N=159 chicks, 32 nests, 2004 data

After hatching, the reliability of gape size as a signal of body size fluctuates. The strength of the relationship between gape and overall size decreases as chicks age, and decreases more quickly for broods hatched later in the breeding season (95% CI -7.26 to

-1.44, $p=0.004^{**}$; Table 6.5a; Figure 6.4). Brood size does not influence the strength of this relationship (95% CI -0.07-0.34, $p=0.2$; Table 6.5a).

Table 6.5. Full model results for variation in the relationships between gape size and (a) overall size and (b) body condition.

	Estimate±SE	95% CI	Δ AIC	Pr(Chi)
(a) Strength of the relationship between:				
Gape size and overall size				
<i>Intercept</i>	0.45±0.27	-0.06 to 0.97		
Chick age	-0.83±0.17	-1.17 to -0.50		<i>significant</i>
Hatch date	-1.75±2.25	-6.10 to 2.59		<i>significant</i>
Brood size	0.13±0.11	-0.07 to 0.34	0.30	0.2
Age * hatch date	-4.35±1.49	-7.26 to -1.44	-6.60	0.004**
(b) Strength of the relationship between:				
Gape size and body condition				
<i>Intercept</i>	-0.003±0.07	-0.13 to 0.12		
Chick age	0.09±0.05	-0.01 to 0.19		<i>significant</i>
Hatch date	-0.61±0.55	-1.66 to 0.44		<i>significant</i>
Brood size	0.05±0.07	-0.08 to 0.18		<i>significant</i>
Age * hatch date	0.83±0.42	0.00 to 1.64		<i>significant</i>
Age * brood size	-0.12±0.05	-0.23 to -0.02		<i>significant</i>
Brood size * hatchdate	0.36±0.58	-0.74 to 1.46		<i>significant</i>
Age * hatch date * brood size	-0.98±0.45	-1.86 to -0.10	-2.77	0.03*

(a) The response variable was the slope of overall size on gape area on each measurement day in each nest, controlling for overall body condition. (b) The response variable was the slope of body condition (residual weight by tarsus size) on gape area on each measurement day in each nest, controlling for overall body size. N=306 nest-date combinations, 41 nests, 2009 data.

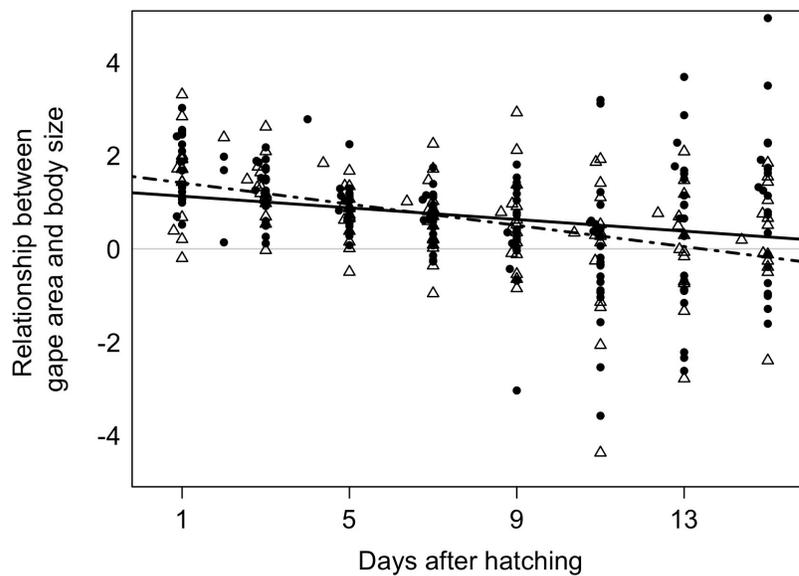


Figure 6.4. Gape size becomes a less reliable signal of body size later in the breeding season and later in the nestling period. The y-axis is a measure of the information content, or reliability, of gape size as a signal of body size. Each data point represents a brood's relationship between gape size and tarsus size on each measurement day, controlling for the effect of chick condition, whether it is fat or thin for its skeletal size (n=306 nest-date combinations, 41 nests). One nest-date combination was excluded because it lay >3 SD from the mean. Solid lines and filled circles represent broods laid in the first half of the breeding season, and dotted lines and open triangles represent broods laid in the second half. The grey line at 0 represents no effect of tarsus size on gape size. As chicks age, the strength of the relationship between gape size and overall size significantly decreases, and it decreases more rapidly in broods that hatched later in breeding season.

Additionally, the reliability of gape size as a signal of body condition is associated with by a three-way interaction between chick age, hatch date and brood size, controlling for the effect of overall size (95% CI -1.86 to -0.10, $p=0.03^*$; Table 6.5b; Figure 6.5). In smaller broods, this relationship begins more negative (i.e. putatively signalling poor condition), while the relationship between gape and condition in larger broods is either positive or approximately null. As chicks age, the strength of the relationship regresses

towards zero for all broods, and this switch more likely to lead to gape area being positively correlated with condition in broods hatched later in the season.

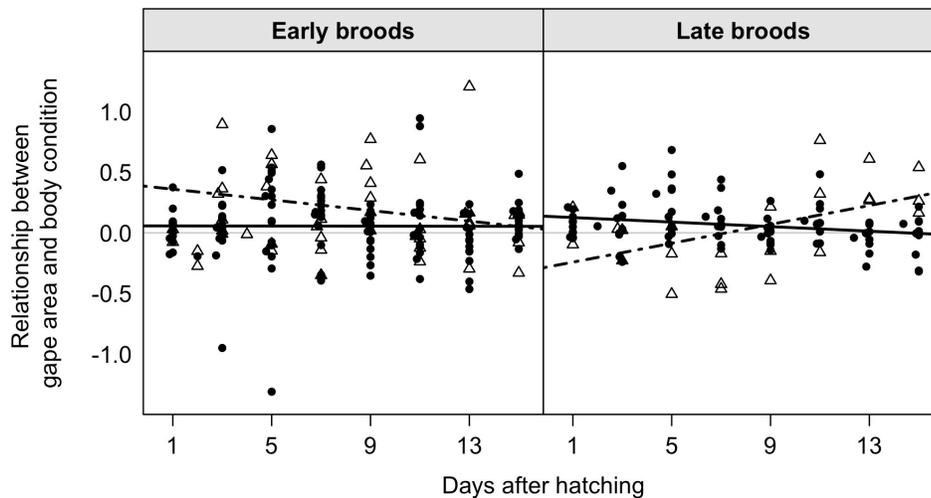


Figure 6.5. Chick age, brood size and hatch date are associated with how reliably gape size signals body condition. The y-axis is a measure of the information content, or reliability, of gape size as a signal of body condition, whether a chick is fat or thin for its skeletal size. Each data point represents a nest's relationship between gape size and body condition on each measurement day, controlling for the effect of overall size (n=306 nest-date combinations, 41 nests). One nest-date combination was excluded because it lay >8 SD from the mean. Dotted lines and open triangles represent small broods of 4 to 6 chicks, and solid lines and filled circles represent large broods of 7 to 11 chicks. The grey line at 0 represents no effect of tarsus size on gape size. Early broods were laid in the first half of the breeding season, and late broods in the second. This is a graphical simplification, as analyses were run on hatch date and clutch size as continuous variables. As chicks in large broods age, the strength of the relationship between gape size and chick condition significantly decreases, and it decreases more rapidly in later broods. In small broods, the strength of the relationship between gape size and body condition significantly decreases as chicks age for early-hatched broods, but increases in late-hatched broods.

Broods that hatch later in the season do not begin shrinking their gape area later as chicks age ($t_{2,34}=0.79$, $p=0.4$). Offspring in smaller broods begin shrinking their gapes earlier ($t_{2,34}=3.27$, $p=0.002^{**}$).

Does the strength of the relationship between gape size and weight gain as within-family conflict increases?

In general, chicks with larger gapes gain more weight, controlling for the effect of overall size ($p < 0.0001^{***}$; Table 6.2). However, the strength of the relationship between gape size and weight gain decreases as offspring age, and this decrease is stronger in smaller broods (95% CI 0.30 to 1.85, $p = 0.007^{**}$; Table 6.6; Figure 6.6). Hatch date does not have an impact on the relationship between gape size and weight gain (95% CI -7.44 to 20.18, $p = 0.6$; Table 6.6).

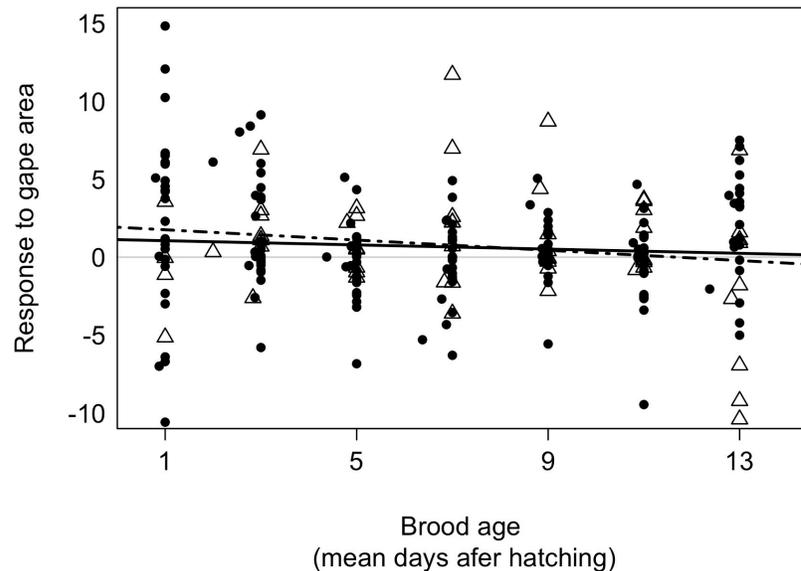


Figure 6.6. The relationship between gape size and weight gain is associated with on brood age and brood size. Each data point represents a nest's relationship between gape size and subsequent weight gain on each measurement day, controlling for the effect of overall size and residual gape size ($n = 259$ nest-date combinations, 40 nests). Dotted lines and open triangles represent small broods of 4 to 6 chicks, and solid lines and filled circles represent large broods of 7 to 11 chicks. This is a graphical simplification, as analyses were run on hatch date and clutch size as continuous variables. The grey line at 0 represents no effect of gape size on weight gain. The effect of gape size on weight gain significantly decreases as broods get older, and this decrease is stronger in smaller broods.

Table 6.6. The relationship between gape size and weight gain

	Estimate±SE	95% CI	Δ AIC	Pr(Chi)
<i>Intercept</i>				
Chick age	-1.15±0.40	-1.92 to -0.37		<i>significant</i>
Brood size	0.02±0.34	-0.65 to 0.69		<i>significant</i>
Hatch date	6.37±7.09	-7.44 to 20.18	1.2	0.4
Age * brood size	1.07±0.40	0.30 to 1.85	-5.3	0.007**

N=259 nest-date combinations, 40 nests. 2009 data

Discussion

We found that parental investment patterns in great tits are not fixed, but instead are highly responsive to the threat of brood reduction and to reliability of a signal of offspring condition. When brood reduction may be more likely, later in the breeding season and in larger clutches, we showed that parents augment the competitive asymmetry of their offspring by beginning incubation earlier and by investing relatively less in eggs laid later within the brood, which creates more of a size hierarchy at hatching. We found that after hatching, offspring with larger gapes gain more weight. However, we found that gape size becomes a less reliable signal as offspring age and when brood reduction is more likely. As might be expected from signalling theory, we found that the relationship between gape size and weight gain is weaker when gape size provides less reliable information. While this study was only correlational, our results are suggestive that parent and offspring behaviours interact in a complementary manner, and that these behaviours are sensitive to the likelihood that parents will be able to provide enough food for the whole brood.

Our study suggests that gape size functions as a signal of non-cryptic information in great tit offspring. Our results supported a signalling function of gape size, and we found stronger support for gape size as a signal of body size than of body condition.

Gape size does not simply scale with body size but instead shrinks several days before fledging. Together with our finding that offspring gain more weight if they have larger gapes, and that the reliability of gape size varies as signalling theory predicts, this supports our hypothesis that gape size functions to help offspring solicit more food from their parents. We found only modest support for gape size as a signal of cryptic information: offspring that are worse body condition have larger than expected gapes, but the effect size was very small. On the other hand, there was very strong relationship between tarsus size and gape size, supporting the hypothesis that gape size signals redundant, non-cryptic information, i.e. body size.

Furthermore, for parents to be responding to gape size as a signal of cryptic condition, they would have to take the time to compare offspring body and gape size, and determine whether each gape was larger or smaller than expected for that size, i.e. parents would need to assess residual gape size. For parents to respond to gape size as a signal of overall size, they only have to find the largest (or smallest) gape. Body size is associated with fledging and recruitment success in passerines, and so parents may be interested in feeding offspring based on size. Given that great tit parents return to a dark cavity nest with a pile of offspring jostling each other at the bottom, the most readily apparent information about offspring size may be the gapes raised above the pile (Figure 6.7). Parents could realise an efficiency bonus from quickly distributing food based on gape size as a signal of body size, giving them more time to forage for the brood (Wild *et al.*, in press). Gape size therefore may function primarily as a signal of body size, although it may also contain additional information about cryptic condition (Wild *et al.*, 2017; Hasson 1989; Bogaardt & Johnstone 2016). Given that most signals likely transmit cryptic information, which researchers can only approximate or guess at, a

signal that transmit obvious, easily measurable information like body size would be invaluable in future experimental studies on what drives dishonesty and defences against dishonesty.

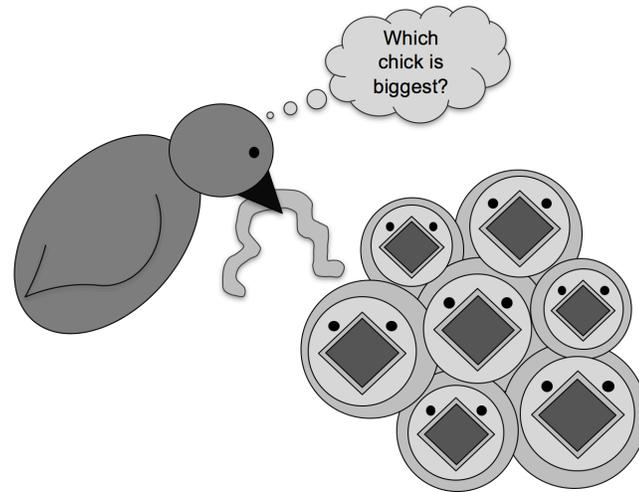


Figure 6.7. Gape area may convey the same information as body size, but more quickly. During the nestling period, gape area may be a signal of non-cryptic condition, allowing parents to distribute food more efficiently.

The reliability of gape size, whether we treat it as a signal of body size or body condition, varies based on local conditions. As offspring age, they could divert investment from skeletal growth to gape size growth, essentially exaggerating their body size and providing a dishonest signal (Gil *et al.* 2008; Mainwaring *et al.* 2012; Carazo & Font 2014; Caro *et al.* 2016b). The decrease in reliability is more extreme when brood reduction is more likely, in broods hatched later in the breeding season. This pattern could be driven either by smaller offspring exaggerating their signals or by larger offspring reducing their investment in the signal. In the first case, needier offspring increase their investment in gape size over time, because they are losing out to their siblings. Bigger siblings are likely getting enough food already, and so they would have no need to likewise divert resources to signal growth over time. In the second case,

bigger siblings begin shrinking their gapes earlier than smaller siblings because they are closer to fledging. Across nests, however, even though overall growth is slower later in the season, gape area begins shrinking at the same time. This suggests that reliability is reduced because needier offspring are exaggerating their gape size, rather than because higher-quality offspring are reducing investment in the signal. Further study of individual growth trajectories would be necessary to reveal exactly how great tit offspring partition resources into signalling and growth, and to determine if these developmental resource allocation decisions vary based local conditions.

Finally, signalling theory predicts that receivers should not respond to signals when they are likely to be dishonest (Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). Regardless of the mechanism, gape size becomes a less reliable signal of body size as offspring age, and parents do respond less to gape size as offspring age. While this study cannot offer conclusive proof of predictions from theory because reliability was not the only condition that differed between early and late broods, it does suggest that parents respond less to signals when those signals are likely unreliable. Mothers may also attempt to influence the reliability of offspring signals (Hinde *et al.* 2010). At hatching there is a stronger relationship between body size and gape size in broods that hatch later in the breeding season, when parents are more likely to be following a brood reduction strategy and thus would prefer to bias food towards the largest offspring. Since this effect was found at hatching, before offspring have had time to adjust their investment in signals, it is likely due to maternal effects in the egg. Further research on how receivers influence the reliability and production of signals, could illuminate this effect more.

DISCUSSION

The preceding chapters each contained their own relevant extensive discussions. This chapter therefore briefly discusses the key results, the broader implications about the connections between theoretical and empirical biology, and future research questions raised by this work.

The aim of this thesis was to identify how signalling can evolve and be maintained even in the face of conflict amongst communicators. Communication provides the foundation for social behaviours across the tree of life, yet it is vulnerable when the interests of the speaker and the listener are not perfectly aligned—as is frequently the case in non-clonal organisms. Understanding the conditions that reduce conflict sufficiently for selection to favour honest signallers and attentive receivers is therefore required for our understanding of social evolution. Through the lens of parent-offspring communication in birds, I present two main findings in this thesis: (i) the more conflict within-families, the more vulnerable offspring signals of condition are to becoming dishonest and/or being ignored; and (ii) even when information is already public knowledge, signals of condition can be stable if their efficiency benefits are high enough.

Summary of main results

Conflict over food distribution governs parent-offspring communication

Begging is a model system for understanding the fundamental selection pressures that drive the evolution of communication. Although it is most commonly thought of as a signal of offspring need, the hundreds of studies devoted to begging frequently contradicted this framework. Indeed, many species show opposite patterns in whether

offspring beg more when they are in better or worse condition and whether parents pay attention to or ignore begging when distributing food. To disentangle the conflicting results found in models and empirical studies alike, I investigated conditions that are predicted to lead to different signalling systems being stable in different species or lead to flexibility in how individuals communicate.

I posited that the conditions that are most likely to influence whether real animals behave how theory predicts they should are those directly related to the assumptions forming the basis for that theory. An underlying assumption in signal-of-need models is that parents are always attempting to rear their entire brood, and are therefore selected to preferentially feed the neediest offspring (Godfray 1991; Kilner & Johnstone 1997; Godfray & Johnstone 2000; Hinde & Godfray 2011; Mock *et al.* 2011). However, this assumption is regularly violated in nature: many bird species engage in strategic brood reduction, the starvation of at least one nestling, as a reaction to unpredictable food availability or unusually poor environmental conditions (Lack 1947; 1954; Drummond & Garcia Chavelas 1989; Mock & Parker 1997; Cotton *et al.* 1999; Mock *et al.* 2011). The threat of brood reduction increases conflict over food distribution, since each nestling may have an incentive to exaggerate signals of need to secure more food for itself and avoid being the one to starve. Therefore, in cases with brood reduction, a key assumption of signal-of-need models is violated, and I predicted that signals of need will not be stable. In cases without brood reduction, I predicted that signals of need will be stable.

To test that prediction, I conducted a comparative analysis across 143 species (Chapter 2). I showed that offspring are more likely to signal need through begging, and parents

are more responsive to begging, in predictable and/or good environments, when conflict over food distribution is low because food is plentiful enough for all (Figures 2.4 and 2.5). Conversely, in unpredictable and/or poor environments, when conflict over scarce food is intense, offspring are more likely to signal their quality through structural ornaments, and parents pay more attention to structural signals or size cues (Figures 2.4 and 2.5).

This work raised the question of how malleable communication strategies are within species (Chapter 3). In a comparative analysis across 57 species, I found that the patterns within species mirror the patterns across species: in general, parents respond less to begging signals of need and more to size cues when environmental conditions are worse (Figure 3.6). To examine this within-species trend in more detail, I used long-term field data from a population of wild great tits, a species that experiences variable environmental conditions. I investigated whether parents facultatively adjust how they respond to offspring signals based on the current risk of brood reduction. Again, I found similar patterns within great tits as I found across species: parents' responsiveness to begging varies based on local ecological conditions and brood size (Figures 3.2, 3.3, 3.4 and 3.5).

I next examined whether offspring signalling strategies vary based on another potential source of conflict within-families, brood size and relatedness (Chapter 4). The alignment of parent and offspring interests can be disrupted by increased sibling competition, but need not be (Mock & Parker 1997). This competition can arise from having a higher number of competitors, or from receiving fewer inclusive fitness benefits when those competitors are fed because they are only half ($r=0.25$) rather than

full siblings ($r=0.50$) (Parker *et al.* 1989; Johnstone & Grafen 1993; Godfray 1995b; Rodríguez-Gironés *et al.* 1998; Godfray & Johnstone 2000; Royle *et al.* 2002; Parker *et al.* 2002a; Johnstone 2004; Kilner & Hinde 2012; Grodzinski & Johnstone 2012). This increased competition could favour exaggerated or dishonest signals of need. In a comparative study across 60 species, I showed that offspring were relatively less honest about need when they had more nestmates, when their parents could produce more broods over their whole lifetimes, and when future broods were likely to contain half, rather than full, siblings (Figures 4.1, 4.2 and 4.3).

Information does not need to be cryptic for signals to be stable

Signals transmit information. One of the main findings of my comparative analyses (Chapters 2 and 4) was that different signals transmit different information about offspring condition, specifically that behavioural begging appears to function as a signal of need but structural signals appear to function as a signal of quality (but see Kilner 1999 and Kilner & Davies 1998). In both cases, theory assumes that the information about offspring condition must be cryptic. Producing signals entails at least minimal costs, and so signalling should be favoured only when this information could not be obtained otherwise, and is ‘cryptic’ or ‘private’ (e.g., Grafen 1990; Godfray 1991; Kilner & Johnstone 1997; Bergstrom *et al.* 2002; Johnstone 2004). In essence, the common view is that the function of signals is to increase the amount of information available to organisms.

However, I argue that this view does not sufficiently consider that signals may have benefits other than giving receivers new information. I showed that selection can theoretically favour signalling about information that is not private—if signals increase

the efficiency, or speed, with which ‘public’ or ‘redundant’ information can be transmitted (Chapter 5). In our simple game, parents must choose which of two offspring to invest in under resource-limited conditions. These offspring differ in quality, such that parents should prefer feeding the higher-quality offspring. Condition could be assessed through a public cue, or through a signal that offspring could produce. Parents receive the same information from both, but they gain an efficiency benefit from using the signal rather than cue. We found that this form of signalling can be at equilibrium under certain conditions, such as a high efficiency benefit, low signal cost, and high relatedness between offspring (Figures 5.3 and 5.4).

In Chapter 6, I presented a potential example of such a signal in nature: gape size in great tit nestlings. In great tits, parents tend to prefer feeding larger offspring, and so a signal that increases the efficiency with which parents can assess body size in dark nest cavities could be favoured, even if parents could instead take the time to investigate actual body size. Parents returning to the nest are faced with a jumble of offspring presenting wide-open gapes. These gapes may be their brood’s most conspicuous body parts, and so could potentially function as a signal for body size. However, in order to be classified as a signal, a trait should: (i) reliably convey some information; (ii) alter the behaviour of the receiver in a way that benefits the receiver and the signaller; and (iii) have evolved in the signaller *because* the receiver’s response benefits the signaller, rather than for some other function (Maynard Smith & Harper 2003). I showed that: (i) gape size contains information about body size (Figure 6.1); (ii) parents may be responding to gape size by preferentially feeding offspring with larger gapes, since chicks with larger gapes gain more weight (Figure 6.6); and (iii) gape width shrinks prior to fledging, indicating that gape size has a function specific to the nestling period

and is not simply scaling with body size (Figure 6.1). Furthermore, I found that the reliability of gape size fluctuates with the degree of within-family conflict, as expected from signalling theory and my findings in Chapters 2-4 (Figure 6.4). Taken together, these findings indicate that gape size could function as a signal of body size, which is a public cue of quality. I also found that the reliability of gape size as a signal of body size decreased as offspring aged, and decreased more rapidly for broods that hatch under worse environmental conditions (Figure 6.4). I found that parents relied less on gape size as offspring aged, when gape becomes less honest (Figure 6.6). Partially informative signals like this one, whose honesty fluctuates over time in response to the degree of conflict amongst communication, may be common in nature.

In summary, Chapters 5 and 6 suggest that the biological function of signals may be broader than is currently considered. Some signals may have evolved not because they increase the amount of information available to receivers, but because they increase the speed at which receivers can learn that information. Furthermore, given that offspring are predicted to stop investing in signals if parents stop responding (Chapters 2, 3 and 6), and given that parents should stop responding to begging if it is less honest (Chapters 4 and 6), my thesis highlights how vulnerable communication is to conflict, even within family groups.

Bridging the gap between theory and empirical work

‘All models are wrong, but some are useful.’

George Box, 1978

‘All models are right, most are useless.’

Thaddeus Tarpey, 2009

The appeal of theory is the simplification of the real world. Theory gives us simple, definitive answers to complex questions, and within the mathematical world of a model, all its conclusions are true: ‘all models are right’. We also do not expect these simple answers to fit the real world perfectly, since no biological system will ever perfectly fit the assumptions of a model: ‘all models are wrong’. This combination of models being both right and wrong can lead empiricists to getting stuck in a framework rut—especially when the dominant models are also intuitively appealing because they feel right, and when contradictory data can be explained away by the slight wrongness of models. Continual empirical support for one framework can then lead to theorists getting stuck in the same rut, where they refine the same basic models over and over, without exploring mathematical worlds with fundamentally different starting assumptions.

For example, biologists studying parent-offspring communication have largely settled on the explanation that offspring beg to show their parents how needy they are, and that parents respond to that begging by giving offspring more food (Kilner & Johnstone 1997; Wright & Leonard 2002; Hinde & Godfray 2011; Johnstone & Kilner 2011; Mock *et al.* 2011). This explanation comes with strong theoretical backing: model after model found that signals of need could be stable, particularly when signals are costly enough to outweigh the benefits of misrepresenting offspring need (e.g. Godfray 1991; 1995b). Alternative explanations have been put forward, the most influential of which was a non-signalling explanation for begging as scramble competition between siblings (Grafen 1990; Rodríguez-Gironés *et al.* 1996; 1998; Rodríguez-Gironés 1999; Royle *et al.* 2002; Wright & Leonard 2002). Yet such alternatives received relatively little attention compared to studies supporting the dominant paradigm, despite a significant

amount of data that seemed to directly contradict the predictions of the signal-of-need framework (Cotton *et al.* 1999; Wright & Leonard 2002; Mock *et al.* 2011; Caro *et al.* 2016a). Indeed, the signal-of-need framework seems to have become so entrenched the burden of proof seems to have shifted, so that empiricists needed to prove begging is **not** an honest signal of need, rather than that it is.

My comparative analyses exposed the pitfalls in such a strong acceptance and application of a theoretical framework (Chapters 2, 4; Caro *et al.* 2016a, b). I showed that although offspring signalling looks almost identical across birds, it functions in opposite ways based on whether parents can expect their whole brood to survive or not. I also showed that different signal modalities, such as vocalisation and coloration, contain different information, and that parents respond to these different signals in a context-dependent way. While others have previously noted that signals of needs are only expected when conflict within families is low and when there are fewer sources of information about offspring condition (e.g., Royle *et al.* 2002), this point was not fully incorporated into practice. I believe this is because there has not been enough constructive interchange between theory and empirical work, particularly around how applicable models are to nature.

The trick for empiricists is sifting between ‘useful’ and the ‘useless’ models on a case-by-case basis. This can only be done by a critical examination of the foundations of a model and determining how likely its assumptions are to be invalid (‘useless’ models), as opposed to normal variation within acceptable parameter space (‘useful’ models). In the case of offspring signalling, if a key assumption of signal-of-need models is that offspring condition only varies in a narrow range, above the viability threshold, but

offspring regularly starve in your species, those models are likely to be useless for your species. If, conversely, offspring regularly survive in your species, albeit with some variation, those models are likely to be useful for your species. Consequently, researchers interpreting their empirical results based on their fit to the predictions of a model may also want to explicitly address how well the model assumptions fit their study system.

Theorists also need to be explicit about the assumptions that go into building their models, and those models should reflect the latest advances in empirical research. For example, including a table that explicitly lists all model assumptions in one place could make it easier for empiricists to know whether the model is likely to be useful for understanding their study system. In order to avoid falling into a framework rut, theorists should also regularly consider how realistic their model assumptions are. For models that aim to explore the realms of possibility, realistic assumptions are unnecessary, but such models should be explicit about their purpose and potential applications (Godfray 1995a). But for models that aim to explain real-world phenomena, assumptions need to be realistic enough to generate useful predictions, which implies that theorists need to incorporate more input from empiricists during the model-building stage (Godfray 1995a). Empirical data can also identify promising avenues for extending theory. If theorists find that their assumptions are regularly violated in nature, then they can explore how adjusting such assumptions impacts their model's solutions.

Comparative studies can play a large role in facilitating the conversation between empiricists and theorists. The power of comparative analyses is that they can

incorporate data from species experiencing different selection pressures. This variation could mean that one model is useful for some species, while another model applies in others, because of variation along one biological parameter. By assessing how well species fit the predictions of different models, this could reveal whether that biological parameter actually impacts evolution—if species behave identically regardless of violations of an assumption about that parameter, then that parameter likely does not exert selective pressure. If they do behave differently based on that violation of an assumption, in the ways predicted by the different models, then that parameter likely does exert selection pressure. Thus comparative studies can generate testable hypotheses about the fundamental selection pressures that have driven the evolution of traits. By utilizing the greater degree of variation in ecology and life history traits present across species compared to within species, these hidden pressures can be uncovered. Empiricists can then experimentally test the effects of these factors, and theorists can build models that more explicitly account for their effects.

Furthermore, one of the most important patterns that emerged from my thesis (Chapters 2, 3, 4, and 6) is that communication falls along a continuum, rather than at the extremes (Caro *et al.* 2016a, b). Parent-offspring signalling theory has typically dealt with all-or-nothing solutions: honest signals are either stable or not, and parents are either responsive or not. The goal of many signalling models has been to identify the conditions under which honest signalling can be an evolutionary stable strategy at equilibrium (Harper & Maynard-Smith 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). And while parent-offspring signalling might be at equilibrium in nature, it is also possible that parents and offspring are engaged in an evolutionary arms race (Haig 1993; Godfray 1995a; Haig 1996; Kilner & Hinde 2008). There are two

important consequence if signalling is not at equilibrium: first, varying degrees of honesty and responsiveness are possible; and second, we cannot use equilibrium models directly to make predictions about real-world situations. I found that intermediate levels of honesty and responsiveness are the norm in nature. I therefore assumed that parent-offspring signalling is not at equilibrium. In order to use existing equilibrium models to make predictions about non-equilibrium biology, I assumed that the same conditions that make signalling equilibria more mathematically restrictive would also tend to shift parents and offspring further from honest and responsive signalling behaviours. For example, if lower relatedness between siblings means that the threshold cost for signals needs to be higher in order to achieve an equilibrium resolution (for example, Chapter 5 and Wild *et al.* 2017), I extrapolated that lower relatedness between siblings should decrease honesty. However, this kind of extrapolation may not lead to valid predictions. New theory that incorporates more biological complexity or explore non-equilibrium possibilities would be useful in explaining the gradual variation observed across species, within species, and even within individuals (Johnstone & Grafen 1993; West *et al.* 2002b; Caro *et al.* 2016b). Additionally, this variation within individuals (Chapters 3 and 6) re-emphasises the need for dynamic models, which incorporate the repeated and cumulative nature of parent-offspring interactions (Godfray 1995a; Godfray & Johnstone 2000; Royle *et al.* 2002; Searcy & Nowicki 2005; Mock *et al.* 2011; Wild 2011). Although such models are more technically difficult and intensive, they are possible (see Wild 2011 for an example), and necessary for the next generation of useful models of parent-offspring signalling.

In conclusion, all models are both right and wrong but only narrowly useful, and we can better explain the complexity of the real world if theorists and empiricists work together more closely.

Weaknesses of comparative and correlational data

I used correlational comparative data (Chapters 2, 4 and 5) and empirical data (Chapters 4 and 6) in this thesis. Comparative data is valuable because it can be used to identify broad patterns across species and to synthesise findings from many studies. Comparative data is vulnerable, however, to biases in which studies are published (the ‘file drawer problem’), which species or populations are studied, which phylogeny is used, and which factors are considered in statistical analyses (Borenstein *et al.* 2011; Nakagawa & Santos 2012; Koricheva *et al.* 2013; Hadfield *et al.* 2014). Similarly, correlational data can demonstrate patterns and provide suggestive evidence for a hypothesis, but the results of analyses, especially post-hoc analyses, may be confounded by hidden factors. Consequently, findings from comparative and correlational data cannot be considered as conclusive as data from a controlled experiment, and there are several important caveats which need to be made.

Publication bias—when non-significant effects are not reported less frequently—can be identified by asymmetric effect size funnel plots (Borenstein *et al.* 2011). While I did not find any evidence of publication bias in my comparative analyses (Chapters 2 and 4), I cannot exclude the possibility that it existed and influenced my results for three reasons. First, tests for publication bias assume that the true effect size is the same across all species and studies, and I have no a priori reason to believe that all species are behaving identically. Second, these tests assume that studies with larger sample sizes

are more likely to approach the true effect size, but sample size is not independent of species or study methodology (for instance, randomized controlled experiments may be higher quality but tend to have smaller sample sizes than correlational studies). Finally, the species researchers have chosen to study are non-random, and this cannot be corrected for by any statistical test. While my comparative study included published data on species from 51 families in 19 orders, this still represents a tiny fraction of extant species.

A related issue is that the quality of meta-analyses depends on the quality of the studies published, which is colloquially known as the ‘garbage in, garbage out’ problem. There are several possible solutions to this problem, including weighting or excluding studies by some qualitative metric of quality. In an attempt to limit the impact of my own biases on analyses, I decided not to weight or exclude any studies based on my qualitative assessment of quality, and assumed that poor quality studies would simply add noise to the analyses. If the poor quality studies were not randomly distributed by species, life history traits or environmental quality, this could have biased my findings. In the future, an individual blind to the hypotheses of the meta-analyst could rate the quality of included studies, and this rating could be used to weight or exclude studies. The only long-term solution to publication issues would be to collect data from more species, engage in rigorous peer review of articles, and ensure that all valid findings, even non-significant ones, are reported in the literature.

A more fundamental question is whether comparative and correlational data on birds can ever be considered hypothesis-testing, rather than hypothesis-generating. In many cases, especially with comparative analyses that attempt to infer the evolutionary past,

controlled experiments are impossible. Furthermore, fitness is typically estimated using measures such as growth and survival, which may not be adequate proxies. In a world of infinite resources and time, scientists could use existing patterns across species to predict how evolution may proceed under a long-term experimental selection study across hundreds of birds species, and fitness could be measured directly. Insect models of parent-offspring interactions offer a promising and realistic alternative, given their shorter generation time and ability to thrive under laboratory controlled settings. As a general rule, and assuming there is enough plasticity in traits within or across individuals, findings from comparative or correlational data should be validated by controlled experiments within a population.

Future directions

Parental responsiveness to whole-brood begging

This thesis investigated how parents use begging when determining which of their offspring to feed, but parents also use begging when determining how much they should be feeding the whole brood. Parents face a trade-off between investing in parental care for their current brood and saving energy for future reproduction, and the balance of this trade-off may vary across species (Stearns 1992). However, there have been no studies on the diversity of how parents of different species increase provisioning effort based on whole-brood begging. My preliminary, exploratory comparative analyses indicate that responsiveness to this other function of begging may have evolved differently in different species. In general, parents seem to increase their total provisioning effort when their offspring beg more, but there is considerable variation across species in just how much they increase provisioning effort (Figure 7.1).

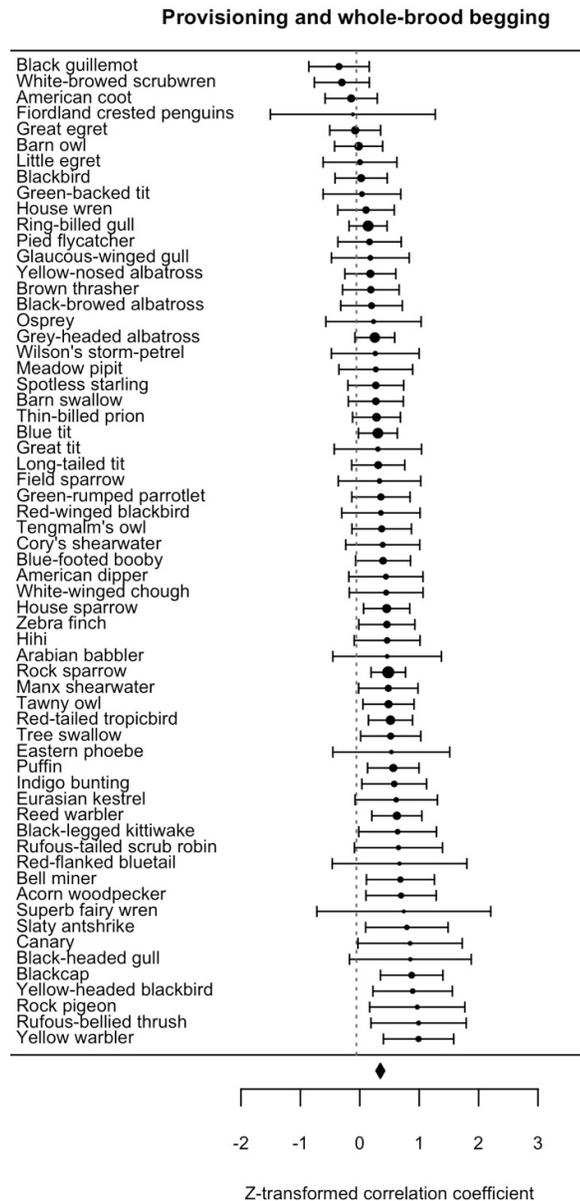


Figure 7.1. Species vary in how much they respond to whole-brood begging. The x-axis is the strength of the relationship between total provisioning (e.g. number of nest visits per hour) and begging intensity (e.g. begging playbacks). Circles represent a species' weighted mean relationship between total provisioning and begging, and circles are scaled by sample size. Lines indicate the 95% CI for each estimate. The dotted line at 0 indicates no effect of begging on total provisioning, negative values indicate parents reduce total provisioning the more their offspring beg, and positive values indicate parents increase total provisioning the more their offspring beg, with greater values indicating a stronger response. The diamond at the bottom represents the mean response to whole-brood begging across species. This is preliminary data. N = 62 species, 100 studies, 335 effect sizes.

I would like to explain this variation in a future phylogenetic comparative analysis. Specifically, I would like to investigate whether parental responsiveness varies based on the total number of broods parents can produce over their whole lifetime, as parents may value the current brood more if they can, for example, produce only two broods as opposed to ten broods over their lifetime (Grodzinski & Johnstone 2012; Caro *et al.* 2016b). Parents may also respond differently to whole brood begging based on whether they are following a whole-brood survival or a brood-reducing strategy (Lack 1954; Caro *et al.* 2016a), as the demands of the whole brood matters less if parents do not expect marginal offspring to survive.

Signalling systems will collapse if they become too dishonest, because parents do not benefit from responding to false information (Maynard Smith & Harper 2003; Searcy & Nowicki 2005; Bradbury & Vehrencamp 2011). I will therefore also test whether offspring honesty, as measured in my previous comparative study (Caro *et al.* 2016b), explains any variation in how much parents respond to whole-brood begging.

In some species, males and females may also respond to whole-brood begging differently (Figures 7.2 and 7.3). The sexes may differ in how highly they value their current brood, based on differences in the potential for future reproduction and their average relatedness to the brood (Queller 1997; Kokko & Jennions 2003; 2008; Lessells & McNamara 2012; Santos & Nakagawa 2012; Griffin *et al.* 2013; Liker *et al.* 2015). For example, in a species with a male-biased adult sex ratio, males may have a difficult time finding a new mate and may therefore prefer to invest in their current brood rather than save energy for a hypothetical second brood (Kokko & Jennions 2008). Males may also adjust their care based on how promiscuous females are, since they benefit less

from parental care if they are provisioning another male's offspring, although this effect will be mediated by how costly care is (Hamilton 1964; Queller 1997; Lessells & McNamara 2012; Griffin *et al.* 2013). Promiscuous females may also compensate for lower investment from their male partners (Hinde & Kilner 2007). Males and females may also vary in how costly it is to increase their provisioning effort (Santos & Nakagawa 2012). I will therefore test for any effects of adult sex ratio, mating system, and sex differences in the cost of care.

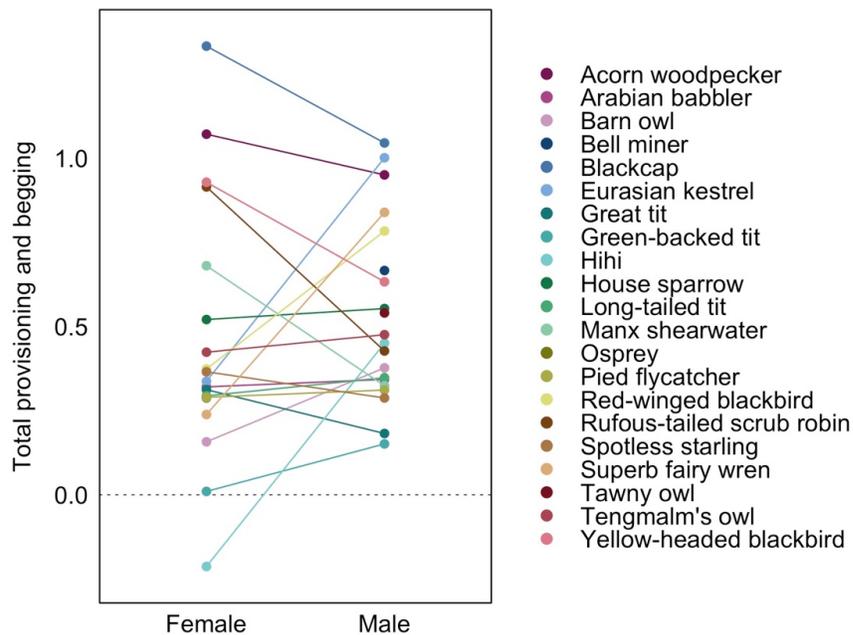


Figure 7.2. Males and females respond differently to whole-brood begging. The y-axis is the strength of the relationship between total provisioning (e.g. number of nest visits per hour) and begging intensity: Z-transformed correlation coefficient. Circles represent species' mean responsiveness to whole-brood begging for each sex. Lines connect females and males of the same species; Figure 7.3 depicts the magnitude of any sex difference. Three species have data from only one sex. The dotted line at 0 indicates no effect of begging on total provisioning, and more positive values indicate a stronger relationship between begging and an increase in total provisioning. This is preliminary data. N = 21 species, 31 studies, 95 effect sizes.

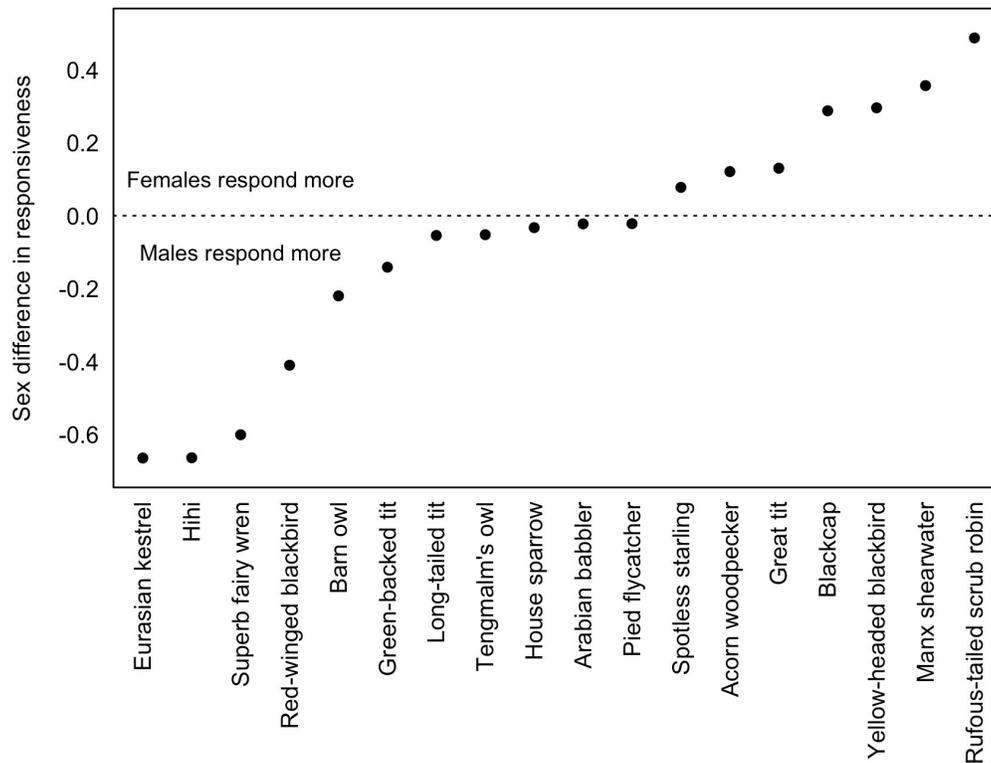


Figure 7.3. Species differ in whether males or females respond more to whole-brood begging. Circles represent the difference between mean female and mean male responsiveness to begging in each species; Figure 7.2 depicts the absolute values for each sex. The dotted line at 0 indicates no sex difference, and positive values indicate females respond more, and negative values indicate males respond more. This is preliminary data. N = 18 species with data from both sexes.

Experimental manipulations of environmental quality

My previous work (Chapters 2 and 3) found that environmental quality is associated with whether species have evolved to respond more to begging, or more to chick size or signals of high quality. If individuals of a given species experience high variation in these factors within their lifetimes, they could benefit from being flexible in how they use offspring signals and cues. In collaboration with Camilla Hinde at Wageningen University, I plan to experimentally manipulate environmental quality in great tits, a species exposed to highly variable environmental conditions, to test whether the relationships I found were causal. The more food available, the more parents should

distribute food based on begging signals of need (Caro *et al.* 2016a). To test this, I will do experimental fieldwork using an established population of wild great tits in The Netherlands. I will manipulate brood size and give some great tit parents access to supplemental food. I will then quantify how much begging and offspring size rank affect food allocation in broods experiencing different experimental treatments.

Mechanisms involved in parent-offspring signalling

My thesis was concerned with the function of signals and determining when different strategies are likely to be adaptive, rather than the mechanisms regulating communication. Understanding the mechanisms involved in determining both parent and offspring strategies could lead to a deeper understanding of the evolution of signalling (Smiseth *et al.* 2008; Kilner & Hinde 2012; Stucki & Kölliker 2013). For instance, recent work on population genetics and maternal effects has shown positive covariance between begging and responsiveness in some species (e.g. canaries, Hinde *et al.* 2010) but not others (e.g. house sparrows, Dor & Lotem 2010). If species differ in how parent and offspring signalling traits co-evolve, this could illuminate deeper aspects of how parent-offspring conflict influences selection on parent-offspring communication. Some factors that may prove important are whether parents or offspring control this co-evolution; whether it is arms race; whether only mothers, and not fathers, influence offspring begging rules; how environmental variability influences selection for maternal effects on signalling; and what influence other life history traits have on the potential for signalling co-evolution (Smiseth *et al.* 2008; Hinde *et al.* 2010; Kilner & Hinde 2012; Stucki & Kölliker 2013). It is also possible that this covariance could have made the comparative analyses in Chapters 2 and 4 more noisy or confounded species-level estimates of parental responsiveness and offspring honesty, and so knowing the

degree of covariance within each species would let us investigate and potentially control for these effects. More species-level data on parent-offspring covariance in signalling are needed before comparative work can be done to identify broad evolutionary patterns and to add another layer of complexity to the existing comparative work.

How parents provision their young may also have a large impact on the form of parent-offspring communication, and indeed, on whether begging is a signal at all. Whether parents or offspring control resource distribution ultimately determines whether begging can be considered communication or is better thought of as scramble competition (Royle *et al.* 2002; Parker *et al.* 2002a; Johnstone 2004; Mock *et al.* 2011; Kilner & Hinde 2012). Animals vary in the balance of power between parents and offspring across class, species, and even time as offspring develop. However, we do not yet have a generalizable way of classifying or quantifying where exactly organisms fall on the spectrum of parent vs. offspring control of food distribution, and so we cannot yet test predictions about how begging should evolve based on this balance. More data on the mechanisms of resource allocation across species are necessary to provide the framework for analyses of these predictions. Data from non-avian species with more drastically different modes of resource distribution than we can observe within birds (such as lactating mammals) would be particularly useful for such analyses.

Concluding remarks

Offspring begging is used as a model for studying communication in general. My thesis shows that signalling strategies vary based on the degree of conflict between communicators, a result that is likely to apply in other signalling contexts. For instance, the stability of quorum-sensing signalling systems are likely to be sensitive to

relatedness within bacterial communities, and to how resource-stressed those communities are. My thesis also showed that it is possible for offspring signals containing non-cryptic information to be stable. The efficiency with which organisms can access information through different channels may therefore play a vital role in the evolution of signalling. Male sexual signals, for example, may have evolved in part to facilitate faster mate choice than if females had to spend more time investigating male quality, rather than having evolved to provide females with additional information about quality.

To conclude, this thesis emphasises the importance of considering empirical data when constructing models, considering model assumptions when matching theory to empirical data, and considering empirical data from multiple species when drawing broader conclusions about natural phenomena. It also demonstrates the key role of conflict in the evolution of social behaviour within families and communication, and it provides a framework for a novel function of signals.

BIBLIOGRAPHY

1. Akaike, H. (2011). Akaike's Information Criterion. In: *International Encyclopedia of Statistical Science*. Springer Berlin Heidelberg, pp. 25–25.
2. Akçay, E. (2012). Incentives in the family II: behavioral dynamics and the evolution of non-costly signaling. *Journal of Theoretical Biology*, 294, 9–18.
3. Barba, E., Atienzar, F., Marin, M., Monros, J.S. & Gil-Delgado, J.A. (2009). Patterns of nestling provisioning by a single-prey loader bird, Great Tit *Parus major*. *Bird Study*, 56, 187–197.
4. Bates, D., Maechler, M., Bolker, B. & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software*, 67, 1–48.
5. Bengtsson, H. & Rydén, O. (1983). Parental Feeding Rate in Relation to Begging Behavior in Asynchronously Hatched Broods of the Great Tit *Parus major*: An Experimental Study. *Behav Ecol Sociobiol*, 12, 243–251.
6. Bergstrom, C.T. & Lachmann, M. (1997). Signalling among Relatives. I. Is Costly Signalling Too Costly? *Philosophical Transactions: Biological Sciences*, 352, 609–617.
7. Bergstrom, C.T., Szamado, S. & Lachmann, M. (2002). Separating equilibria in continuous signalling games. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357, 1595–1606.
8. Biernaskie, J.M., Grafen, A. & Perry, J.C. (2014). The evolution of index signals to avoid the cost of dishonesty. *Proceedings of the Royal Society B: Biological Sciences*, 281, 20140876–20140876.
9. Bize, P., Piau, R., Moureau, B. & Heeb, P. (2006). A UV signal of offspring condition mediates context-dependent parental favouritism. *Proceedings of the Royal Society B: Biological Sciences*, 273, 2063–2068.
10. Bogaardt, L. & Johnstone, R.A. (2016). Amplifiers and the origin of animal signals. *Proceedings of the Royal Society B: Biological Sciences*, 283, 20160324–6.
11. Boncoraglio, G. & Saino, N. (2008). Barn swallow chicks beg more loudly when broodmates are unrelated. *J. Evol. Biol.*, 21, 256–262.
12. Borenstein, M., Hedges, L.V., Higgins, J.P.T. & Rothstein, H.R. (2011). *Introduction to Meta-Analysis*. John Wiley & Sons, Sussex, UK.
13. Bossan, B., Hammerstein, P. & Koehncke, A. (2013). We were all young once: an intragenomic perspective on parent-offspring conflict. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20122637–20122637.
14. Bradbury, J.W. & Vehrencamp, S.L. (2011). *Principles of animal communication*. 2nd edn. Sinauer Associates, Sunderland, USA.
15. Brinkhof, M.W.G., Heeb, P., Kölliker, M. & Richner, H. (1999). Immunocompetence of nestling great tits in relation to rearing environment and parentage. *Proceedings of the Royal Society B: Biological Sciences*, 266, 2315–2322.
16. Briskie, J.V., Naugler, C.T. & Leech, S.M. (1994). Begging Intensity of Nestling Birds Varies with Sibling Relatedness. *Proceedings of the Royal Society B: Biological Sciences*, 258, 73–78.
17. Bro-Jørgensen, J. (2010). Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends in Ecology & Evolution*, 25, 292–300.
18. Broom, M., Ruxton, G.D. & Schaefer, H.M. (2013). Signal verification can promote reliable signalling. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20131560–

20131560.

19. Bulmer, E., Celis, P. & Gil, D. (2007). Parent-absent begging: evidence for sibling honesty and cooperation in the spotless starling (*Sturnus unicolor*). *Behavioral Ecology*, 19, 279–284.
20. Butler, D.G., Cullis, B.R., Gilmour, A.R. & Gogel, B.J. (2009). *ASReml-R reference manual: mixed models for S language environments*. The State of Queensland, Department of Primary Industries and Fisheries, Brisbane, AU.
21. Carazo, P. & Font, E. (2014). “Communication breakdown”: the evolution of signal unreliability and deception. *Animal Behaviour*, 87, 17–22.
22. Caro, S.M., Griffin, A.S., Hinde, C.A. & West, S.A. (2016a). Unpredictable environments lead to the evolution of parental neglect in birds. *Nature Communications*, 7, 1–10.
23. Caro, S.M., West, S.A. & Griffin, A.S. (2016b). Sibling conflict and dishonest signaling in birds. *Proceedings of the National Academy of Sciences of the United States of America*, 113, 13803–13808.
24. Chappell, M.A. & Bachman, G.C. (2002). Energetic Costs of Begging Behaviour. In: *The Evolution of Begging*. Springer Netherlands, Dordrecht, pp. 143–162.
25. Clutton-Brock, T. (1991). *The evolution of parental care*. Oxford University Press, Princeton, NJ.
26. Cohen, J., Cohen, P., West, S.G. & Aiken, L.S. (2003). *Applied multiple correlation/regression analysis for the behavioral sciences*. UK: Taylor & Francis.
27. Cotton, P.A., Kacelnik, A. & Wright, J. (1996). Chick begging as a signal: are nestlings honest? *Behavioral Ecology*, 7, 178–182.
28. Cotton, P.A., Wright, J. & Kacelnik, A. (1999). Chick Begging Strategies in Relation to Brood Hierarchies and Hatching Asynchrony. *The American Naturalist*, 153, 412–420.
29. Culina, A., Radersma, R. & Sheldon, B.C. (2014). Trading up: the fitness consequences of divorce in monogamous birds. *Biological Reviews*, 90, 1015–1034.
30. Davis, J.N., Todd, P.M. & Bullock, S. (1999). Environment quality predicts parental provisioning decisions. *Proceedings of the Royal Society B: Biological Sciences*, 266, 1791–1797.
31. Dor, R. & Lotem, A. (2010). Parental effort and response to nestling begging in the house sparrow: repeatability, heritability and parent-offspring co-evolution. *Journal of Evolutionary Biology*, 23, 1605–1612.
32. Dor, R., Kedar, H., Winkler, D.W. & Lotem, A. (2006). Begging in the absence of parents: a “quick on the trigger” strategy to minimize costly misses. *Behavioral Ecology*, 18, 97–102.
33. Dreiss, A., Lahlah, N. & Roulin, A. (2010). How siblings adjust sib-sib communication and begging signals to each other. *Animal Behaviour*, 80, 1049–1055.
34. Drummond, H. & Garcia Chavelas, C. (1989). Food shortage influences sibling aggression in the blue-footed booby. *Animal Behaviour*, 37, 806–819.
35. Du, B., Liu, C.J. & Bao, S.J. (2015). Begging form and growth pattern of nestlings correlate with parental food-allocation patterns in the Horned Lark (*Eremophila alpestris*). *Canadian Journal of Zoology*, 93, 273–279.
36. Dugas, M.B. & Rosenthal, G.G. (2009). Carotenoid-rich mouth colors influence the conspicuousness of nestling birds. *Behavioural Ecology and Sociobiology*, 64, 455–462.
37. Fawcett, T.W. & Johnstone, R.A. (2003). Optimal assessment of multiple cues. *Proceedings*

- of the Royal Society B: Biological Sciences, 270, 1637–1643.
38. Fenoglio, S., Cucco, M. & Malacarne, G. (2002). The effect of a carotenoid-rich diet on immunocompetence and behavioural performances in Moorhen chicks. *Ethology Ecology & Evolution*, 14, 149–156.
 39. Flower, T.P., Gribble, M. & Ridley, A.R. (2014). Deception by flexible alarm mimicry in an African bird. *Science*, 344, 513–516.
 40. Forbes, L.S. & Ydenberg, R.C. (1992). Sibling rivalry in a variable environment. *Theoretical Population Biology*, 41, 135–160.
 41. Forbes, S., Thornton, S., Glassey, B., Forbes, M. & Buckley, N.J. (1997). Why parent birds play favourites. *Nature*, 390, 351–352.
 42. García-Navas, V., Ferrer, E.S. & Jose Sanz, J. (2013). Prey choice, provisioning behaviour, and effects of early nutrition on nestling phenotype of titmice. *Ecoscience*, 20, 9–18.
 43. Ghalambor, C.K. & Martin, T.E. (2001). Fecundity-survival trade-offs and parental risk-taking in birds. *Science*, 292, 494–497.
 44. Gil, D., Bulmer, E., Celis, P. & Lopez-Rull, I. (2008). Adaptive developmental plasticity in growing nestlings: sibling competition induces differential gape growth. *Proceedings of the Royal Society B: Biological Sciences*, 275, 549–554.
 45. Glassey, B. & Forbes, S. (2002). Muting individual nestlings reduces parental foraging for the brood. *Animal Behaviour*, 63, 779–786.
 46. Godfray, H.C. (1995a). Evolutionary theory of parent-offspring conflict. *Nature*, 376, 133–138.
 47. Godfray, H.C.J. (1991). Signalling of need by offspring to their parents. *Nature*, 352, 328–330.
 48. Godfray, H.C.J. (1995b). Signaling of Need Between Parents and Young: Parent-Offspring Conflict and Sibling Rivalry. *The American Naturalist*, 146, 1–24.
 49. Godfray, H.C.J. & Johnstone, R.A. (2000). Begging and bleating: the evolution of parent-offspring signalling. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 355, 1581–1591.
 50. Grafen, A. (1990). Biological signals as handicaps. *Journal of Theoretical Biology*, 144, 517–546.
 51. Griffin, A.S., Alonzo, S.H. & Cornwallis, C.K. (2013). Why Do Cuckolded Males Provide Paternal Care? *PLoS Biology*, 11, 1–9.
 52. Grissom, R.J. & Kim, J.J. (2011). *Effect Sizes for Research: Univariate and Multivariate Applications; 2nd ed.* Taylor & Francis, Hoboken, NJ.
 53. Grodzinski, U. & Johnstone, R. A. (2007). The adaptive value of parental responsiveness to nestling begging. *Proceedings of the Royal Society B: Biological Sciences*, 274, 2449–2456.
 54. Grodzinski, U. & Johnstone, R.A. (2012). Parents and offspring in an evolutionary game: the effect of supply on demand when costs of care vary. *Proceedings of the Royal Society B: Biological Sciences*, 279, 109–115.
 55. Guilford, T. & Dawkins, M.S. (1991). Receiver Psychology and the Evolution of Animal Signals. *Animal Behaviour*, 42, 1–14.
 56. Hadfield, J.D. (2010). MCMC Methods for Multi-Response Generalized Linear Mixed Models: The MCMCglmm R Package. *Journal of Statistical Software*, 33, 1–22.
 57. Hadfield, J.D., Krasnov, B.R., Poulin, R. & Nakagawa, S. (2014). A Tale of Two

- Phylogenies: Comparative Analyses of Ecological Interactions. *The American Naturalist*, 183, 174–187.
- 58.Haff, T.M. & Magrath, R.D. (2011). Calling at a cost: elevated nestling calling attracts predators to active nests. *Biology Letters*, 7, 493–495.
- 59.Haig, D. (1993). Genetic conflicts in human pregnancy. *Quarterly Review of Biology*, 68, 495–532.
- 60.Haig, D. (1996). Placental hormones, genomic imprinting, and maternal- fetal communication. *Journal of Evolutionary Biology*, 9, 357–380.
- 61.Hamilton, W.D. (1964). The genetical evolution of social behaviour. I. *Journal of Theoretical Biology*, 7, 1–16.
- 62.Hasson, O. (1989). Amplifiers and the handicap principle in sexual selection: a different emphasis. *Proceedings of the Royal Society B: Biological Sciences*, 235, 383–406.
- 63.Heeb, P., Schwander, T. & Faoro, S. (2003). Nestling detectability affects parental feeding preferences in a cavity-nesting bird. *Animal Behaviour*, 66, 637–642.
- 64.Higgins, J.P.T., Thompson, S.G., Deeks, J.J. & Altman, D.G. (2003). Measuring Inconsistency In Meta-Analyses. *British Medical Journal*, 327, 557–560.
- 65.Hill, G.E. & McGraw, K.J. (2006). Mechanics of carotenoid-based coloration. *Bird coloration*, 1, 177–242.
- 66.Hinde, C.A. (2006). Negotiation over offspring care? --a positive response to partner-provisioning rate in great tits. *Behavioral Ecology*, 17, 6–12.
- 67.Hinde, C.A. & Godfray, H.C.J. (2011). Quality, need, or hunger; begging the question. *Behavioral Ecology*, 22, 1147–1148.
- 68.Hinde, C.A. & Kilner, R.M. (2007). Negotiations within the family over the supply of parental care. *Proceedings of the Royal Society B: Biological Sciences*, 274, 53–60.
- 69.Hinde, C.A., Johnstone, R.A. & Kilner, R.M. (2010). Parent-Offspring Conflict and Coadaptation. *Science*, 327, 1373–1376.
- 70.Hinks, A.E., Cole, E.F., Daniels, K.J., Wilkin, T.A., Nakagawa, S. & Sheldon, B.C. (2015). Scale-Dependent Phenological Synchrony between Songbirds and Their Caterpillar Food Source. *The American Naturalist*, 186, 84–97.
- 71.Jetz, W., Thomas, G.H., Joy, J.B., Redding, D.W., Hartmann, K. & Mooers, A.O. (2014). Global distribution and conservation of evolutionary distinctness in birds. *Current Biology*, 24, 919–930.
- 72.Jimeno, B., Muriel, J., Pérez-Rodríguez, L. & Gil, D. (2013). Sexual Differences in Parental Investment in Response to Parent-Absent Calls. *Ethology*, 120, 258–265.
- 73.Johnstone, R.A. (1995). Honest advertisement of multiple qualities using multiple signals. *Journal of Theoretical Biology*, 177, 87–94.
- 74.Johnstone, R.A. (1996). Begging Signals and Parent-Offspring Conflict: Do Parents Always Win? *Proceedings of the Royal Society B: Biological Sciences*, 263, 1677–1681.
75. Johnstone, R. A. (1996b). Multiple displays in animal communication: 'backup signals' and multiple messages'. *Philosophical Transactions of the Royal Society of London B: Biological Sciences* 351, 329-338.
- 76.Johnstone, R.A. (1999). Signaling of need, sibling competition, and the cost of honesty. *Proceedings of the National Academy of Sciences*, 96, 12644–12649.
- 77.Johnstone, R.A. (2004). Begging and Sibling Competition: How Should Offspring Respond to Their Rivals? *The American Naturalist*, 163, 388–406.

78. Johnstone, R.A. & Grafen, A. (1993). Dishonesty and the Handicap Principle. *Animal Behaviour*, 46, 759–764.
79. Johnstone, R.A. & Kilner, R.M. (2011). New labels for old whines. *Behavioral Ecology*, 22, 918–U1500.
80. Johnstone, R.A. & Roulin, A. (2003). Sibling negotiation. *Behavioral Ecology*.
81. Johnstone, R.A., Manica, A., Fayet, A.L., Stoddard, M.C., Rodríguez-Gironés, M.A. & Hinde, C.A. (2013). Reciprocity and conditional cooperation between great tit parents. *Behavioral Ecology*, 25, 216–222.
82. Kacelnik, A., Cotton, P.A., Stirling, L. & Wright, J. (1995). Food Allocation among Nestling Starlings: Sibling Competition and the Scope of Parental Choice. *Proceedings of the Royal Society B: Biological Sciences*, 259, 259–263.
83. Kilner, R. (1997). Mouth colour is a reliable signal of need in begging canary nestlings. *Proceedings of the Royal Society B: Biological Sciences*, 264, 963–968.
84. Kilner, R.M. (2001). A Growth Cost of Begging in Captive Canary Chicks. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 11394–11398.
85. Kilner, R., & Davies, N. B. (1998). Nestling mouth colour: Ecological correlates of a begging signal. *Animal Behaviour*, 56(3), 705–712.
86. Kilner, R.M. & Hinde, C.A. (2008). Information warfare and parent-offspring conflict. *Advances in the Study of Behavior*, 68, 283–336.
87. Kilner, R.M. & Hinde, C.A. (2012). Parent-offspring conflict. In: *The evolution of parental care* (eds. Royle, N.J., Smiseth, P.T. & Kölliker, M.). Princeton University Press, Oxford, UK.
89. Kilner, R. & Johnstone, R.A. (1997). Begging the question: are offspring solicitation behaviours signals of need? *Trends in Ecology & Evolution*, 12, 11–15.
90. Kilner, R. M., Madden, J. R., & Hauber, M. E. (2004). Broad parasitic cowbird nestlings use host young to procure resources. *Science*, 305(5685), 877–879. <http://doi.org/10.1126/science.1098487>
91. Kilner, R.M., Noble, D.G. & Davies, N.B. (1999). Signals of need in parent-offspring communication and their exploitation by the common cuckoo. *Nature*, 397, 667–672.
92. Klug, H., Bonsall, M.B. & Alonzo, S.H. (2013). The origin of parental care in relation to male and female life history. *Ecology and Evolution*, 3, 779–791.
93. Koenig, W.D., Walters, E.L. & Haydock, J. (2009). Helpers and egg investment in the cooperatively breeding acorn woodpecker: testing the concealed helper effects hypothesis. *Behavioural Ecology and Sociobiology*, 63, 1659–1665.
94. Kokko, H. & Jennions, M. (2003). It takes two to tango. *Trends in Ecology & Evolution*, 18, 103–104.
95. Kokko, H. & Jennions, M.D. (2008). Parental investment, sexual selection and sex ratios. *Journal of Evolutionary Biology*, 21, 919–948.
96. Koricheva, J., Gurevitch, J. & Mengersen, K. (2013). *Handbook of Meta-analysis in Ecology and Evolution*. Princeton University Press, Princeton, USA.
97. Kölliker, M. (2011). On the meaning of hunger and behavioral control in the evolution of honest begging. *Behavioral Ecology*, 22, 919–920.
98. Krist, M. (2010). Egg size and offspring quality: a meta-analysis in birds. *Biological Reviews*, 86, 692–716.
99. Lachmann, M. & Bergstrom, C.T. (1998). Signalling Among Relatives II. Beyond the Tower of Babel. *Theoretical Population Biology*, 54, 146–160.

- 100.Lachmann, M., Szamado, S. & Bergstrom, C.T. (2001). Cost and conflict in animal signals and human language. *Proceedings of the National Academy of Sciences of the United States of America*, 98, 13189–13194.
- 101.Lack, D. (1947). The Significance of Clutch-size. *Ibis*, 89, 302–352.
- 102.Lack, D. (1954). *The natural regulation of animal numbers*. Clarendon Press, Oxford, UK.
- 103.Lee, S.Y. & Song, X.Y. (2004). Evaluation of the Bayesian and maximum likelihood approaches in analyzing structural equation models with small sample sizes. *Multivariate Behavioral Research*, 39, 653–686.
- 104.Leech, S.M. & Leonard, M.L. (1996). Is There an Energetic Cost to Begging in Nestling Tree Swallows (*Tachycineta bicolor*)? *Proceedings of the Royal Society B: Biological Sciences*, 263, 983–987.
- 105.Leonard, M. & Horn, A. (1996). Provisioning rules in tree swallows. *Behavioural Ecology and Sociobiology*, 38, 341–347.
- 106.Leonard, M.L. & Horn, A.G. (1998). Need and nestmates affect begging in tree swallows. *Behavioural Ecology and Sociobiology*, 42, 431–436.
- 107.Leonard, M.L. & Horn, A.G. (2001). Begging calls and parental feeding decisions in tree swallows (*Tachycineta bicolor*). *Behavioural Ecology and Sociobiology*, 49, 170–175.
- 108.Leonard, M.L., Horn, A.G., Gozna, A. & Ramen, S. (2000). Brood size and begging intensity in nestling birds. *Behavioral Ecology*, 11, 196–201.
- 109.Lessells, C.M. & McNamara, J.M. (2012). Sexual conflict over parental investment in repeated bouts: negotiation reduces overall care. *Proceedings of the Royal Society B: Biological Sciences*, 279, 1506–1514.
- 110.Liker, A., Freckleton, R.P., Remeš, V. & Székely, T. (2015). Sex differences in parental care: Gametic investment, sexual selection, and social environment. *Evolution*, 69, 2862–2875.
- 111.Lockie, J.D. (1955). The Breeding Habits and Food of Short-Eared Owls after a Vole Plague. *Bird Study*, 2, 53–69.
- 112.Parker, G. A., & Macnair, M. R. (1979). Models of parent-offspring conflict. IV. Suppression: evolutionary retaliation by the parent. *Animal Behaviour*, 27, 1210–1235.
- 113.Magrath, R.D. (1990). Hatching asynchrony in altricial birds. *Biological Reviews*, 65, 587–622.
- 114.Magrath, R.D. (1992). Roles of Egg Mass and Incubation Pattern in Establishment of Hatching Hierarchies in the Blackbird (*Turdus merula*). *The Auk*, 109, 474–487.
- 115.Mainwaring, M.C., Dickens, M. & Hartley, I.R. (2012). Sexual dimorphism and offspring growth: smaller female Blue Tit nestlings develop relatively larger gapes. *Journal of Ornithology*, 153, 1011–1016.
- 116.Marques, P.A.M., Leonard, M.L., Horn, A.G. & Contasti, A. (2011). How Nestling Tree Swallows (*Tachycineta bicolor*) Integrate their Responses to Hunger and Signalling by Nestmates. *Ethology*, 117, 163–170.
- 117.Marques, P.A.M., Marquez, R. & Vicente, L. (2006). Brood size and nestling vocal begging behaviour in the Spanish Sparrow *Passer hispaniolensis*. *Ardea*, 94, 203–210.
- 118.Martin-Galvez, D., Perez-Contreras, T., Soler, M. & Soler, J.J. (2011). Benefits associated with escalated begging behaviour of black-billed magpie nestlings overcompensate the associated energetic costs. *Journal of Experimental Biology*, 214, 1463–1472.
- 119.Martin-Vivaldi, M., Palomino, J.J., Soler, M. & Soler, J.J. (1999). Determinants of reproductive success in the Hoopoe *Upupa epops*, a hole-nesting non-passerine bird with

- asynchronous hatching. *Bird Study*, 46, 205–216.
120. Mathevon, N. & Charrier, I. (2004). Parent-offspring conflict and the coordination of siblings in gulls. *Proceedings of the Royal Society B: Biological Sciences*, 271, S145–S147.
 121. Maynard Smith, J. (1982). *Evolution and the Theory of Games*. Cambridge University Press, Cambridge, UK.
 122. Maynard Smith, J. (1991a). Honest signalling: the Philip Sidney game. *Animal Behaviour*, 42, 1034–1035.
 123. Maynard Smith, J. (1991b). Honest signalling: the Philip Sidney game. *Animal Behaviour*, 42, 1034–1035.
 124. Maynard Smith, J. & Harper, D. (2003). *Animal signals*. Oxford University Press, Oxford, UK.
 125. McCarty, J.P. (1996). The energetic cost of begging in nestling passerines. *The Auk*, 113, 178–188.
 126. McNamara, J.M., Gasson, C. & Houston, A. (1999). Incorporating rules for responding into evolutionary games. *Nature*, 401, 368–371.
 127. Merckling, T., Perrot, C., Helfenstein, F., Ferdy, J.-B., Gaillard, L., Lefol, E., *et al.* (2016). Maternal effects as drivers of sibling competition in a parent-offspring conflict context? An experimental test. *Ecology and Evolution*, 6, 3699–3710.
 128. Mock, D.W. & Parker, G.A. (1997). *The evolution of sibling rivalry*. Oxford University Press, Oxford, UK.
 129. Mock, D.W., Dugas, M.B. & Strickler, S.A. (2011). Honest begging: expanding from Signal of Need. *Behavioral Ecology*, 22, 909–917.
 130. Mokkonen, M. & Lindstedt, C. (2015). The evolutionary ecology of deception. *Biological Reviews*, 000–000.
 131. Monaghan, P. & Nager, R.G. (1997). Why don't birds lay more eggs? *Trends in Ecology & Evolution*, 12, 270–274.
 132. Mondloch, C. (1995). Chick hunger and begging affect parental allocation of feedings in pigeons. *Animal Behaviour*, 49, 601–613.
 133. Moreno-Rueda, G. (2006). Is there empirical evidence for the cost of begging? *Journal of Ethology*, 25, 215–222.
 134. Moreno-Rueda, G., Soler, M., Martín-Vivaldi, M. & Palomino, J.J. (2009). Brood provisioning rate and food allocation rules according to nestling begging in a clutch-adjusting species, the Rufous-tailed Scrub-robin *Cercotrichas galactotes*. *Acta Ornithologica*, 44, 167–175.
 135. Nager, R.G. & van Noordwijk, A.J. (1995). Proximate and Ultimate Aspects of Phenotypic Plasticity in Timing of Great Tit Breeding in a Heterogeneous Environment. *The American Naturalist*, 146, 454–474.
 136. Nakagawa, S. & Santos, E.S.A. (2012). Methodological issues and advances in biological meta-analysis. *Evolutionary Ecology*, 26, 1253–1274.
 137. Nakagawa, S. & Schielzeth, H. (2013). A general and simple method for obtaining R² from generalized linear mixed-effects models. *Methods in Ecology and Evolution*, 4, 133–142.
 138. Neuenschwander, S., Brinkhof, M.W.G., Kölliker, M. & Richner, H. (2003). Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). *Behavioral Ecology*, 14, 457–462.

139. Nöldeke, G. & Samuelson, L. (1999). How Costly is the Honest Signaling of Need? *Journal of Theoretical Biology*, 197, 527–539.
140. Parker, G.A., Mock, D.W. & Lamey, T.C. (1989). How Selfish Should Stronger Sibs Be? *The American Naturalist*, 133, 846.
141. Parker, G.A., Royle, N.J. & Hartley, I.R. (2002a). Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecology Letters*, 5, 206–215.
142. Parker, G.A., Royle, N.J. & Hartley, I.R. (2002b). Intrafamilial conflict and parental investment: a synthesis. *Philosophical Transactions of the Royal Society B: Biological Sciences*, 357, 295–307.
143. Perrins, C.M. (1970). The timing of birds' breeding seasons. *Ibis*, 112, 242–255.
144. Peterson, C.C., Nagy, K.A. & Diamond, J. (1990). Sustained metabolic scope. *Proceedings of the National Academy of Sciences of the United States of America*, 87, 2324–2328.
145. Price, K. (1996). Begging as competition for food in yellow-headed blackbirds. *The Auk*, 113, 963–967.
146. Price, K. & Ydenberg, R. (1995). Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. *Behavioural Ecology and Sociobiology*, 37, 201–208.
147. Price, K., Harvey, H. & Ydenberg, R. (1996). Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Animal Behaviour*, 51, 421–435.
148. Queller, D.C. (1997). Why do females care more than males? *Proceedings of the Royal Society B: Biological Sciences*, 264, 1555–1557.
149. Quillfeldt, P. (2002). Begging in the absence of sibling competition in Wilson's storm-petrels, *Oceanites oceanicus*. *Animal Behaviour*, 64, 579–587.
150. Quillfeldt, P., Everaert, N., Buyse, J., Masello, J.F. & Dridi, S. (2009). Relationship between plasma leptin-like protein levels, begging and provisioning in nestling thin-billed prions *Pachyptila belcheri*. *General and Comparative Endocrinology*, 161, 171–178.
151. R Core Team. (2013). R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
152. Rodríguez-Gironés, M.A. (1999). Sibling competition stabilizes signalling resolution models of parent-offspring conflict. *Proceedings of the Royal Society B: Biological Sciences*, 266, 2399–2402.
153. Rodríguez-Gironés, M.A., Cotton, P.A. & Kacelnik, A. (1996). The evolution of begging: Signaling and sibling competition. *Proceedings of the National Academy of Sciences of the United States of America*, 93, 14637–14641.
154. Rodríguez-Gironés, M.A., Enquist, M. & Cotton, P.A. (1998). Instability of signaling resolution models of parent-offspring conflict. *Proceedings of the National Academy of Sciences of the United States of America*, 95, 4453–4457.
155. Romano, A., Caprioli, M., Boncoraglio, G., Saino, N. & Rubolini, D. (2012). With a little help from my kin: barn swallow nestlings modulate solicitation of parental care according to nestmates' need. *Journal of Evolutionary Biology*, 25, 1703–1710.
156. Roulin, A., Kölliker, M. & Richner, H. (2000). Barn owl (*Tyto alba*) siblings vocally negotiate resources. *Proceedings of the Royal Society B: Biological Sciences*, 267, 459–463.
157. Royle, N.J., Alonzo, S.H. & Moore, A.J. (2016). Co-evolution, conflict and complexity:

- what have we learned about the evolution of parental care behaviours? *Current Opinion in Behavioral Sciences*, 12, 30–36.
158. Royle, N.J., Hartley, I.R. & Parker, G.A. (2002). Begging for control: when are offspring solicitation behaviours honest? *Trends in Ecology & Evolution*, 17, 434–440.
 159. Russell, A.F., Langmore, N.E., Cockburn, A., Astheimer, L.B. & Kilner, R.M. (2007). Reduced Egg Investment Can Conceal Helper Effects in Cooperatively Breeding Birds. *Science*, 317, 941–944.
 160. Saino, N., Incagli, M., Martinelli, R., Ambrosini, R. & Møller, A.P. (2001). Immunity, growth and begging behaviour of nestling Barn Swallows *Hirundo rustica* in relation to hatching order. *Journal of Avian Biology*, 32, 263–270.
 161. Santos, E.S.A. & Nakagawa, S. (2012). The costs of parental care: a meta-analysis of the trade-off between parental effort and survival in birds. *Journal of Evolutionary Biology*, 25, 1911–1917.
 162. Searcy, W.A. & Nowicki, S. (2005). *The evolution of animal communication: reliability and deception in signaling systems*. Princeton University Press, Princeton, USA.
 163. Shizuka, D. & Lyon, B.E. (2012). Family dynamics through time: brood reduction followed by parental compensation with aggression and favouritism. *Ecology Letters*, 16, 315–322.
 164. Slagsvold, T., Sandvik, J., Rofstad, G. & Lorentsen, Ö. (1984). On the adaptive value of intraclutch egg-size variation in birds. *The Auk*, 101, 685–697.
 165. Smiseth, P.T., Kölliker, M. & Royle, N.J. (2012). What is parental care? In: *The evolution of parental care* (eds. Royle, N.J. & Smiseth, P.T.). Oxford University Press, Oxford, pp. 1–14.
 166. Smiseth, P.T., Wright, J. & Kölliker, M. (2008). Parent-offspring conflict and co-adaptation: behavioural ecology meets quantitative genetics. *Proceedings of the Royal Society B: Biological Sciences*, 275, 1823–1830.
 167. Smith, H.G. & Montgomerie, R. (1991). Nestling American robins compete with siblings by begging. *Behavioural Ecology and Sociobiology*, 29, 307–312.
 168. Sockman, K.W. (2012). Hatching Order and Seasonal Timing of Development Predict Bill Morphology of Nestling and Adult Lincoln's Sparrows - El Orden de Eclosión y la Temporalidad Estacional de Desarrollo Predicen la Morfología del Pico de los Pichones y Adultos de *Melospiza lincolnii*. *Condor*, 114, 645–653.
 169. Soler, M., Ruiz-Raya, F., Carra, L.G., Medina-Molina, E., Ibáñez-Álamo, J.D. & Martín-Gálvez, D. (2014). A Long-Term Experimental Study Demonstrates the Costs of Begging That Were Not Found over the Short Term. *PLoS ONE*, 9, e111929–11.
 170. Stearns, S.C. (1992). *The Evolution of Life Histories*. Oxford University Press, Oxford, UK.
 171. Sternalski, A., Mougeot, F., Pérez-Rodríguez, L. & Bretagnolle, V. (2012). Carotenoid-Based Coloration, Condition, and Immune Responsiveness in the Nestlings of a Sexually Dimorphic Bird of Prey. *Physiological and Biochemical Zoology*, 85, 364–375.
 172. Stoddard, M.C., Fayet, A.L., Kilner, R.M. & Hinde, C.A. (2012). Egg speckling patterns do not advertise offspring quality or influence male provisioning in great tits. *PLoS ONE*, 7, e40211.
 173. Stoleson, S.H. & Beissinger, S.R. (1995). Hatching Asynchrony and the Onset of Incubation in Birds, Revisited. In: *Current Ornithology* (ed. Power, D.M.). Springer US, Boston, MA, pp. 191–270.
 174. Stucki, D. & Kölliker, M. (2013). Coevolutionary feedbacks between family interactions and life history. *Evolution*, 67, 3208–3220.

175. Tanaka, K.D., Morimoto, G. & Ueda, K. (2005). Yellow wing-patch of a nestling Horsfield's hawk cuckoo *Cuculus fugax* induces miscognition by hosts: mimicking a gape? *Journal of Avian Biology*, 36, 461–464.
176. Thorogood, R., Ewen, J.G. & Kilner, R.M. (2011). Sense and sensitivity: responsiveness to offspring signals varies with the parents' potential to breed again. *Proceedings of the Royal Society B: Biological Sciences*, 278, 2638–2645.
177. Trivers, R.L. (1974). Parent-Offspring Conflict. *American Zoologist*, 14, 249–264.
178. Van Noordwijk, A.J., McCleery, R.H. & Perrins, C.M. (1995). Selection for the Timing of Great Tit Breeding in Relation to Caterpillar Growth and Temperature. *Journal of Animal Ecology*, 64, 451–458.
179. Verhulst, S., van Balen, J.H. & Tinbergen, J.M. (1995a). Seasonal Decline in Reproductive Success of the Great Tit: Variation in Time or Quality? *Ecology*, 76, 2392–2403.
180. Verhulst, S., Vanbalen, J.H. & Tinbergen, J.M. (1995b). Seasonal Decline in Reproductive Success of the Great Tit - Variation in Time or Quality. *Ecology*, 76, 2392–2403.
181. Viechtbauer, W. (2010). Conducting Meta-Analyses in R with the metafor Package. *Journal of Statistical Software*, 36, 1–48.
182. Weathers, W.W., Hodum, P.J. & Anderson, D.J. (1997). Is the Energy Cost of Begging by Nestling Passerines Surprisingly Low? *The Auk*, 114, 133–133.
183. Wells, J.C. (2003). Parent-offspring conflict theory, signaling of need, and weight gain in early life. *The Quarterly Review of Biology*, 78, 169–202.
184. West, S.A. (2009). *Sex Allocation*. Princeton University Press, Princeton, USA.
185. West, S.A., Pen, I. & Griffin, A.S. (2002a). Conflict and cooperation - Cooperation and competition between relatives. *Science*, 296, 72–75.
186. West, S.A., Reece, S.E. & Sheldon, B.C. (2002b). Sex ratios. *Heredity*, 88, 117–124.
187. Wiebe, K.L. & Slagsvold, T. (2009). Mouth coloration in nestling birds: increasing detection or signalling quality? *Animal Behaviour*, 78, 1413–1420.
188. Wiebe, K.L. & Slagsvold, T. (2012a). Brood parasites may use gape size constraints to exploit provisioning rules of smaller hosts: an experimental test of mechanisms of food allocation. *Behavioral Ecology*, 23, 391–396.
189. Wiebe, K.L. & Slagsvold, T. (2012b). Parents take both size and conspicuousness into account when feeding nestlings in dark cavity nests. *Animal Behaviour*, 84, 1307–1312.
190. Wild, G. (2011). Direct fitness for dynamic kin selection. *Journal of Evolutionary Biology*, 24, 1598–1610.
191. Wild, G., Caro, S.M. & West, S.A. (2017). Honest signaling of information that is neither cryptic nor private. *Journal of Evolutionary Biology*.
192. Wild, G. & West, S.A. (2007). A Sex Allocation Theory for Vertebrates: Combining Local Resource Competition and Condition-Dependent Allocation. *Am Nat*, 170, E112–E128.
193. Williams, T.D. (1994). Intraspecific Variation in Egg Size and Egg Composition in Birds - Effects on Offspring Fitness. *Biological Reviews*, 69, 35–59.
194. Wright, J. (2011). Honest begging: signals of need, quality, and/or hunger? *Behavioral Ecology*, 22, 920–921.
195. Wright, J. & Leonard, M.L. (2002). *The evolution of begging: competition, cooperation and communication*. Kluwer Academic Publishers, Dordrecht, The Netherlands.
196. Wright, J., Hinde, C., Fazey, I. & Both, C. (2002). Begging signals more than just short-

term need: cryptic effects of brood size in the pied flycatcher (*Ficedula hypoleuca*).
Behavioural Ecology and Sociobiology, 52, 74–83.

197. Zahavi, A. (1975). Mate selection—A selection for a handicap. *Journal of Theoretical Biology*, 53, 205–214.
198. Zollman, K.J.S., Bergstrom, C.T. & Huttegger, S.M. (2012). Between cheap and costly signals: the evolution of partially honest communication. *Proceedings of the Royal Society B: Biological Sciences*, 280, 20121878–20121878.

APPENDICES

ARTICLE

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OPEN

Unpredictable environments lead to the evolution of parental neglect in birds

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A nest of begging chicks invites an intuitive explanation: needy chicks want to be fed and parents want to feed them. Surprisingly, however, in a quarter of species studied, parents ignore begging chicks. Furthermore, parents in some species even neglect smaller chicks that beg more, and preferentially feed the biggest chicks that beg less. This extreme variation across species, which contradicts predictions from theory, represents a major outstanding problem for the study of animal signalling. We analyse parent-offspring communication across 143 bird species, and show that this variation correlates with ecological differences. In predictable and good environments, chicks in worse condition beg more, and parents preferentially feed those chicks. In unpredictable and poor environments, parents pay less attention to begging, and instead rely on size cues or structural signals of quality. Overall, these results show how ecological variation can lead to different signalling systems being evolutionarily stable in different species.

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In many species, including our own, the production of offspring represents the most energetically demanding stage of an animal's life. Raising a brood successfully puts a metabolic demand on breeding birds that is the equivalent to a human cycling the Tour de France¹. Success or failure often depends on parents' ability to determine which offspring to invest in, when to invest in them and how much to invest. Offspring attempt to influence the feeding behaviour of their parents by begging for food through a variety of mechanisms, including vocal calls, behavioural displays and physical structures².

Different species, however, appear to beg and respond to begging in different ways (Fig. 1)^{3–9}. In many species, such as the tree swallow, smaller nestlings beg more, and are preferentially fed by their mothers^{10,11}. In other species, such as the hoopoe, mothers sometimes force food into the beaks of larger, silent chicks, ignoring the persistent begging from their smaller offspring¹². In many siblicidal species, such as the blue-footed booby, the largest offspring beg and are fed the most¹³.

Evolutionary theory has been unable to account for this diversity across species, as highlighted by Mock *et al.*³. The dominant paradigm, 'signal of need', predicts that chicks in worse condition beg with greater intensity and that parents respond to this begging^{3,14–17}. However, these signal of need models assume that parents are trying to rear all their offspring and that offspring in better condition reduce their begging^{3,4,9,14,17}. This is clearly not the case in species where

parents let the neediest offspring starve and offspring in better condition beg more^{3,13,18–21}. The pattern in those species may be better explained by 'signal of quality' models^{3,20,21}. However, neither signal of need nor quality models predict that parents should flexibly ignore begging, as the hoopoe does^{12,17,19}. While each model is consistent with observations in some species, it is inconsistent with others³.

A possible explanation for this diversity is that different ecological conditions, in different species, favour different signalling systems^{8,22–25}. When food is relatively plentiful, parents can be selected to preferentially feed the offspring signalling the greatest need⁸. In contrast, when food is scarce, parents can be predicted to ignore begging and preferentially feed bigger chicks⁸. Consequently, a single factor—the extent to which parents can acquire enough food to feed all their offspring—could lead to the stability of different signalling systems, and hence explain the extreme variation across species in who begs and how parents respond to begging (Fig. 2)^{3,8,25}.

There has, however, been no empirical test of whether different signalling systems have evolved in response to differences in relative food availability. While many studies have been conducted within species, it is hard to generalize their findings because of differences in environmental context and life history variables between species. We therefore conducted a comparative study to test whether signalling and provisioning correlate with the likelihood that parents can acquire enough food to rear a



Figure 1 | Variation in parental provisioning. In every species of bird with parental care, chicks appear to have evolved signals designed to maximize their chance of being fed, such as vocalizations, begging postures and bright mouths. However, the way parents respond to information about their offspring differs markedly across species. Tree swallows *Tachycineta bicolor* feed the chick begging the most (a). Others sometimes neglect begging offspring, such as the blue-footed booby *Sula neboouxii* (b) and the hoopoe *Upupa epops* (c) which instead preferentially feed larger chicks. Gouldian finch *Erythrura gouldiae* parents (d) may preferentially feed offspring with elaborate structural ornaments around their mouths. (Photos courtesy of (a) M. Sodicoff. (b) This figure is not covered by the CC BY licence ©Damschen/ARCO/naturepl.com. All rights reserved, used with permission. (c) This figure is not covered by the CC BY licence © L.M.R. Gordón. All rights reserved, used with permission; and (d) This figure is not covered by the CC BY licence (c) G. Grall, National Aquarium, Baltimore. All rights reserved, used with permission.

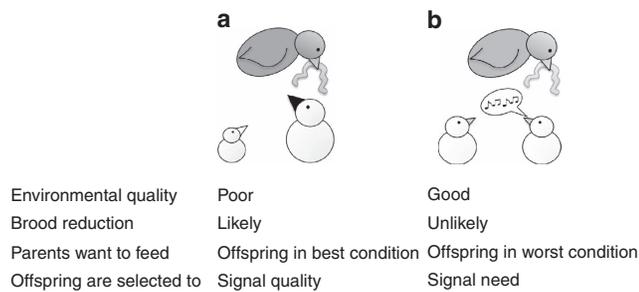


Figure 2 | Ecological variation and diversity in signalling systems. (a) In unpredictable environments, parents may produce a larger brood than future environmental conditions will support. This selects for parents to preferentially feed the offspring with the highest chance of survival. We predict parents will assess quality by cues such as body size, or structural signals such as dark mouths. Offspring may still beg, but parents should ignore begging in favour of other information. (b) In contrast, in predictable environments, parents will lay an appropriate number of eggs and food will be plentiful enough to rear all their offspring. Here parents will be selected to preferentially feed offspring in the worst condition. We predict offspring should signal need through begging, and parents will feed those begging more.

complete brood. We collected data on 143 bird species, examining how offspring signalling relates to their condition, and how parents respond to signals and cues of offspring condition. Our aim was to test the hypothesis that variation in food availability can explain variation in offspring communication and parental provisioning strategies.

We examined two possible determinants of parents' ability to acquire enough food to rear all their offspring: environmental predictability and environmental quality^{8,18,26–28}. First, in species where environmental conditions are more predictable, parents are more likely to produce the clutch size that leads to all of their offspring surviving^{27–29}. Conversely, in unpredictable environments, parents may lay an optimistic number of eggs, and are only able to rear all their offspring in particularly good years^{18,19,27–29}. Such species often begin egg incubation before they have completed a clutch, creating a size hierarchy: when conditions are worse, only the biggest and best quality chicks survive to fledge^{18,27–29}. We classified species as 'brood reducing' if hatching is asynchronous or if the later-hatched offspring die at greater rate, as is expected with low environmental predictability^{18,27–29}. If this information was not available, we used a conservative cutoff of 75% broods in the population typically experiencing the starvation of at least one chick. We classed all other species as having a 'whole-brood survival' strategy, as is expected with relatively high environmental predictability.

Our second determinant of food availability was current environmental quality⁸. In unusually good conditions, parents are more likely to be able to acquire enough food to feed all their offspring, even if they are typically brood reducing. We categorized environmental quality as good, average or poor compared with the norm for that population, dependent upon ecological measures or experimental manipulations. For example, owls experiencing a crash in the vole population³⁰ are in a poor environment, and pigeons supplemented with mealworms and grain³¹ are experiencing a good environment.

We found that the strategies of both offspring and parents depend upon environmental predictability and quality. In relatively stable and unusually good environments, offspring signal their need and parents distribute food according to begging. In contrast, in relatively unpredictable and unusually poor environments, offspring signal their quality and parents are

more likely to feed offspring based on signals or cues of quality. These results allow us to explain why opposite patterns have been observed in different species, with parents preferentially feeding offspring in either worse or better condition.

Results and Discussion

Offspring signalling strategies. To determine what information is encoded in chick signals, we calculated the correlation coefficient (effect size) between offspring long-term condition and (1) begging and (2) structural signals (Fig. 3). The coefficient varies between ± 1 , with positive values meaning that chicks in better condition beg more or have larger structural signals, and negative values implying that chicks in worse condition beg more or have larger structural signals. Long-term condition, or the likelihood that offspring will survive to adulthood and reproduce, is information that obviously influences parents' fitness^{3,6,17,32}. Long-term condition was captured by health, body condition, changes to food intake over multiple days, weight and rank within the brood. These different measures reflect factors that parents may or may not be able to assess directly to different degrees^{3,4,14}.

Our first prediction was that chicks in worse condition should be more likely to beg, or beg more intensely, in better environmental contexts and in species that generally rear the whole brood. Under these conditions, all offspring will be more likely to survive to maturity, and hence honest signalling of need can be favoured. We examined vocal begging and posture, as birds could adjust these behaviours flexibly in response to need.

As predicted, we found that chicks in worse condition were more likely to beg in species that rear a complete brood (phylogeny-based, Bayesian generalized linear mixed models with Markov chain Monte Carlo methods: pMCMC = 0.001; Table 1a; Fig. 4a). In contrast, in brood-reducing species, there is no general correlation between chick long-term condition and begging intensity (pMCMC = 1; Table 1a). Furthermore, across all species, chicks in worse condition were more likely to beg more intensely in better environments (pMCMC = 0.001; Table 1a). None of our results were influenced by the measure of condition or begging used in the original studies (Supplementary Tables 1–2). These results are consistent with a greater likelihood of signalling of need in species trying to rear all their offspring.

We then examined a mode of parent-offspring communication that we predicted could function as a signal of quality: structures such as mouth colour, ultraviolet reflectance and mouth size^{22,33,34}. These require a relatively long-term investment of resources such as carotenoids, and so are more likely to reflect long-term quality rather than short-term need³³. Consequently, these structural signals are more likely to be used as signals of quality, and so we predict that they will be greater in species living in unpredictable and poor environments, where only a fraction of the brood will be reared.

As predicted, we found that chicks in better condition tended to produce more intense structural signals in brood-reducing species (pMCMC = 0.02), but not in species that rear the whole brood (pMCMC = 0.4; Table 1b; Fig. 4b). This is consistent with structural signals being used to signal quality when brood reduction is possible. Furthermore, there was a significant interaction between brood reduction strategy and environmental quality in the predicted direction (pMCMC = 0.003; Table 1b). Specifically, brood-reducing species showed an increased tendency for better condition chicks to produce greater structural signals in poorer environments, which is when brood reduction is most likely. These results are consistent with a decrease in relative food availability selecting for chicks to signal quality to their parents, to avoid being the chick left to starve.

Our analyses support our hypothesis that when raising a complete brood is likely, selection should favour chicks that signal

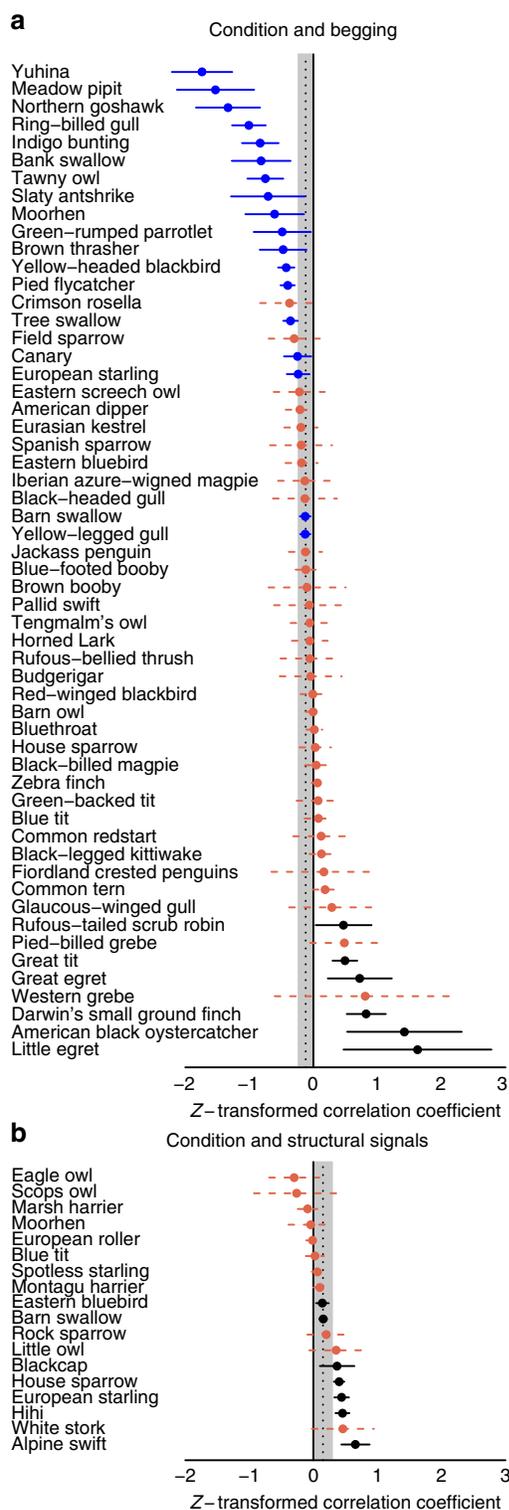


Figure 3 | Variation in offspring signals across species. Circles represent species' mean z-transformed correlation coefficient between condition and (a) begging intensity ($N=56$ species) and (b) structural signal intensity ($N=18$ species). The grand mean and 95% credible interval (CI) are denoted by the shaded bar. Blue, solid lines indicate that chicks that in worse condition signal more. Black, solid lines indicate that chicks in better condition signal more. Red, dashed lines indicate no effect of condition on signals. Lines show 95% CI (\pm s.e. $\times t_{critical}$). s.e. was estimated from the pooled number of broods across all studies.

need through behavioural begging. In contrast, when parents are unlikely to raise a complete brood, selection appears to favour chicks that signal quality through structural signals. However, caution is required when interpreting these results, because signalling theory predicts that signals must transmit information about a cryptic aspect of quality that parents cannot otherwise detect^{4,15,20}. While researchers may have captured this with measures such as immunocompetence^{33,35}, measures such as body mass may be less likely to reflect some cryptic aspect of condition. A stronger approach to test our hypothesis would be to examine parental response to begging signals, structural signals and body size cues, in terms of how parents distribute food among offspring.

Parental feeding strategies. To determine what information parents use when allocating food, we estimated the strength of the correlation between feeding and three sources of information about chick condition: begging, structural signals and body size cues (Fig. 5). Parents may respond to all, none or a combination of these signals and cues when allocating food. As far as possible, we included only data that isolated the individual effects of each of these information sources; for example, begging height, which combines both body size and begging posture, was excluded. The direction of each correlation coefficient was based solely on whether chicks signalling more were fed more, and our analyses of parental response made no assumptions about what information was included in the signal or cue.

On average, parents preferentially feed chicks that beg more (pMCMC < 0.0001; Table 2a), have brighter and more saturated mouths (pMCMC = 0.009; Table 2b), and are larger (pMCMC < 0.0002; Table 2c). The responsiveness to begging varied across species, with parents not preferentially feeding the chicks that beg the most in 17 of the 61 species studied (Fig. 6a; total heterogeneity (I^2), the proportion of observed variance that reflects true differences in correlation coefficients: 23.2%; Supplementary Table 6). Responsiveness to structural signals was also variable across species, with no effect of signal intensity on feeding in almost half of species studied ($I^2 = 16.9\%$; Fig. 6b; Supplementary Table 6). Surprisingly, given the common assumption that parents want to feed the neediest offspring, parents almost universally prefer feeding larger offspring: only 2 of 120 species feed smaller chicks more ($I^2 = 15.4\%$; Fig. 7; Supplementary Table 6). None of our results were influenced by the measure of feeding preference used in the original studies (Supplementary Tables 3–5).

We predict that parents will preferentially feed chicks in the greatest need when there is a relatively high likelihood that parents will have enough food to rear a complete brood. Given that that chicks signal need behaviourally with vocal calls and posturing (Fig. 4a), we expect that parents should be more likely to respond to such begging in relatively good environments. In contrast, when parents are unlikely to have enough food to rear a complete brood, we predict that parents should prefer to feed the better quality chicks, irrespective of begging intensity. Quality could be assessed by a cue such as body size or by chicks signalling quality with structures (Fig. 4b). In this context, we expect a positive correlation between food allocation and offspring size and/or structural signals.

As predicted, we found that parents preferentially fed the chicks that begged the most in good environments, but were less responsive to begging in poor environments (pMCMC = 0.01; Table 2a; Fig. 5a). This pattern did not differ depending upon whether a species was brood reducing or rears the whole brood (pMCMC = 0.5; Table 2a).

Table 1 | Environmental and life history influences on offspring signalling strategies.

	Posterior mean Z	95% Credible interval	pMCMC
(a) Begging			
Brood reducing	0.01	− 0.19 to 0.17	0.95
Whole-brood survival	− 0.30	− 0.47 to − 0.14	0.001***
Reduction difference	− 0.37	− 0.66 to − 0.05	0.02*
Environment	− 0.29	− 0.50 to − 0.07	0.001**
Reduction × environment	− 0.07	− 0.33 to 0.22	0.62
Grand mean	− 0.12	− 0.26 to 0.01	0.09.
(b) Structural signals			
Brood reducing	0.31	0.08 to 0.57	0.02*
Whole-brood survival	0.10	− 0.13 to 0.36	0.4
Reduction difference	− 0.21	− 0.47 to 0.09	0.18
Environment	− 0.53	− 0.77 to − 0.28	0.0001***
Reduction × environment	0.49	0.16 to 0.80	0.003**
Grand mean	0.15	− 0.00 to 0.32	0.06.

Results of MCMCgmm analyses on Fisher’s Z-transformed correlation coefficients (manuscript and figures report correlation coefficients). $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.
 (a) Behavioural begging: $n = 56$ species, 96 studies, 247 effect sizes.
 (b) Structural signals: $n = 18$ species, 33 studies, 140 effect sizes.

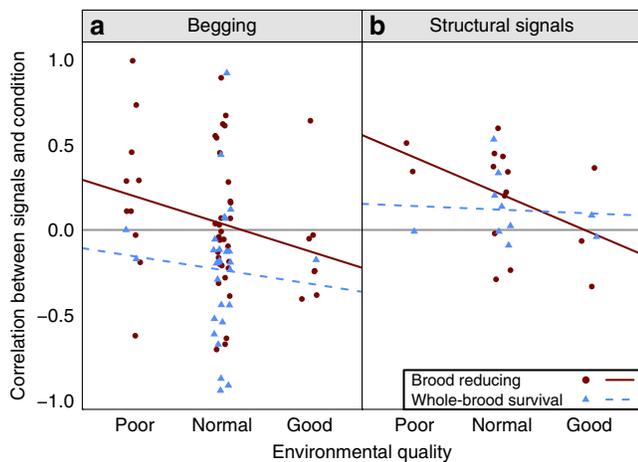


Figure 4 | Brood reduction likelihood determines whether low or high condition chicks signal more. Data points represent each species’ mean correlation coefficient (effect size) of offspring condition on signal intensity in that environment. Positive correlations indicate chicks in better condition signal at a higher intensity, and negative correlations indicate chicks in worse condition signal more. This is a graphical simplification; analyses were run on the full data set per effect size reported, not species’ means. **(a)** Chicks in worse condition were more likely to beg the most in good environments (MCMCgmm, pMCMC = 0.001), and in species which tend to raise the whole brood (MCMCgmm, pMCMC = 0.02, $N = 56$ species). This represents the scenario where brood reduction is least likely. **(b)** Chicks in better condition were more likely produce more intense structural signals in brood-reducing species in poor environments (MCMCgmm, pMCMC = 0.003, $N = 18$ species). This represents the scenario where brood reduction is most likely.

In contrast, we expect the opposite pattern with structural signals of quality and body size: when parents are unlikely to have enough food to rear all of their offspring, we predict they will respond more to structural signals and body size. As predicted, we found that parents preferentially fed chicks with more colourful mouths and/or larger bodies in poor environments, and responded less to structural signals and body size cues in good environments (structural signals: pMCMC = 0.007; size: pMCMC = 0.006; Table 2b,c; Fig. 5b,c). Furthermore, the preference for larger chicks was greater in brood-reducing species than in species where the whole brood survives (pMCMC

< 0.0002; Table 2c). Parents in brood-reducing species were also more likely to feed chicks based on structural signals, although not significantly, perhaps because of low sample size for this comparison (pMCMC = 0.09, $n = 6$ whole-brood survival species, 9 brood-reducing species; Table 2b).

Overall, a clear pattern emerges: the probability of successfully raising all offspring from a nest determines the system of communication between parents and their offspring across species. In predictable and/or unusually good environments, offspring in worse condition are more likely to beg (Fig. 4a), and parents are more likely to feed individuals begging at a higher rate (Fig. 5a). These results are predicted by signal of need models, where parents expect to rear a complete brood^{3,14–16}. In contrast, in unpredictable and/or poor environments, offspring in better condition have more intense structural signals (Fig. 4b), and parents are more likely to feed chicks that are larger or have more intense structural signals (Fig. 7b,c). These results are predicted by signal of quality models, where parents rear only a fraction of their offspring, or by models where signalling is not stable, and parents just respond to cues of quality^{3,8,21,36,37}. Another possibility is that parents respond less to variation in begging when food availability is low simply because all chicks are hungry, and therefore beg at similar rates. Irrespective of whether begging provides less information or parents are selected to ignore it, the outcome is the same: begging becomes a less useful signal in worse environments, while body size and structural signals become more important.

Our study relied on the fact that there was sufficient variation across species in food availability to produce different evolutionary outcomes. In some cases, there may even be sufficient environmental variation within a species that individuals will be selected to adjust their behaviour conditionally in response to local conditions. For example, hibi parents become less sensitive to their offspring’s mouth colour when they are supplemented with additional food³⁸. Similarly, alpine swifts who breed early in the season, when food availability is greater, prefer nestlings with lower ultraviolet reflectance, while parents who breed later, under worse conditions, switch to preferring nestlings with greater reflectance³⁹.

Conclusions

More generally, one of the major outstanding challenges for our understanding of how communication evolves is to explain why

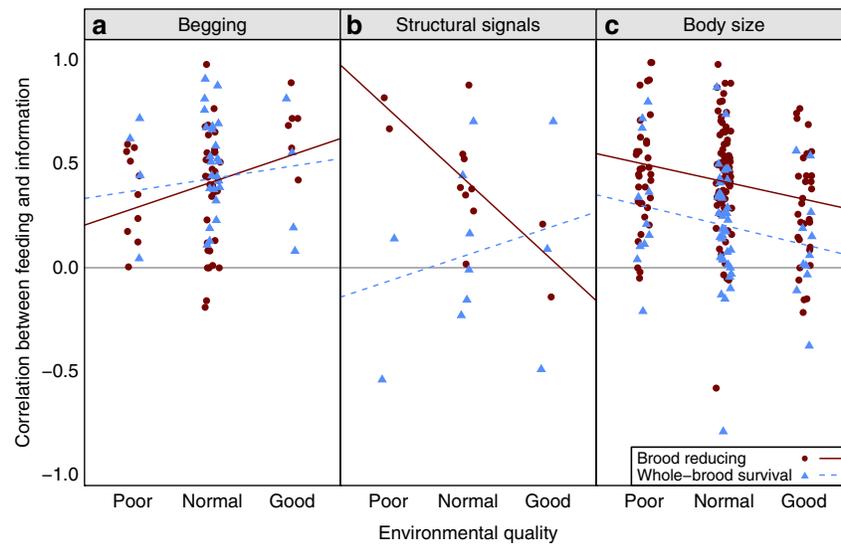


Figure 5 | Brood reduction likelihood determines how parents respond to chick signals and cues. Data points represent species' mean correlation coefficient (effect size) of signal intensity or body size on food allocation in that environment. Positive correlations indicate larger chicks or those signalling more intensely receive more food. This is a graphical simplification; analyses were run on the full data set per effect size reported, not species' means. **(a)** Parents respond more to begging as the environment improves (MCMCglmm, $p\text{MCMC} = 0.01$, $N = 61$ species). **(b)** Brood-reducing species paid more attention to structural signals in poorer environments, whereas species that rear the whole brood show a consistently low response, though low sample size keeps this interaction non-significant (MCMCglmm, $p\text{MCMC} = 0.09$, $N = 15$ species). **(c)** Parents showed a stronger preference for larger chicks in poorer environments (MCMCglmm, $p\text{MCMC} = 0.006$) and brood-reducing species (MCMCglmm, $p\text{MCMC} < 0.0002$ and $N = 120$ species).

Table 2 | Environmental and life history influences on parental response strategies.

	Posterior mean Z	95% Credible interval	pMCMC
(a) Begging			
Brood reducing	0.70	0.52 to 0.89	0.0004***
Whole-brood survival	0.61	0.38 to 0.87	0.0002***
Reduction difference	-0.11	-0.40 to 0.16	0.5
Environment	0.35	0.05 to 0.61	0.01*
Reduction \times environment	-0.16	-0.67 to 0.33	0.5
Grand mean	0.62	0.48 to 0.76	<0.0001***
(b) Structural signals			
Brood reducing	0.79	0.34 to 1.2	0.0006***
Whole-brood survival	0.34	-0.09 to 0.80	0.12
Reduction difference	-0.45	-0.97 to 0.08	0.09
Environment	-0.71	1.22 to -0.20	0.007**
Reduction \times environment	0.70	-0.10 to 1.50	0.09
Grand mean	0.36	0.10 to 0.61	0.009**
(c) Body size			
Brood reducing	0.50	0.40 to 0.59	<0.0002***
Whole-brood survival	0.19	0.07 to 0.32	0.003**
Reduction difference	-0.30	-0.43 to -0.17	<0.0002***
Environment	-0.14	-0.25 to -0.04	0.006**
Reduction \times environment	0.001	-0.20 to 0.18	0.98
Grand mean	0.43	0.31 to 0.54	<0.0002***

Results of MCMCglmm analyses on Fisher's Z-transformed correlation coefficients. $p < 0.10$, * $p < 0.05$, ** $p < 0.01$, *** $p < 0.001$.

(a) Behavioural begging: $n = 61$ species, 92 studies, 301 effect sizes.

(b) Structural signals: $n = 15$ species, 20 studies, 60 effect sizes.

(c) Body size: $n = 120$ species, 218 studies, 795 effect sizes.

species have such diverse communication systems. We have shown how variation in environmental quality can explain differences in communication between offspring and their parents. In relatively good environments, there is less conflict, and offspring can be selected to signal need to their parents. In contrast, in relatively poor environments, there is more conflict,

and parents are expected to respond to quality rather than need. Furthermore, this can occur via either offspring signalling quality or parents ignoring signals and instead relying on cues such as body size. This variation is why hundreds of empirical studies on begging and parental response have not yet led to a consensus on exactly what information is transmitted through offspring signals,

or how parents respond to various signals^{3–7}. Our results suggest that this variation reflects different communication systems being stable in different species.

Methods

Data collection. We conducted a literature search on Web of Science and Google Scholar using the keywords ‘beg’, ‘parent–offspring’, ‘bird’, ‘begging’, ‘communication’ and ‘provision’ (see Supplementary Fig. 1 for PRISMA flowchart detailing data collection). We performed backwards and forwards citation searches on all studies. We included studies published before August 2014, as well as unpublished data sets from five researchers. We included all papers with any measure relating to the relationship between chick long-term condition and (1) behavioural begging or (2) structural signals, and food allocation and (3) behavioural begging, (4) structural signals or (5) size cues (see Supplementary Table 9 for a list of excluded of studies). We excluded studies if it was impossible to determine whether parents were responding to begging or to size cues. We excluded effect sizes where the only measure of chick condition was proximate hunger rather than long-term condition. We only included effect sizes for the relationship of begging on within-brood food allocation, rather than on increases in overall parental feeding effort, as these represent fundamentally different aspects of parental care. We excluded data on species that lay only one egg per brood, as selective pressures on these offspring are likely to differ from species laying multiple eggs per brood. If relevant data were given in papers without statistical tests, such as raw means and s.e.’s, we estimated effect sizes. This resulted in a data set of 1,544 effect sizes (correlation coefficients) from 306 studies on 143 species (Supplementary Data 1). The data set contains a diverse range of species, spanning 51 families in 19 different orders.

Measures of offspring condition. We examined the effect of long-term condition on signalling intensity³². Our proxies for long-term condition were health (for example, experimental immune challenge, parasite load, carotenoid supplementation), body condition (for example, body mass to skeletal size ratio, blood glucose levels), weight (for example, body mass), rank within the brood (for example, hatching rank, dominance rank, body mass or skeletal size rank) and experimental manipulations that affected food intake over multiple days (for example, experimentally reduced or enlarged broods, with the assumption that chicks in larger broods receive less food per capita).

We excluded studies that examined only the effect of short-term food deprivation, that is, hunger. While hunger and condition may not be truly separable, they represent very different selection pressures^{3–6,17,32,40}. For example, although each piece of food eaten contributes to the likelihood that a chick will survive, the fitness benefit of food to fatally diseased chicks is zero, because they will not live to breed^{3,34,40}. Furthermore, the influence of hunger on begging is already well established^{2,3}. Consequently, we focused on the influence of long-term condition, and so data on the relationship between hunger and signal intensity were not included in analyses of offspring strategies. For example, we excluded data such as Kilner³⁴ finding that canary chicks’ mouths get redder as they become hungrier over 40 min. However, our analyses of parental behaviour made no assumptions about what information was transmitted by signals. Therefore, feeding in response to mouth redness would be included in analyses on parental behaviour, just as the response to begging calls, which may be influenced by both hunger and condition, was included. It would be an interesting task for the future to examine whether and how hunger interacts with measures of long-term condition⁴.

Measures of signalling and provisioning. Many aspects of the behavioural and structural signalling suite were reported in the literature, such as begging amplitude, duration, latency, likelihood, call structure, posture, ultraviolet reflectance of the gape or flange, carotenoid saturation of the gape or flange, or colouration of specialized skin patches and feathers only present during the nestling period. Different measures of food allocation were also reported, such as weight gain over a short time period, actual food intake, number of food items received, likelihood of being fed, growth rate and mortality. We assumed that all measures of signal intensity and food allocation were driving towards the same biological phenomenon, and so included all reported statistics in our analyses. Parents’ responses to begging signals, structural signals and body size cues were analysed separately. Because measures of feeding preference such as mortality could have been partially confounded by how we classified environmental predictability, we tested whether the measure of feeding affected the strength of the correlation coefficient, but found no difference between any of the proxies for feeding preference ($pMCMC > 0.05$, see Supplementary Tables 3–5). Because test statistics were converted to a standardized scale, differences between the various measures of begging intensity or feeding preferences should not influence the overall trends seen. Study methodology, such as which measure of long-term condition was reported or whether the study was experimental or observational, had no impact on effect size ($pMCMC > 0.05$ in all cases, see Supplementary Tables 3–5).

Data on brood reduction strategy. We classified species as brood reducing if hatching is asynchronous (24 h or more passes between the hatching of the first and last chick in the brood) and if nestling mortality follows a stereotypical pattern

of later-hatched nestlings dying at a greater rate due to starvation, siblicide or infanticide²⁷. If that data were not available, we assessed whether partial brood mortality is typical (at least one chick starves in at least 75% of broods in the population)^{18,27,28}. Many brood-reducing species experience lower rates of starvation³, but this conservative criterion allows us to identify species with a very clear strategy of brood reduction based on environmental factors, rather than incidental starvation. The combination of hatching and mortality patterns allowed us to distinguish between species employing a true brood reduction strategy and those with asynchronous hatching for other reasons, such as spreading offspring demand evenly over the nestling period or avoiding chilling earlier-laid eggs²⁸.

Data on environmental quality. To evaluate how environmental conditions interact with life history traits across species, we categorized populations as experiencing normal, better than normal or worse than normal environments, based on experimental manipulations (parents were fed reduced or supplemented diets or chick demand was artificially increased or decreased), ecological measures (such as prey density, date or rainfall), or average mortality across different years in long-term observational studies. Only long-term manipulations of food availability over multiple days were included, to ensure chick condition, and not simply hunger, was affected by the ecological variation. If no information on environmental quality was available, studies were conservatively classified as normal conditions.

Statistical analyses. To evaluate the strength of the relationships across studies and species, we transformed any test statistic measuring either an effect of long-term condition on signal intensity, or an effect of chick signals or cues on feeding into a standardized effect size (Fisher’s Z-transformed correlation coefficient)^{41–44}. These correlation coefficients follow a normal distribution, account for different scales in their original measurements, are well suited to the ordered nature of the data and are more straightforward to interpret than standardized difference in means⁴¹. Before analyses, we decided not to exclude potential outliers. Fisher’s Z-transformed correlation coefficients were analysed using the MCMCglmm package in R, which implements Bayesian generalized linear mixed models with Markov chain Monte Carlo methods^{45,46}. Models were weighted by sample size and controlled for phylogeny and repeated measures on the same study and species. Sample size was determined as the number of broods used to generate the original test statistic, because this is a standard measure across studies. It also conservatively avoids pseudoreplication if chick number or number of observations were used as the sample size. Environmental quality was treated as a three-level ordered categorical variable, and brood reduction strategy as a two-level categorical factor. We obtained phylogenies from Birdtree.org, and models were run on 100 random phylogenetic trees with Ericson and Hackett backbones, and then averaged⁴⁷. Analyses were run separately for each relationship.

Forest plots and species-level analyses were conducted with the metafor package in R^{45,48}. We assessed the heterogeneity of our data using I^2 , which is a descriptive measure of the proportion of observed variance that reflects true differences in correlation coefficients^{41,49,50}. Results related to heterogeneity and random effects can be found in Supplementary Tables 6–7. Example R code can be found in Supplementary Note 1 or requested from authors. We used ASReml analyses to confirm the results of our meta-analysis (Supplementary Methods; Supplementary Table 8)^{51–53}.

Tests for publication bias. Although we did not expect to find one true effect size across all studies and species⁴¹, we tested our meta-analysis for publication bias using the regression test for funnel plot asymmetry (Egger’s test) in the ‘metafor’ package in R⁴⁸. We calculated the average effect size per study and compared it with its variance to determine whether studies with smaller sample sizes were more likely to show extreme effects. We found no evidence of publication bias in the relationships between: (1) offspring condition and begging ($z = 0.54$, $P = 0.59$); (2) offspring condition and structural signals ($z = 0.93$, $P = 0.35$); (3) feeding and begging ($z = -0.49$, $P = 0.63$); (4) feeding and structural signals ($z = 0.91$, $P = 0.36$); and (5) feeding and body size cues ($z = -1.59$, $P = 0.11$).

Tests for confounding methodological factors. We recorded additional information on study methodology for each effect size, including the following: the sample size (number of broods) of that measurement; the type of begging variable (three-level factor: whether or not begging occurred; any continuous intensity measure (for example, duration, amplitude and posture); hunger treatment: experimentally deprived or satiated, with the assumption that hungry chicks beg more); the type of feeding variable (four-level factor: whether or not feeding occurred; any continuous measure of feeding (feeding rate or weight of food received); growth of mass or body structures (tarsus and primary feather), either rate or final size attained, with the assumption that growth rates reflect feeding rates at least in part; and mortality risk before fledging, with the assumption that mortality rates reflect feeding rates at least in part. Nestlings typically died of starvation. Predation risk was excluded as much as possible by considering only partial brood losses); the type of long-term condition variable (five-level factor: health, rank, weight, condition and long-term changes to food intake); whether the offspring contrast was dichotomous (bigger versus smaller) or continuous

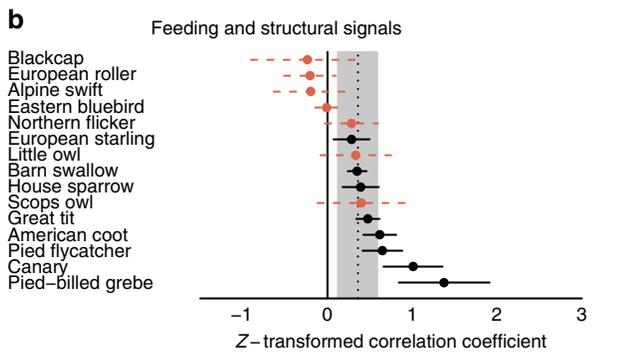
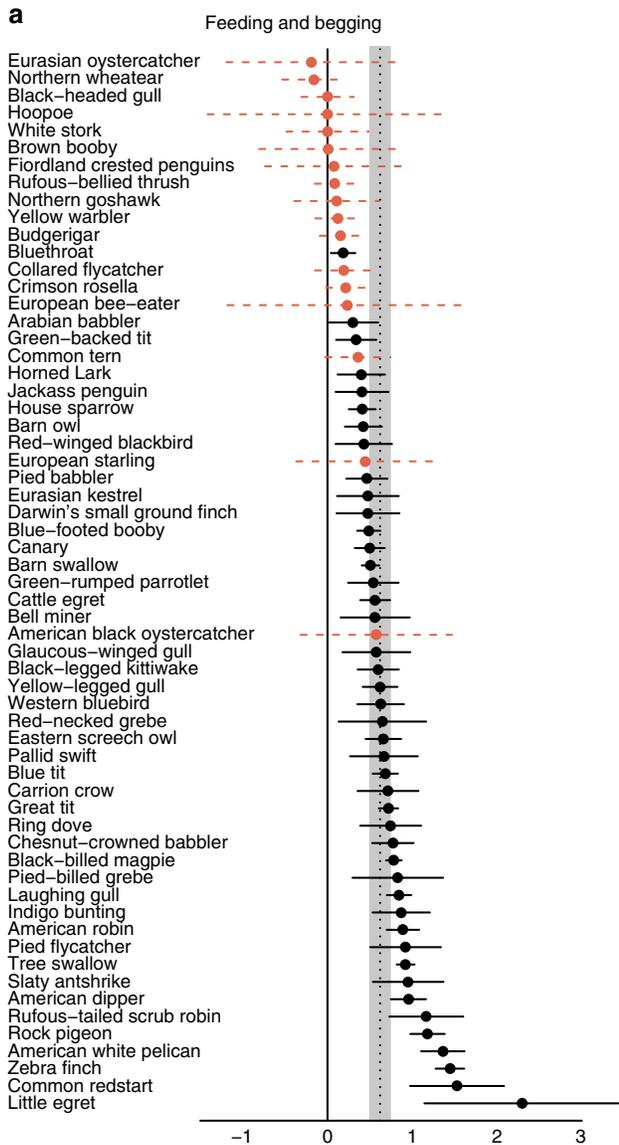


Figure 6 | Variation in parental responsiveness to offspring signals across species. Circles represent species' mean z-transformed correlation coefficient between feeding and (a) begging ($N = 61$ species), and (b) structural signals ($N = 15$ species). The grand mean and 95% credible interval (CI) are denoted by the shaded bar. Black, solid lines indicate chicks that signal more and are preferentially fed more. Red, dashed lines indicate no effect of signals on feeding. Lines show 95% CI ($\pm \text{s.e.} \times t_{\text{critical}}$). s.e. was estimated from the pooled number of broods across all studies.

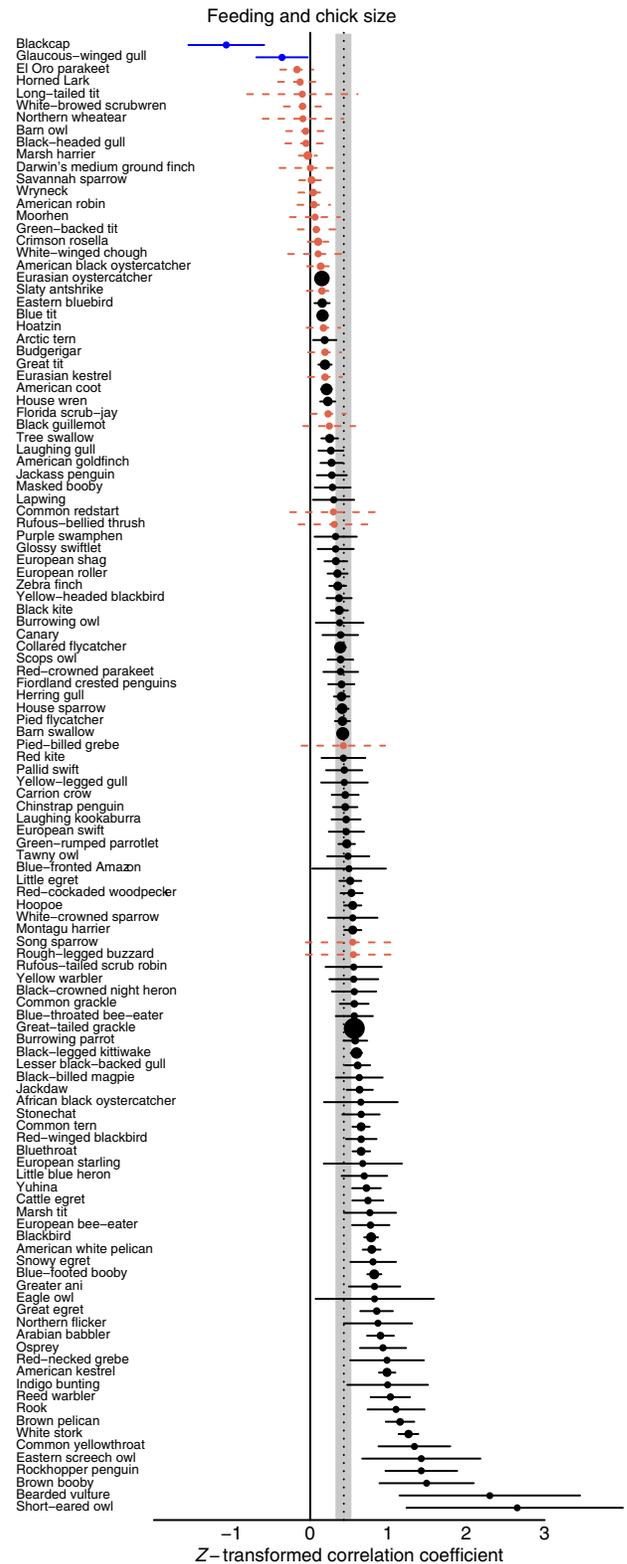


Figure 7 | Variation in parental responsiveness to offspring size across species. Circles represent species' mean z-transformed correlation coefficient between feeding and chick body size ($N = 120$ species). The grand mean and 95% credible interval (CI) are denoted by the shaded bar. Black, solid lines indicate chicks that signal more and are preferentially fed more. Red, dashed lines indicate no effect of signals on feeding. Lines show 95% CI ($\pm \text{s.e.} \times t_{\text{critical}}$). s.e. was estimated from the pooled number of broods across all studies.

(all offspring included); whether the female, male, both sexes combined or a helper was the responder (four-level factor); and whether the data were experimental or observational (two-level factor). Not all study methodology variables were relevant for all aspects of this communication system. Analyses of potential confounding factors were only run if at least two factor levels had at least 10 effect sizes.

No methodological factors had an impact on any of the five relationships tested in this communication system (MCMCglmm phylogenetically controlled and weighted regression: $pMCMC > 0.05$). The 95% credible intervals of the correlation coefficients for each methodological factor are presented in Supplementary Tables 1–5.

Because measures of feeding preference such as mortality and growth rate may be partially confounded by how we classified environmental predictability, we ran models excluding all effect sizes generated using these measures. There was no change in the significance of results for any parental responsiveness model, despite a reduction in sample size of 50 species. In the model of how much parents feed their offspring in response to size cues, the slope for environmental quality changed from -0.14 ($pMCMC < 0.0002$) to -0.25 ($pMCMC = 0.005$), and the difference between brood reducing and whole-brood survival changed from -0.30 ($pMCMC = 0.006$) to -0.26 ($pMCMC = 0.018$). In the model of how much parents feed their offspring in response to begging, the slope for environmental quality changed from 0.35 ($pMCMC = 0.01$) to 0.34 ($pMCMC = 0.01$). In the model of how much parents feed their offspring in response to structural signals, the slope for environmental quality did not change, the difference between brood reducing and whole-brood survival changed from -0.45 ($pMCMC = 0.09$) to -0.46 ($pMCMC = 0.06$), and the interaction from 0.61 ($pMCMC = 0.09$) to 0.58 ($pMCMC = 0.10$).

Heterogeneity. We measured the heterogeneity in our data set with I^2 , the proportion of observed variance due to true differences in effect sizes, rather than measurement errors (Supplementary Table 6)^{41,49,50}. Total I^2 was calculated by dividing the summed variance attributed to phylogeny, species, study and units by the overall variance observed in the data (variance attributed to measurement error, phylogeny, species, study and units). Higher values of I^2 indicate that more of the observed variance is true rather than due to measurement error, with 25%, 50% and 75% as low, moderate and high benchmarks, respectively^{41,49}.

I^2 describes the amount of true heterogeneity seen, but these results should be interpreted with caution. I^2 is independent of the absolute value of the variance observed, which is good because it does not vary based on the scale or number of studies included in the meta-analysis⁴¹. However, this measure does not take into account the dispersion of effect sizes, only the precision with which effect sizes were measured⁵. Thus, identical I^2 values could be obtained even if the between-species variance differed by an order of magnitude⁴¹. If the true effect size for each species or study is spread over a wide range, I^2 cannot capture this dispersion.

References

- Peterson, C. C., Nagy, K. A. & Diamond, J. Sustained metabolic scope. *Proc. Natl Acad. Sci. USA* **87**, 2324–2328 (1990).
- Wright, J. & Leonard, M. L. *The Evolution of Begging: Competition, Cooperation and Communication* (Springer Science & Business Media, 2002).
- Mock, D. W., Dugas, M. B. & Strickler, S. A. Honest begging: expanding from Signal of Need. *Behav. Ecol.* **22**, 909–917 (2011).
- Hinde, C. A. & Godfray, H. C. J. Quality, need, or hunger; begging the question. *Behav. Ecol.* **22**, 1147–1148 (2011).
- Johnstone, R. A. & Kilner, R. M. New labels for old whines. *Behav. Ecol.* **22**, 918–919 (2011).
- Wright, J. Honest begging: signals of need, quality, and/or hunger? *Behav. Ecol.* **22**, 920–921 (2011).
- Koelliker, M. On the meaning of hunger and behavioral control in the evolution of honest begging. *Behav. Ecol.* **22**, 919–920 (2011).
- Davis, J. N., Todd, P. M. & Bullock, S. Environment quality predicts parental provisioning decisions. *Proc. Biol. Sci.* **266**, 1791–1797 (1999).
- Kilner, R. & Johnstone, R. A. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol. Evol.* **12**, 11–15 (1997).
- Leonard, M. L. & Horn, A. G. Begging calls and parental feeding decisions in tree swallows (*Tachycineta bicolor*). *Behav. Ecol. Sociobiol.* **49**, 170–175 (2001).
- Leonard, M. & Horn, A. Provisioning rules in tree swallows. *Behav. Ecol. Sociobiol.* **38**, 341–347 (1996).
- Martin-Vivaldi, M., Palomino, J. J., Soler, M. & Soler, J. J. Determinants of reproductive success in the Hoopoe *Upupa epops*, a hole-nesting non-passerine bird with asynchronous hatching. *Bird Study* **46**, 205–216 (1999).
- Drummond, H. & Garcia Chavelas, C. Food shortage influences sibling aggression in the blue-footed booby. *Anim. Behav.* **37**, 806–819 (1989).
- Godfray, H. C. J. Signalling of need by offspring to their parents. *Nature* **352**, 328–330 (1991).
- Godfray, H. Signaling of need between parents and young - parent-offspring conflict and sibling rivalry. *Am. Nat.* **146**, 1–24 (1995).
- Johnstone, R. A. Begging and sibling competition: how should offspring respond to their rivals? *Am. Nat.* **163**, 388–406 (2004).
- Godfray, H. C. J. & Johnstone, R. A. Begging and bleating: the evolution of parent-offspring signalling. *Philos. Trans. R. Soc. B Biol. Sci.* **355**, 1581–1591 (2000).
- Mock, D. W. & Parker, G. A. *The Evolution of Sibling Rivalry* (Oxford Univ. Press, 1997).
- Cotton, P. A., Wright, J. & Kacelnik, A. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. *Am. Nat.* **153**, 412–420 (1999).
- Grafen, A. Biological signals as handicaps. *J. Theor. Biol.* **144**, 517–546 (1990).
- Royle, N. J., Hartley, I. R. & Parker, G. A. Begging for control: when are offspring solicitation behaviours honest? *Trends Ecol. Evol.* **17**, 434–440 (2002).
- Johnstone, R. A. Honest advertisement of multiple qualities using multiple signals. *J. Theor. Biol.* **177**, 87–94 (1995).
- Fawcett, T. W. & Johnstone, R. A. Optimal assessment of multiple cues. *Proc. Biol. Sci.* **270**, 1637–1643 (2003).
- Bro-Jørgensen, J. Dynamics of multiple signalling systems: animal communication in a world in flux. *Trends Ecol. Evol.* **25**, 292–300 (2010).
- Grodzinski, U. & Johnstone, R. A. Parents and offspring in an evolutionary game: the effect of supply on demand when costs of care vary. *Proc. Biol. Sci.* **279**, 109–115 (2012).
- Forbes, L. S. & Ydenberg, R. C. Sibling rivalry in a variable environment. *Theor. Popul. Biol.* **41**, 135–160 (1992).
- Lack, D. *The Natural Regulation of Animal Numbers* (Clarendon Press, 1954).
- Stoleson, S. H. & Beissinger, S. R. in *Current Ornithology* (ed. Power, D. M.) 191–270 (Plenum Press, 1995).
- Magrath, R. D. Hatching asynchrony in altricial birds. *Biol. Rev. Camb. Philos. Soc.* **65**, 587–622 (1990).
- Lockie, J. D. The breeding habits and food of short-eared owls after a vole plague. *Bird Study* **2**, 53–69 (1955).
- Mondloch, C. Chick hunger and begging affect parental allocation of feedings in pigeons. *Anim. Behav.* **49**, 601–613 (1995).
- Price, K., Harvey, H. & Ydenberg, R. Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Anim. Behav.* **51**, 421–435 (1996).
- McGraw, K. J. & Hill, G. E. Mechanics of carotenoid-based coloration. *Bird coloration* **1**, 177–242 (2006).
- Kilner, R. Mouth colour is a reliable signal of need in begging canary nestlings. *Proc. Biol. Sci.* **264**, 963–968 (1997).
- Saino, N., Incagli, M., Martinelli, R., Ambrosini, R. & Møller, A. P. Immunity, growth and begging behaviour of nestling Barn Swallows *Hirundo rustica* in relation to hatching order. *J. Avian Biol.* **32**, 263–270 (2001).
- Rodriguez-Girones, M. A., Cotton, P. A. & Kacelnik, A. The evolution of begging: Signaling and sibling competition. *Proc. Natl Acad. Sci. USA* **93**, 14637–14641 (1996).
- Parker, G. A., Royle, N. J. & Hartley, I. R. Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecol. Lett.* **5**, 206–215 (2002).
- Thorogood, R., Ewen, J. G. & Kilner, R. M. Sense and sensitivity: responsiveness to offspring signals varies with the parents' potential to breed again. *Proc. Biol. Sci.* **278**, 2638–2645 (2011).
- Bize, P., Pialut, R., Moureau, B. & Heeb, P. A UV signal of offspring condition mediates context-dependent parental favouritism. *Proc. Biol. Sci.* **273**, 2063–2068 (2006).
- Wells, J. C. Parent-offspring conflict theory, signaling of need, and weight gain in early life. *Q. Rev. Biol.* **78**, 169–202 (2003).
- Borenstein, M., Hedges, L. V., Higgins, J. P. T. & Rothstein, H. R. *Introduction to Meta-Analysis* (John Wiley & Sons, 2011).
- Grissom, R. J. & Kim, J. J. *Effect Sizes for Research: Univariate and Multivariate Applications*. 2nd ed. (Taylor & Francis, 2011).
- Koricheva, J., Gurevitch, J. & Mengersen, K. *Handbook of Meta-analysis in Ecology and Evolution* (Princeton Univ. Press, 2013).
- Nakagawa, S. & Schielzeth, H. A general and simple method for obtaining R^2 from generalized linear mixed-effects models. *Methods Ecol. Evol.* **4**, 133–142 (2013).
- R Core Team. *R: A Language and Environment For Statistical Computing* (R Foundation for Statistical Computing, 2013).
- Hadfield, J. D. MCMC methods for multi-response generalized linear mixed models: the MCMCglmm R Package. *J. Stat. Software* **33**, 1–22 (2010).
- Jetz, W. *et al.* Global distribution and conservation of evolutionary distinctness in birds. *Curr. Biol.* **24**, 919–930 (2014).
- Viechtbauer, W. Conducting Meta-Analyses in R with the metafor Package. *J. Stat. Software* **36**, 1–48 (2010).
- Higgins, J., Thompson, S. G., Deeks, J. J. & Altman, D. G. Measuring inconsistency in meta-analyses. *BMJ* **327**, 557–560 (2003).
- Nakagawa, S. & Santos, E. S. A. Methodological issues and advances in biological meta-analysis. *Ecol. Evol.* **26**, 1253–1274 (2012).

51. Butler, D., Cullis, B., Gilmour, A. & Gogel, B. *ASReml-R Reference Manual* (VSN International Ltd., 2009).
52. Hadfield, J. D., Krasnov, B. R., Poulin, R. & Nakagawa, S. A tale of two phylogenies: comparative analyses of ecological interactions. *Am. Nat.* **183**, 174–187 (2014).
53. Lee, S.-Y. & Song, X.-Y. Evaluation of the Bayesian and maximum likelihood approaches in analyzing structural equation models with small sample sizes. *Multivariate Behav. Res.* **39**, 653–686 (2004).

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Author contributions

All authors designed the study. S.M.C. conducted the meta-analysis and wrote the first draft. S.M.C., A.S.G. and S.A.W. wrote the manuscript. All authors discussed the manuscript.

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Sibling conflict and dishonest signaling in birds

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Offspring survival can often depend on successful communication with parents about their state of need. Theory suggests that offspring will be less likely to honestly signal their need when they experience greater competition from either a greater number of nestmates or less-related nestmates. We found support for this hypothesis with a comparative analysis, examining data from across 60 species of birds. We found that offspring are less honest about their level of need when (i) they face competition from current siblings; (ii) their parents are likely to breed again, and so they are in competition with future siblings; and (iii) parental divorce or death means that they are likely to be less related to future siblings. More generally, these patterns highlight the sensitivity of communication systems to conflict between signaler and receiver while also suggesting that when there is little conflict, natural selection favors the honest.

parent-offspring communication | signaling | begging | parent-offspring conflict | meta-analysis

In almost every species where offspring live with their parents in family groups, they beg or signal to their parents for food (1, 2). Evolutionary theory suggests that signaling between offspring and their parents will evolve in response to the environment. At one extreme, if parents have enough resources to rear all their offspring, then offspring can be selected to honestly signal their need for food, so the offspring in the worst condition is fed (1–8). At the other extreme, if parents only have enough resources to rear one offspring, then offspring can be selected to competitively signal their quality or scramble for food, so the offspring in the best condition is fed (7–14). Empirical data support these predictions: offspring appear more likely to signal need when resources are relatively plentiful and quality when resources are scarce (15).

Theory also provides an understanding of when signals of need between offspring and parents are expected to break down or become distorted. If the self-interest of an offspring conflicts sufficiently with the interests of its parents, then it can be selected to exaggerate its need (4–7, 11, 13, 16–20). Increased competition between siblings can disrupt the alignment of interests between parents and their offspring. Competition between siblings can reduce the benefit of allowing needier siblings to be fed, selecting for each offspring to try to maximize its own share of parental resources, such that honest signaling of need is not stable. Both increased numbers of siblings and lower relatedness between those siblings could lead to greater sibling competition (4–6, 11, 13, 14, 16–20). Competition between siblings could also lead to exaggerated and dishonest signals of need, rather than the complete collapse of honest signaling (16). However, there is a lack of consistent empirical evidence demonstrating that sibling competition leads to either the breakdown of honest signaling or less honest signals (7, 21–33). One problem is that these hypotheses can be hard to test within a single species, where there may not be sufficient variation in offspring number and relatedness.

We exploited the variation in breeding behavior across birds to test whether offspring beg less honestly in species where there is greater competition between siblings. We estimated the honesty of offspring signals by calculating the strength of the relationship (correlation coefficient) between signals and long-term condition (Fig. S1) (34–37). “Condition,” “need,” and “quality” refer to the

ultimate fitness effects of receiving additional food; our measures of long-term condition (body condition, health, rank within the brood and long-term food intake) therefore reflect the total requirement for food to improve overall quality before fledging and are likely to reflect both cryptic and public aspects of condition (*SI Materials and Methods*) (3, 4, 7, 9, 24, 38, 39). An advantage of focusing on the correlation between signaling and condition is that correlation coefficients are less likely to be influenced by nonsocial differences between species, such as body size, which can affect absolute measures of begging intensity, such as call volume (34). Our hypotheses were based on signal-of-need models (4–6, 11, 13, 14, 17–20), and so we first analyzed behavioral signals, such as begging calls and postures, which are more likely to be signals of need (15). We then analyzed structural signals, such as mouth color, which are more likely to be signals of quality (15).

Results and Discussion

We compared the strength of species’ correlation coefficients (effect sizes) between begging intensity and long-term need using phylogeny-based, linear mixed models, which were weighted by study sample size (34, 40, 41). A positive effect size indicates that offspring in worse condition beg more and therefore are more honestly signaling their need (37). Larger positive effect sizes suggest a clearer, more honest signal of need. In contrast, an effect size of zero indicates no correlation with begging intensity, such that begging provides no honest information about long-term need. A negative correlation indicates that offspring with less need beg more intensely.

Honesty and Sibling Rivalry. We first tested whether sibling conflict leads to less honest signaling. We estimated the effect of competition by dividing species into two categories: “siblings present” and “siblings always absent” (42). This categorization

Significance

Should a chick beg for food even if it isn’t struggling to grow? Does it have anything to lose? The answer could be “yes” if it risks losing indirect fitness through the starvation of siblings. Evolutionary theory suggests that offspring may be more likely to exaggerate signals of need when they compete with less-related nestmates or a greater number of nestmates. We found clear support for this hypothesis in an analysis across 60 bird species. Offspring begging was less reliable in species where parents produce larger broods and more broods and where parental divorce or death reduces between-brood relatedness. This result helps explain why chicks of some species are more honest than others and tests general predictions of signaling theory.

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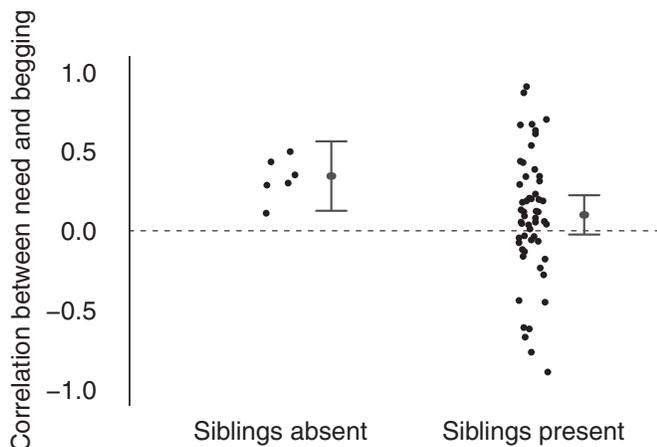


Fig. 1. The presence of siblings is associated with a reduction in offspring honesty. Data points represent species' mean correlation coefficients of long-term need and begging intensity for species where parents rear only one ($n = 6$ species) or more than one offspring per brood ($n = 54$ species). Positive correlations indicate that offspring in worse condition beg more intensely, providing honest information about need. Gray lines represent the 95% CIs from the model, run on the full dataset, controlling for phylogeny and repeated measures. Species with siblings present have a weaker correlation between need and begging, suggesting less honest signaling of need (Wald = 6.69, $P = 0.0097$).

represents a true biological distinction, because some species of birds obligately lay only one egg per breeding attempt (42). Theory suggests that the difference between brood sizes of one and two will be substantially large, going from no to appreciable sibling competition (3, 4). Consistent with this, we found that the presence of siblings is correlated with less honest offspring: the relationship between need and begging is weaker in species with multiple offspring per brood (mean Wald statistic = 6.69, $P = 0.0097$,

$n = 60$ species; Fig. 1 and Table 1, model 1). Offspring in worse condition beg more intensely in species where offspring never interact with siblings (95% CI of the correlation coefficient = 0.13–0.56, $P = 0.0055$) than in species where siblings compete for food (95% CI = -0.02 to 0.22, $P = 0.075$). Phylogeny did not influence how honest offspring are (Table S1).

We then examined whether increasing intensity of sibling competition led to a corresponding decrease in honesty using data on average brood size. The intensity of within-family conflict may increase as more offspring compete for food in bigger broods, and this conflict could favor exaggerated signals of need (13, 17, 18). For instance, offspring sharing a nest with ten siblings may experience more intense competition than those with only one sibling. It has also been suggested that parent-offspring communication can be affected in more complicated ways in larger broods, with only offspring in the most need selected to invest in costly signaling (18, 43, 44). We found that the strength of the correlation between need and begging was lower in species with larger brood sizes: offspring with more siblings are less honest with their parents about their level of need (mean Wald statistic = 4.57, $P = 0.033$; Table 1, model 2).

We might expect to see similar patterns within species that exhibit consistent variation in the intensity of sibling competition if individuals can assess the relative intensity of competition from siblings in their environment. Consistent with this, offspring of several species have been found to adjust their level of begging facultatively: American robins (21), great tits (30), tree swallows (27–29), and yellow-headed blackbirds (24, 45) all escalate their begging intensity when competing against more or needier nestmates. In contrast, barn swallows (33) and black-headed gulls (31) show the opposite pattern, reducing their begging intensity when faced with more or needier nestmates, and European starling offspring do not change how they beg at all based on the begging of their nestmates (25, 26). These discrepancies may be due to biological differences between species,

Table 1. Results for all models: fixed effects

Model no.	Fixed effects	Results	<i>N</i> species	<i>N</i> study	<i>N</i> observations
1	Siblings present y/n	$F_{1,71.8} = 6.69, P = 0.0097$	60	108	336
2	Brood size	$F_{1,31.0} = 4.57, P = 0.033$			
3	Siblings present y/n	$F_{1,67.0} = 8.45, P = 0.0050$	51	98	317
	<i>No. of future broods possible</i>	$F_{1,87.9} = 3.13, P = 0.080$			
4	Brood size	$F_{1,82.2} = 11.87, P = 0.0009$			
	No. of future broods possible	$F_{1,83.5} = 7.22, P = 0.0087$			
5	Siblings present y/n	$F_{1,84.2} = 0.42, P = 0.42$	49	96	314
	No. of future broods possible	$F_{1,95.4} = 9.39, P = 0.0028$			
	Full vs. half siblings likelihood	$F_{1,112.5} = 6.94, P = 0.0096$			
6	<i>Brood size</i>	$F_{1,87.1} = 3.07, P = 0.083$			
	No. of future broods possible	$F_{1,86.4} = 13.09, P = 0.0005$			
	Full vs. half siblings likelihood	$F_{1,89.6} = 5.98, P = 0.016$			
7	Siblings present y/n	$F_{1,60.5} = 0, P = 1$	31	68	230
	<i>No. of future broods possible</i>	$F_{1,58.4} = 3.10, P = 0.083$			
	<i>Full vs. half siblings likelihood</i>	$F_{1,76.0} = 3.77, P = 0.056$			
	Extrapair paternity	$F_{1,58.5} = 0.04, P = 0.84$			
8	<i>Brood size</i>	$F_{1,66.2} = 3.87, P = 0.053$			
	No. of future broods possible	$F_{1,58.3} = 4.94, P = 0.038$			
	<i>Full vs. half siblings likelihood</i>	$F_{1,67.1} = 1.00, P = 0.32$			
	Extrapair paternity	$F_{1,58.5} = 0.27, P = 0.61$			

Mean results (conditional Wald statistics) of 500 ASReml linear mixed models. Models controlled for phylogeny, repeated measures on studies, and species, and were weighted by study sample size (the number of broods used to calculate the original test statistic). Fixed effects in bold are significant at the $P < 0.05$ level and in italics at the $P < 0.10$ level. Models are grouped by the dataset used for analysis, as sample size decreased in later analyses due to unavailable life history data.

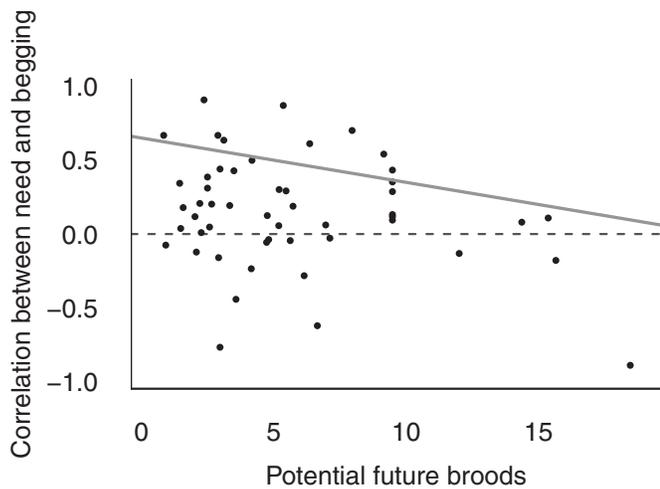


Fig. 2. Conflict with future siblings is associated with a reduction in offspring honesty. Data points show species' mean correlation coefficient of long-term need and begging intensity. The number of potential future broods is the adult life expectancy multiplied by the number of successful broods that can be reared each breeding season ($n = 51$ species). The gray line is the regression coefficient from the model, run on the full dataset, controlling for phylogeny and repeated measures. Positive correlations indicate that offspring in worse condition beg more intensely, providing honest information about need. The dashed line at zero indicates no relationship between condition and begging. The correlation between need and begging is weaker in species where parents can potentially produce more broods over their lifetimes (Wald = 7.22, $P = 0.0087$), suggesting that future reproduction selects for less honest signaling of need.

particularly whether parents or offspring control offspring food distribution (18, 25). For instance, in black-headed gulls, parents regurgitate food to the nest floor, rather than distributing it, and so offspring completely determine food distribution (31). Because offspring control food distribution, they do not fit the assumptions of standard signal-of-need models; instead, theory predicts that offspring in better condition are selected to decrease, rather than increase, begging when their needier siblings beg more (18).

Honesty and Future Siblings. Parental investment is not only shared within a brood, but also between broods produced throughout a parent's lifetime. Therefore, unborn siblings, which may potentially exist in the future, could potentially impact the honesty of signaling between current offspring and their parents. If parents are saving resources for future breeding attempts, then this could make them less responsive to their current brood's begging, and hence select for their offspring to exaggerate their signals (3, 6, 46, 47). We estimated conflict with future siblings from the relative number of potential future breeding attempts: adult life expectancy multiplied by the maximum number of successful broods parents can raise each year. These data were available for 51 of the 60 species in our dataset, and we controlled for current sibling competition (brood size) in these analyses.

As we predicted, offspring were less honest with parents in species where offspring compete against more future siblings. The correlation between begging and need was significantly lower in species where parents can rear more broods over their lifetime (mean Wald statistic = 7.22, $P = 0.0087$; Fig. 2 and Table 1, model 4), and species with larger broods (mean Wald statistic = 11.87, $P = 0.0009$). Offspring compete with both their current and future siblings for resources by manipulating parental behavior through their begging. Overall, our analysis suggests that the honesty of offspring signaling varies in response to how parental investment is distributed over the parents' lifetime.

We might also expect to see individuals adjusting their behavior conditionally in response to variation in the likelihood of competition with future siblings. For example, offspring born to younger parents, with greater reproductive potential, might make less reliable signals than offspring that represent a parents' terminal investment (48). Previous studies within species that produce multiple broods in a season have found such patterns. For example, European starlings can lay two broods per year, and offspring only signal need honestly if they are in the second brood, when parents cannot lay another brood (49). Hihi bird parents' response to offspring signals in their first brood decreases if their likelihood of breeding again is experimentally increased (50).

Honesty and Relatedness to Siblings. When relatedness is lower between offspring sharing the same parent or parents, there will be stronger selection to monopolize parental investment and weaker selection on higher-quality offspring to show restraint in begging for food (3–7, 13, 18–20, 47). The survival of unrelated nestmates or brood fails to enhance the inclusive fitness of a focal offspring. Consequently, we predict that decreased relatedness between offspring will lead to less honest signaling of need. We examined the consequences of two factors that can reduce relatedness within families: (i) parents breeding with different partners, such that all future broods can only contain half (genetic relatedness, $r = 0.25$), rather than full ($r = 0.50$), siblings; and (ii) parents being promiscuous, such that some brood-mates are only half siblings.

We determined the likelihood of parents changing breeding partners by combining the rates of mortality and divorce. Divorce is the rate at which pairs mate with different partners when both original partners are still present in the population (51). In nine species where data on divorce rates were unavailable, we used mating system (lifetime vs. seasonal monogamy) to estimate the likelihood that parents will breed together again. Because the divorce rate was estimated in some cases, we binned species

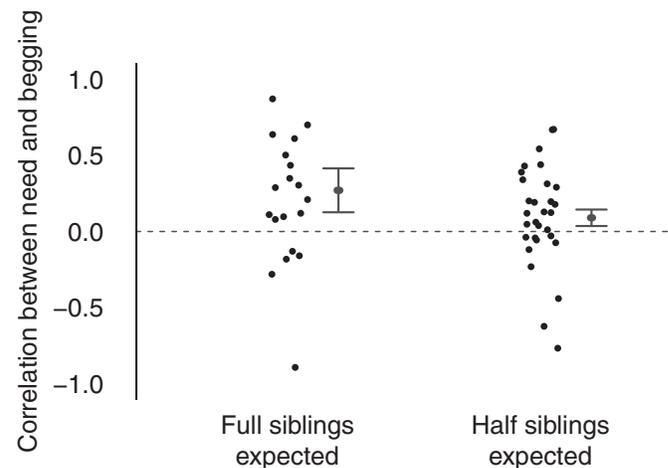


Fig. 3. Parental divorce and death is associated with a reduction in offspring honesty. Data points represent species' mean correlation coefficients of long-term need and begging intensity for species. We divided species by whether there is a higher or lower than 50% chance that parents will breed together again in the next year, based on survival and divorce rates ($n = 19$ species where full siblings are expected; $n = 30$ species where half siblings are expected). Positive correlations indicate that offspring in worse condition beg more intensely, providing honest information about need. Gray lines represent the 95% CIs from our analyses. The correlation between need and begging is weaker in species with higher rates of divorce and lower rates of survival, where half siblings are expected (Wald = 5.98, $P = 0.016$), suggesting less honest signaling of need.

according to whether pairs had a higher or lower than 50% chance of breeding together again. Data on the likelihood of breeding together again were available for 49 of the 60 species in our original data set, and so we carried out analyses on this subset, controlling for the number of current and future siblings.

Offspring whose parents are unlikely to breed together again, through either death or divorce, are significantly less honest with their parents (mean Wald statistic = 5.98, $P = 0.016$; Fig. 3 and Table 1, model 6). The number of potential future siblings predicts species' honesty in this model as well (Wald statistic = 13.09, $P = 0.0005$), but brood size was no longer significant, perhaps due to the reduction in sample size (Wald statistic = 3.07, $P = 0.083$). Overall, this suggests that an increased conflict of interest, due to lower relatedness between siblings, favors less honest signaling.

We next looked at whether variation in within-brood relatedness due to promiscuity also impacts offspring honesty (3–6, 18–20). We used the percentage of broods with at least one extrapair offspring as our measure of promiscuity. These data were available for only 31 of the species in our dataset, and so we ran our analyses on this subset, controlling for the number of current and future siblings and the likelihood that parents will breed together again. We did not find an effect of extrapair paternity (mean Wald statistic = 0.27, $P = 0.61$; Table 1, model 8). Of the control variables, only the number of future broods remained significant in this model, again potentially because we are examining a much smaller data set (mean Wald statistic = 4.94, $P = 0.038$).

A possible explanation for a lack of a significant influence of promiscuity is that it selects relatively weakly on honesty. The likelihood that parents will breed together again could be a more consistent and reliable predictor of relatedness: although extrapair paternity may reduce relatedness to a proportion of nestmates, divorce or death means that all future offspring produced by a mother or a father must be half siblings ($r \leq 0.25$). However, an experimental study on barn swallows found that offspring were less honest about their hunger when their nestmates were nonrelatives (52), and a previous comparative study on 11 species found that absolute begging intensity was significantly correlated with promiscuity, as would be expected if lower relatedness led to escalation in begging (22). This discrepancy may be because we assessed changes in honesty, rather than changes in absolute begging levels. Another possible reason we did not see an effect of promiscuity is that the influence of sibling number could obscure the influence of relatedness to those siblings. Specifically, species with larger broods may be less honest, irrespective of how many of those nestmates are half siblings (Fig. S2). This effect of brood size is a specific case of the more general point that local competition can reduce the importance of relatedness between interacting individuals (53).

Ecology and Life History. Our above analyses explored the link between life history variables and signal honesty. Previous analyses have suggested that environmental quality and environmental predictability can also influence the extent to which offspring signal need (15). If these environmental variables covary with sibling number or relatedness, our results could have been driven purely by environmental variation. We tested whether environmental quality and predictability confounded our results in two ways: by assessing their relationship with life history traits (Table S2) and by comparing models with and without these variables (Table S3). We found no relationships between life history traits and environmental quality/predictability in our dataset, except for the presence/absence of siblings (Table S2). The obligate absence of siblings was nested within the “predictable” level of environmental predictability, and so this relationship was unavoidable. Models that included both environmental predictability and the presence/absence of siblings had somewhat variable results, as expected if these factors are

partially collinear (models 1, 3, 5 and 7; Table S3). However, when we used brood size, rather than the presence/absence of siblings, the coefficients of fixed effects were equivalent across models, and both environmental factors and life history traits generally remained significant (models 2, 4, 6 and 8; Table S3). This result suggests that both life history and ecology influence parent-offspring communication.

Signaling Theory and Empirical Data. The hypotheses tested here are based on existing theory that examines the conditions required for the evolutionary stability of honest signaling of need (3–6, 11, 13, 16–20). These previous models tend to predict that honest signaling is either stable or not, rather than a continuum of more gradual shifts between these extremes (43). In contrast, the empirical data show much more gradual variation, with a wide range of correlation coefficients between condition and signaling (Figs. 1–3). Our extrapolation is to take predictions for when stable signaling is or is not favored (extremes) and use them to make predictions about how honest signaling should be (variation across intermediates). This mismatch between the predictions of theoretical models (extremes), and the patterns observed empirically (intermediates) has previously been analyzed in the context of sex allocation. Sex allocation represents a much simpler game theoretic case, where it was found that by increasing biological complexity, models were able to move from the prediction of extremes (all or nothing) to the prediction of more gradual and realistic variation (54, 55). We suggest that increased biological complexity could similarly lead to the prediction of more gradual shifts in signaling models, and further theory is clearly required to examine the evolutionary stability of intermediate levels of honesty (16). Another complication is that many signaling models predict multiple possible equilibria (56) without distinguishing which of the possible equilibria natural

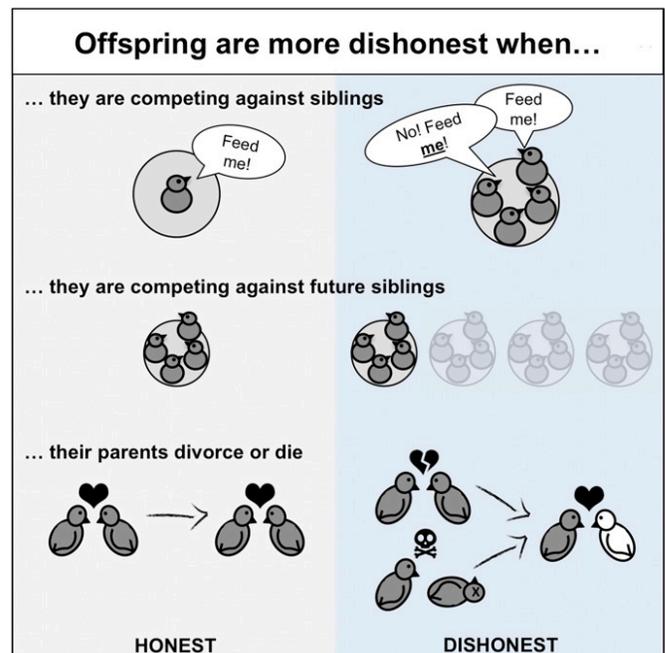


Fig. 4. Family conflict is associated with a reduction in the honesty of offspring signals of need. Offspring in species with siblings present are less honest when signaling need (Wald statistic = 6.69, $P = 0.0097$). The probability that parents will breed again is also associated with more dishonest offspring, as the current brood competes against future broods for parental investment (Wald = 7.22, $P = 0.0087$). Finally, offspring are less honest in species where parents are likely to divorce or die before breeding again, and all future siblings will be half siblings (Wald = 5.98, $P = 0.016$).

selection will lead to (57). There is clearly also a need for signaling theory that can be better linked to the kind of variation in signaling systems that is observed in empirical studies.

Another complication with linking to data to theory is that empirical estimates of need could be unreliable or fail to capture character states in a way that is relevant to theory (7). These errors would, however, be most likely to obscure any underlying biological pattern, and it is unlikely that such error would have produced the patterns we observe. Indeed, by finding patterns in the predicted direction, our results suggest that empirical researchers have successfully managed to capture biologically relevant aspects of condition.

Signals of Quality. Offspring can solicit food using either signals of need or quality, and the same life history traits may influence the evolution of both kinds of signals (1, 2). Our predictions were derived from signal-of-need models, where parents are assumed to have enough food to feed all their offspring and are selected to feed the offspring with the greatest need (1–8). In contrast, when parents do not have enough food to feed all their offspring, they are expected to pay attention to signals of quality and to feed the highest quality offspring (7–14). Consequently, we predict the opposite patterns with signals of quality as those we observed with signals of need. For example, when relatedness is higher, chicks in better condition should reduce their signaling to allow related nestmates in worse condition to be fed. This restraint could create a situation where chicks in worse condition give more intense signals—increasing the correlation between need and signals but decreasing the correlation between quality and signals.

To determine whether signals of quality respond to life history traits, we repeated our above analyses, but examining structural signals, such as mouth size or color, which are more likely to represent measures of quality (15). We could not find an effect of any of our life history traits on structural signals, whether or not environmental factors were included as covariates (Tables S4 and S5). Our null result could be because the evolution of structural signaling is influenced by other factors or because our sample size was too low to identify true effects: we only had data on 18 species and had no data on species without siblings present. More empirical studies on structural signals could help reveal the selection pressures on such signals. Furthermore, theory that explicitly models offspring signals of quality, without the assumption that all offspring will survive, is necessary to generate testable predictions about which life history traits could influence the evolution of signals of quality.

Conclusion

We found support for the prediction that increased conflict between siblings disfavors honest signaling of need from offspring to their parents (Fig. 4). Specifically, offspring are less likely to honestly signal their need when they have more siblings, when their parents are more likely to breed again, and when they are less related to

their future siblings, due to parental divorce or death. These results suggest that siblings that are not even born yet, and, indeed, may never be born, cast a competitive shadow back in time, which selects for exaggerating need to parents. The logical next step would be to explore how parents' response to begging is affected by the same life history factors (6, 49, 50, 58). Longevity and lifetime fecundity have already been shown to influence other aspects of parental care, such as how parents respond to nest predators, with species that have less potential for future reproduction engaging in riskier defense behavior (59). The results of this study suggest that parents within a stable pair-bond may be selected to be the most responsive parents, especially if they produce few offspring.

Materials and Methods

We searched the literature for data relating to the effect of offspring condition on begging intensity, leading to a dataset of 336 test statistics from 108 studies on 60 species of birds (see Fig. S3 for Preferred Reporting Items for Systematic Reviews and Meta-Analyses (PRISMA) flowchart of study selection, Dataset S1 for the data included in the meta-analysis and life history references, and Dataset S2 for a list of excluded studies). We included any reported measures of behavioral begging, such as vocalizations and postures. We also collected data on the effect of condition on structural signals, leading to a dataset of 140 effect sizes from 33 studies on 18 species. We included any reported measures of structural signals, such as mouth color or UV reflectance. We calculated the correlation coefficient between condition and signals to generate a standardized effect size across studies and species (34–37). This coefficient varies between ± 1 , with positive values indicating that offspring in worse condition signal more, and negative values indicating that offspring in better condition signal more. We assumed offspring were dishonest if there was no correlation between condition and signal intensity. We used health, body condition, rank within the brood, and experimental manipulations that affected food intake over multiple days as proxies for long-term condition (*SI Materials and Methods*).

We analyzed differences in honesty across species using ASReml linear mixed models in R that were weighted by sample size and controlled for phylogeny and repeated measures on studies and species (40, 60). We averaged the results of 500 models using different trees to account for uncertainty in the phylogeny, which we obtained from www.Bird.tree.org, with both Ericson and Hackett backbones (61). Results relating to random effects can be found in Table S1. We compared honesty to a variety of relevant life history traits related to sibling completion and relatedness. We estimated current sibling competition in two ways: (i) presence or obligate absence of siblings and (ii) mean brood size of the study population, or species if population data were unavailable. We estimated species-level competition against potential future siblings by multiplying annual adult survival and the maximum number of broods parents can raise each year. We estimated species-level relatedness to siblings in two ways: (i) whether parents have a better than 50–50 chance of mating together again based on mortality and divorce rates, leading to half siblings; and (ii) the percentage of broods with extrapair paternity. We classified environmental predictability and quality following our previous comparative study (15).

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- Wright J, Leonard ML (2002) *The Evolution of Begging: Competition, Cooperation and Communication*, eds Wright J, Leonard ML (Kluwer Academic Publishers, Dordrecht, The Netherlands).
- Bradbury JW, Vehrencamp SL (2011) *Principles of Animal Communication* (Sinauer Associates, Sunderland, MA.), 2nd Ed.
- Godfray HCJ (1991) Signalling of need by offspring to their parents. *Nature* 352:328–330.
- Godfray HCJ (1995) Signaling of need between parents and young: Parent-offspring conflict and sibling rivalry. *Am Nat* 146(1):1–24.
- Godfray HCJ, Johnstone RA (2000) Begging and bleating: The evolution of parent-offspring signalling. *Philos Trans R Soc Lond B Biol Sci* 355(1403):1581–1591.
- Grodzinski U, Johnstone RA (2012) Parents and offspring in an evolutionary game: The effect of supply on demand when costs of care vary. *Proc Biol Sci* 279(1726):109–115.
- Mock DW, Dugas MB, Strickler SA (2011) Honest begging: Expanding from signal of need. *Behav Ecol* 22(5):909–917.
- Moreno-Rueda G, Soler M, Martín-Vivaldi M, Palomino JJ (2009) Brood provisioning rate and food allocation rules according to nestling begging in a clutch—adjusting species, the Rufous-tailed Scrub-robin *Cercotrichas galactotes*. *Acta Ornithol* 44(2):167–175.
- Grafen A (1990) Biological signals as handicaps. *J Theor Biol* 144(4):517–546.
- Davis JN, Todd PM, Bullock S (1999) Environment quality predicts parental provisioning decisions. *Proc Biol Sci* 266(1430):1791–1797.
- Royle NJ, Hartley IR, Parker GA (2002) Begging for control: When are offspring solicitation behaviours honest? *Trends Ecol Evol* 17(9):434–440.
- Mock DW, Parker GA (1997) *The Evolution of Sibling Rivalry* (Oxford Univ Press, Oxford, NY).
- Parker GA, Royle NJ, Hartley IR (2002) Begging scrambles with unequal chicks: Interactions between need and competitive ability. *Ecol Lett* 5(2):206–215.
- Parker GA, Mock DW, Lamey TC (1989) How selfish should stronger sibs be? *Am Nat* 133(6):846.
- Caro SM, Griffin AS, Hinde CA, West SA (2016) Unpredictable environments lead to the evolution of parental neglect in birds. *Nat Commun* 7:10985.
- Johnstone RA, Grafen A (1993) Dishonesty and the handicap principle. *Anim Behav* 46(4):759–764.
- Rodríguez-Girónés MA, Cotton PA, Kacelnik A (1996) The evolution of begging: Signaling and sibling competition. *Proc Natl Acad Sci USA* 93(25):14637–14641.

18. Johnstone RA (2004) Begging and sibling competition: How should offspring respond to their rivals? *Am Nat* 163(3):388–406.
19. Akçay E (2012) Incentives in the family II: Behavioral dynamics and the evolution of non-costly signaling. *J Theor Biol* 294:9–18.
20. Bossan B, Hammerstein P, Koehncke A (2013) We were all young once: An intragenomic perspective on parent-offspring conflict. *Proc Biol Sci* 280(1754):20122637–20122637.
21. Smith HG, Montgomerie R (1991) Nestling American robins compete with siblings by begging. *Behav Ecol Sociobiol* 29(4):307–312.
22. Briskie JV, Naugler CT, Leech SM (1994) Begging intensity of nestling birds varies with sibling relatedness. *Proc Biol Sci* 258(1351):73–78.
23. Price K, Ydenberg R (1995) Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. *Behav Ecol Sociobiol* 37(3):201–208.
24. Price K (1996) Begging as competition for food in yellow-headed blackbirds. *Auk* 113(4):963–967.
25. Kacelnik A, Cotton PA, Stirling L, Wright J (1995) Food allocation among nestling starlings: Sibling competition and the scope of parental choice. *Proc Biol Sci* 259(1356):259–263.
26. Cotton PA, Kacelnik A, Wright J (1996) Chick begging as a signal: Are nestlings honest? *Behav Ecol* 7(2):178–182.
27. Leonard ML, Horn AG (1998) Need and nestmates affect begging in tree swallows. *Behav Ecol Sociobiol* 42(6):431–436.
28. Leonard ML, Horn AG, Gozna A, Ramen S (2000) Brood size and begging intensity in nestling birds. *Behav Ecol* 11(2):196–201.
29. Marques PAM, Leonard ML, Horn AG, Contasti A (2011) How nestling tree swallows (*Tachycineta bicolor*) integrate their responses to hunger and signalling by nestmates. *Ethology* 117(2):163–170.
30. Neuenschwander S, Brinkhof MWG, Kölliker M, Richner H (2003) Brood size, sibling competition, and the cost of begging in great tits (*Parus major*). *Behav Ecol* 14(4):457–462.
31. Mathevon N, Charrier I (2004) Parent-offspring conflict and the coordination of siblings in gulls. *Proc Biol Sci* 271(Suppl. 4):S145–S147.
32. Marques PAM, Marquez R, Vicente L (2006) Brood size and nestling vocal begging behaviour in the Spanish Sparrow *Passer hispaniolensis*. *Ardea* 94(2):203–210.
33. Romano A, Caprioli M, Boncoraglio G, Saino N, Rubolini D (2012) With a little help from my kin: Barn swallow nestlings modulate solicitation of parental care according to nestmates' need. *J Evol Biol* 25(9):1703–1710.
34. Borenstein M, Hedges LV, Higgins JPT, Rothstein HR (2011) *Introduction to Meta-Analysis* (John Wiley & Sons, New York).
35. Koricheva J, Gurevitch J, Mengersen K (2013) *Handbook of Meta-analysis in Ecology and Evolution* (Princeton Univ Press, Princeton).
36. Grissom RJ, Kim JJ (2011) *Effect Sizes for Research: Univariate and Multivariate Applications* (Taylor & Francis, Hoboken, NJ), 2nd Ed.
37. Carazo P, Font E (2014) "Communication breakdown": The evolution of signal unreliability and deception. *Anim Behav* 87(C):17–22.
38. Wells JC (2003) Parent-offspring conflict theory, signaling of need, and weight gain in early life. *Q Rev Biol* 78(2):169–202.
39. Hinde CA, Godfray HCJ (2011) Quality, need, or hunger: Begging the question. *Behav Ecol* 22(6):1147–1148.
40. Butler DG, Cullis BR, Gilmour AR, Gogel BJ (2009) *ASReml-R Reference Manual: Mixed Models for S Language Environments* (DPI&F Publications, Brisbane, Australia).
41. Nakagawa S, Santos ESA (2012) Methodological issues and advances in biological meta-analysis. *Evol Ecol* 26(5):1253–1274.
42. Quillfeldt P (2002) Begging in the absence of sibling competition in Wilson's storm-petrels, *Oceanites oceanicus*. *Anim Behav* 64(4):579–587.
43. Johnstone RA (1999) Signaling of need, sibling competition, and the cost of honesty. *Proc Natl Acad Sci USA* 96(22):12644–12649.
44. Johnstone RA, Roulin A (2003) Sibling negotiation. *Behav Ecol* 14(6):780–786.
45. Price K, Harvey H, Ydenberg R (1996) Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. *Anim Behav* 51(2):421–435.
46. Griffin AS, Alonzo SH, Cornwallis CK (2013) Why do cuckolded males provide paternal care? *PLoS Biol* 11(3):e1001520.
47. Parker GA, Royle NJ, Hartley IR (2002) Intrafamilial conflict and parental investment: A synthesis. *Philos Trans R Soc Lond B Biol Sci* 357(1419):295–307.
48. Stearns SC (1992) *The Evolution of Life Histories* (Oxford Univ Press, Oxford, UK).
49. Bize P, Pialut R, Moureau B, Heeb P (2006) A UV signal of offspring condition mediates context-dependent parental favouritism. *Proc Biol Sci* 273(1597):2063–2068.
50. Thorogood R, Ewen JG, Kilner RM (2011) Sense and sensitivity: Responsiveness to offspring signals varies with the parents' potential to breed again. *Proc Biol Sci* 278(1718):2638–2645.
51. Culina A, Radersma R, Sheldon BC (2015) Trading up: The fitness consequences of divorce in monogamous birds. *Biol Rev Camb Philos Soc* 90(4):1015–1034.
52. Boncoraglio G, Saino N (2008) Barn swallow chicks beg more loudly when broodmates are unrelated. *J Evol Biol* 21(1):256–262.
53. West SA, Pen I, Griffin AS (2002) Cooperation and competition between relatives. *Science* 296(5565):72–75.
54. Wild G, West SA (2007) A sex allocation theory for vertebrates: Combining local resource competition and condition-dependent allocation. *Am Nat* 170(5):E112–E128.
55. West S (2009) *Sex Allocation* (Princeton Univ Press, Princeton).
56. Lachmann M, Bergstrom CT (1998) Signalling among relatives. II. Beyond the tower of Babel. *Theor Popul Biol* 54(2):146–160.
57. Maynard Smith J, Harper D (2003) *Animal Signals* (Oxford Univ Press, New York).
58. Stucki D, Kölliker M (2013) Coevolutionary feedbacks between family interactions and life history. *Evolution* 67(11):3208–3220.
59. Ghalambor CK, Martin TE (2001) Fecundity-survival trade-offs and parental risk-taking in birds. *Science* 292(5516):494–497.
60. R Core Team (2013) R: A language and environment for statistical computing. R Foundation for Statistical Computing. Available at www.R-project.org. Accessed October 1, 2013.
61. Jetz W, et al. (2014) Global distribution and conservation of evolutionary distinctness in birds. *Curr Biol* 24(9):919–930.
62. Nakagawa S, Schielzeth H (2013) A general and simple method for obtaining R2 from generalized linear mixed-effects models. *Methods Ecol Evol* 4(2):133–142.
63. Viechtbauer W (2010) Conducting meta-analyses in R with the metafor package. *J Stat Softw* 36(3):1–48.
64. Wright J, Hinde C, Fazey I, Both C (2002) Begging signals more than just short-term need: Cryptic effects of brood size in the pied flycatcher (*Ficedula hypoleuca*). *Behav Ecol Sociobiol* 52(1):74–83.

Signalling of information that is neither cryptic nor private

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animal communication;
game;
model;
offspring begging;
parental care.

Abstract

It is commonly assumed that in order for animal signals to be advantageous, the information being signalled could not have been obtained otherwise, and is therefore ‘cryptic’ or ‘private’. Here, we suggest a scenario in which individuals can gain an advantage by signalling ‘public’ information that is neither cryptic nor private. In that scenario, signalling increases the efficiency with which that ‘public’ information is transmitted. We formalize our idea with a game in which offspring can signal their condition to their parents. Specifically, we consider a resource-strapped parent who can only invest in one of its two offspring, and we allow offspring the chance to influence parental investment through a signal. A parent in the game seeks to invest in the higher-quality offspring, which it could identify either through a publicly available cue, such as body size, or by relying on a signal provided by the offspring. We find that if the signal can convey information about offspring quality more efficiently than cues, then signalling of condition between offspring and parents can be favoured by selection, even though parents could potentially have acquired the same information from the cue. Our results suggest that the biological function of signals may be broader than currently considered, and provide a scenario where low cost signalling can be favoured. More generally, efficiency benefits could explain signalling across a range of biological and economic scenarios.

Introduction

Animals use signals to communicate information, ranging from their quality as a potential mate to their need for food (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011). Signalling systems are vulnerable to collapse because individuals could potentially signal dishonestly to coerce others in ways that benefit the signaller (Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011). Evolutionary theory has provided solutions to this problem by showing that individuals can be selected to signal honestly for a number of reasons, such as if the signaller and receiver share a common interest, or if dishonest signals are too costly to produce (Zahavi,

1975; Grafen, 1990; Godfray, 1991; Maynard Smith & Harper, 2003; Searcy & Nowicki, 2005; Bradbury & Vehrencamp, 2011). In these cases, signalling can be an evolutionary stable outcome when any potential benefits of signalling dishonestly are outweighed by the costs.

A prevailing explicit assumption in the signalling literature is that in order for signalling to be favoured, the information being signalled could not be obtained otherwise, and is therefore ‘cryptic’ or ‘private’ (e.g. Grafen, 1990; Godfray, 1991; Kilner & Johnstone, 1997; Bergstrom *et al.*, 2002; Johnstone 2004). We challenge this assumption here. Our hypothesis is that individuals can be favoured to signal information that is not cryptic or private, if signalling increases the efficiency with which that information can be transmitted. In order for this hypothesis to hold, it would require that the increase in efficiency outweighs the cost of signalling and that honest (or at least meaningful) signalling is favoured. Our aim was to investigate the theoretical plausibility of this hypothesis.

It is useful to consider our hypothesis in a specific scenario, and so we examine the case of offspring

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signalling their condition to their parents. We pick this scenario because it has been explicitly stated, on numerous occasions, that offspring must be signalling cryptic information (e.g. Godfray, 1991; Kilner & Johnstone, 1997; Johnstone 2004, Royle *et al.*, 2002). We focus on a scenario in which a parent has only enough food to feed one of its two offspring. Parents in this scenario will be favoured to invest in the higher-quality offspring, which they could identify via publicly available cues, such as body size (Lack, 1954; Mock & Parker, 1997; Davis *et al.*, 1999). This kind of scenario is reflected in the biology of bird species like the hoopoe (*Upupa epops*) and blue-footed booby (*Sula nebouxii*), as parents in those species tend to experience brood reduction, and preferentially feed larger, higher-quality, offspring (Drummond & Garcia Chavelas, 1989; Martin-Vivaldi *et al.*, 1999; Caro *et al.*, 2016). If parents in species like the hoopoe or the blue-footed booby could obtain information about offspring quality more quickly via offspring signals, then they would have more time to acquire food for the offspring. This efficiency benefit could potentially outweigh the costs of signalling, and make signalling evolutionarily stable (Fig. 1). We examine the theoretical plausibility of this scenario by proposing and solving a simple game theory model. We specifically want to determine the conditions under which production of the offspring signal will provide the parent with a means for distinguishing offspring on the basis of quality, at evolutionary equilibrium. In this sense, we are looking for an 'honest' signalling solution to the game. We then address the biological plausibility and empirical applications of the model in our discussion.

The model

We consider a parent that has one low-quality offspring and one high-quality offspring. Offspring quality is not cryptic, and the parent can distinguish the low-quality offspring from the high-quality one by investigating some cue (e.g. body size). Our starting point could mirror some natural cases, such as blue-footed boobies, where two eggs hatch asynchronously, leading to a large size disparity (Drummond & Garcia Chavelas, 1989).

We assume, first, that a parent can also distinguish offspring from one another through means other than the cue. Specifically, the parent can respond to a signal (possibly) produced by the offspring. We assume further that assessing the signal is more efficient than assessing the cue, saving the parent time that can be spent acquiring more food. Signalling can, however, be costly to the offspring.

We then assume that the parent, after producing two offspring, is experiencing relatively poor environmental conditions. Conditions are so poor, in fact, that the parent can successfully rear only one of its two offspring. Therefore, the parent must decide which offspring it will invest in, and which offspring it will allow to die. Offspring, in turn, must decide on what information (if any) to attempt to convey to the parent via the signal. We assume that a high-quality offspring who receives parental investment has fitness equal to 1 and that a low-quality offspring who receives parental investment has a fitness equal to $0 < v < 1$. An offspring who does not receive investment has fitness equal to zero. We assume parents have complete

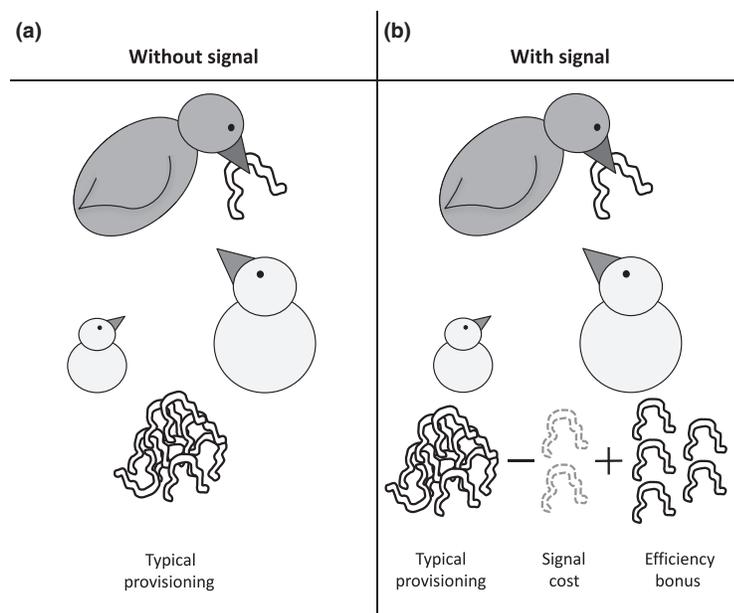
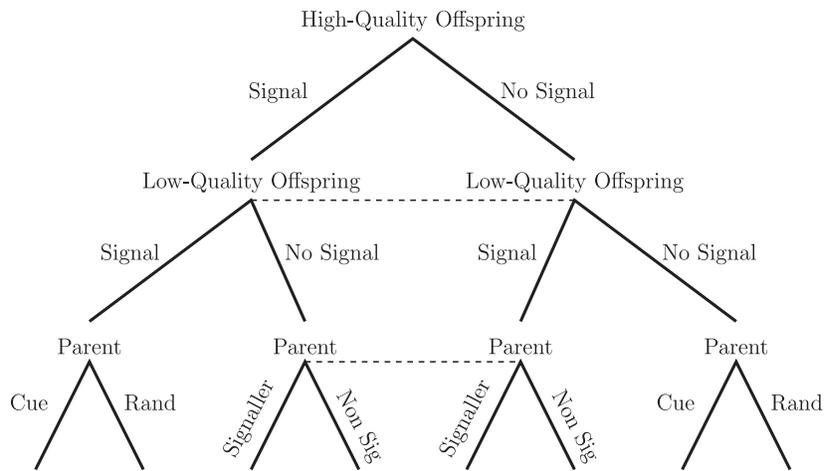


Fig. 1 Costly signals of noncryptic condition are biologically feasible. (a) Parents can distribute food amongst their offspring by relying on a cue of condition, such as body size. (b) Alternatively, parents could distribute food amongst their offspring by relying on a signal of noncryptic condition, such as mouth gape area, begging calls or begging height. If it is much faster for parents to use the signal, they could spend more time foraging for additional caterpillars to feed their brood. As long as the efficiency benefit of using the signal outweighs the cost of producing the signal, this communication system can be advantageous, even if the information encoded in the signal is noncryptic.

Fig. 2 Tree depiction of the game proposed in the main text. Individual decision-makers appear at nodes, and solid branches indicate different actions available to individual decision-makers. Nodes linked by dashed lines indicate that the corresponding decisions are made by individuals who have been given the same information. In particular, the fact that offspring decide upon their respective strategies simultaneously means that the nodes depicting the low-quality offspring's decision must be connected by a dashed line.



control over the distribution of resources like food (e.g. Godfray, 1991).

We model the decisions made by the parent and offspring as moves in a three-player evolutionary game (Fig. 2). In this game, the high-quality offspring moves either by producing a signal (strategy H_1), or by not signalling at all (strategy H_2). At exactly the same time, the low-quality offspring also moves either by producing a signal (strategy L_1), or by not signalling at all (strategy L_2). Any offspring that signals reduces its fitness by a fraction c , which reflects the cost of signal production.

The parent's move in the game follows those made by the offspring, and its available moves vary depending on the situation. If both offspring signal, or if neither offspring signals, then the parent cannot use the signal to distinguish one offspring from the other. In these two cases, the parent moves either by using the cue to direct investment to the high-quality offspring, or by investing in a randomly chosen offspring. Assessing the cue is assumed to incur some time cost, such that investing at random confers an efficiency benefit, which means that the parent is able to improve the fitness of the offspring who receives investment. Here, the improvement is modelled by a multiplicative fitness by $(1 + b)$. If only one offspring signals, then we assume the parent moves either by investing in the signaller, or by investing in the nonsignaller. In this case, the parent also avoids the cost of assessing the cue, and so gains the multiplicative efficiency benefit b . Because the parent can choose between two moves in each of three different situations, there are eight parental strategies in this game (P_1 to P_8 in Table 1).

Method of analysis

We solve the game proposed in the previous section by identifying strategies that are likely to remain fixed in a

Table 1 Description of the eight possible parental strategies, P_1 to P_8 , in the game. Each strategy specifies a course of action given the presence or absence of offspring signals.

Strategy	Both offspring signal	Only one offspring signals	Neither offspring signals
P_1	Feed according to cue	Feed signaller	Feed according to cue
P_2	Feed according to cue	Feed signaller	Feed at random
P_3	Feed according to cue	Feed nonsignaller	Feed according to cue
P_4	Feed according to cue	Feed nonsignaller	Feed at random
P_5	Feed at random	Feed signaller	Feed according to cue
P_6	Feed at random	Feed signaller	Feed at random
P_7	Feed at random	Feed nonsignaller	Feed according to cue
P_8	Feed at random	Feed nonsignaller	Feed at random

population. The solution concept we turn to is the Nash equilibrium. Here, the Nash equilibrium is a strategy profile (H_i, L_j, P_k) that produces a pay-off to each player that cannot be improved upon by a unilateral change in strategy. The Nash equilibrium is a necessary condition of Maynard Smith's (1982) evolutionarily stable strategy (ESS). The Nash equilibrium has also been the solution concept used in other theoretical treatments of signals between offspring and parents (e.g. Rodriguez-Girones, 1999). We are particularly interested in those equilibria in which one, and only one, offspring signals. The signal would then provide a parent with a clear means of distinguishing offspring based on quality. In those cases, the signal conveys meaningful (or, in some sense, 'honest') information to the parent.

To find the Nash equilibrium, we translate the consequences of the various strategies into inclusive fitness pay-offs (Hamilton, 1964). The inclusive fitness pay-off

awarded to an offspring depends upon the relatedness between it and its sibling, $0 < r < 1$. In contrast, relatedness factors out of any inclusive fitness pay off the parent receives, because the parent is equally related to both offspring.

Results

The Nash equilibria we obtain vary according to whether investment using the public cue of quality is more or less profitable than investment at random. If the efficiency benefit b (or potential efficiency benefit) lies below a threshold value of $(1 - v)/(1 + v)$, then using the cue is more profitable and we obtain one set of Nash equilibria. If b exceeds the threshold value of $(1 - v)/(1 + v)$, then investing at random is more profitable and we obtain a different set of Nash equilibria. The details surrounding the equilibria are given below.

Case 1: Following the cue is better than investing at random

We first consider the scenario where the efficiency benefits gained from not investigating the cue are low, $b < (1 - v)/(1 + v)$. In this scenario, following the cue is better than investing at random. Consequently, we are able to examine a reduced game that excludes the parental strategies that rely on random investment (Table 2). In that reduced game, there may be two Nash equilibria at which one, and only one, offspring signals.

The first candidate Nash equilibrium is the triplet (H_1, L_2, P_1) . This triplet corresponds to the situation in which only the high-quality offspring signals, and the parent directs its investment towards that signal in an efficient manner. In keeping with definition of the

Table 2 Reduced pay-off matrix for the case when investing in offspring based on the cue is more profitable than investing at random ($b < (1 - v)/(1 + v)$). Each cell presents the pay-off to the parent (row player), the low-quality offspring (column player) and the high-quality offspring (super-column player), in that order. H_1 and L_1 indicate that high- and low-quality offspring produce the signal, whereas H_2 and L_2 indicate that offspring do not signal. P_1 and P_3 correspond to parental strategies in Table 1.

	H_1		H_2	
	L_1	L_2	L_1	L_2
P_1	$(1 - c)$	$(1 - c)(1 + b)$	$v(1 - c)(1 + b)$	1
	$r(1 - c)$	$r(1 - c)(1 + b)$	$v(1 - c)(1 + b)$	r
P_3	$(1 - c)$	$(1 - c)(1 + b)$	$v(1 - c)(1 + b)$	1
	$(1 - c)$	$v(1 + b)$	$(1 + b)$	1
	$r(1 - c)$	$v(1 + b)$	$r(1 + b)$	r
	$(1 - c)$	$v(1 + b)$	$(1 + b)$	1

Shaded cells indicate Nash equilibria where signalling can be stable.

Nash equilibrium, a unilateral switch from L_2 to L_1 will not increase the low-quality offspring's inclusive fitness pay-off. However, unilateral switches from H_1 to H_2 , or from P_1 to P_3 may be rewarded, and so there is a chance the definition of a Nash equilibrium will not be met. To ensure strategy switches made by the high-quality offspring and the parent, respectively, are not rewarded, we must have $(1 + b)(1 - c) \geq \max\{1, v(1 + b)\}$, or equivalently $c \leq 1 - \max\{1/(1 + b), v\}$. Because we have assumed $b < (1 - v)/(1 + v)$, we can be sure that $v < (1 - b)/(1 + b)$, which implies that $\max\{1/(1 + b), v\} = 1/(1 + b)$. The condition for (H_1, L_2, P_1) to be a NE, therefore, can be stated simply as $c \leq 1 - 1/(1 + b)$. In other words, the cost of signalling cannot be too high. This Nash equilibrium condition is illustrated in Fig. 3 alongside the constraints imposed by other model assumptions. As the figure shows, the largest permissible cost increases as the efficiency benefit rises, and is independent of the relatedness between siblings.

The second Nash equilibrium is the triplet (H_2, L_1, P_3) . It corresponds to the situation in which the low-quality offspring signals in order to efficiently guide the parent's investment towards the nonsignalling, high-quality offspring. The triplet follows the definition of a Nash equilibrium, because:

- 1 a unilateral switch from H_2 to H_1 penalizes the high-quality offspring by an amount $(1 + b) - (1 - c) = (b + c)$;
- 2 a unilateral switch from L_1 to L_2 penalizes the low-quality offspring by an amount $r(1 + b) - r = rb$;
- 3 a unilateral switch from P_3 to P_1 penalizes the parent by an amount $(1 + b) - (1 + b)(1 - c)v = (1 + b)(1 - (1 - c)v)$.

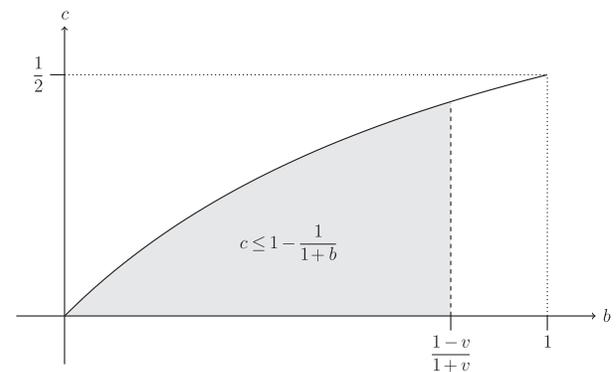


Fig. 3 If the efficiency benefit is small, meaning $b < (1 - v)/(1 + v)$ then the strategy profile (H_1, L_2, P_1) is a Nash equilibrium provided b, c parameters remain in the shaded region. The shaded region is bounded by a curve describing maximum permissible cost, $c = 1 - 1/(1 + b)$, and the maximum b in this case. One can see that the conditions under which (H_1, L_2, P_1) is a Nash equilibrium become more restrictive either as b decreases or as v increases.

The fact that (H_2, L_1, P_3) is a Nash equilibrium is quite intuitive. Indeed, the effective cost of signalling, here, is actually zero, because the offspring who signals ultimately dies.

Case 2: Investing at random is better than following the cue

We now consider the scenario where the efficiency benefits gained from not assessing the cue are high, $b > (1 - v)/(1 + v)$. Under this condition, investing at random is better than following the cue, and so we consider a reduced game that excludes the parental strategies that rely on the cue (Table 3). As in the previous case, we identify two Nash equilibria, at which only one offspring signals.

We first consider the triplet (H_1, L_2, P_6) , where only the high-quality offspring signals, and only the high-quality offspring receives parental investment. In this case, (H_1, L_2, P_6) fails to be a Nash equilibrium when either:

- 1 the signal is so costly that it is better, from the parent’s perspective, to invest in the offspring whose quality is not diminished by the signal,
- 2 it is in the high-quality offspring’s best interest, in an inclusive fitness sense, to stop signalling and suffer the possible consequences of its parent’s random investment, or
- 3 it is in the low-quality offspring’s best interests, in an inclusive fitness sense, to start signalling in order to receive a chance parental investment.

From Table 3, we see that (i) and (ii) can be ruled out when $(1 - c) \geq \max\{v, (1 + rv)/2\}$, whereas (iii)

Table 3 Reduced pay-off matrix for the case when investing in offspring randomly is more profitable than investing based on the cue ($b > (1 - v)/(1 + v)$). Each cell presents the pay-off to the parent (row player), the low-quality offspring (column player) and the high-quality offspring (super-column player), in that order. H_1 and L_1 indicate that high- and low-quality offspring produce the signal, whereas H_2 and L_2 indicate that offspring do not signal. P_1 and P_3 correspond to parental strategies in Table 1.

	H_1		H_2	
	L_1	L_2	L_1	L_2
P_6	$(1 - c)(1 + b)(1 + v)/2$	$(1 - c)(1 + b)$	$v(1 - c)$	$(1 + b)(1 + v)/2$
	$(1 - c)(1 + b)(r + v)/2$	$r(1 - c)(1 + b)$	$v(1 - c)$	$(1 + b)(r + v)/2$
	$(1 - c)(1 + b)(1 + rv)/2$	$(1 - c)(1 + b)$	$rv(1 - c)$	$(1 + b)(1 + rv)/2$
P_8	$(1 - c)(1 + b)(1 + v)/2$	$v(1 + b)$	$(1 + b)$	$(1 + b)(1 + v)/2$
	$(1 - c)(1 + b)(r + v)/2$	$v(1 + b)$	$r(1 + b)$	$(1 + b)(r + v)/2$
	$(1 - c)(1 + b)(1 + rv)/2$	$rv(1 + b)$	$(1 + b)$	$(1 + b)(1 + rv)/2$

Shaded cells indicate Nash equilibria where signalling can be stable.

can be ruled out when $r \geq v$. Furthermore, if we do have $r \geq v$, then we can be sure that $v < 1/(2 - r)$ so that $\max\{v, (1 + rv)/2\} = (1 + rv)/2$. It follows that (H_1, L_2, P_6) is a Nash equilibrium if and only if $r \geq v$ and $c \leq (1 - rv)/2$. The latter condition sets the largest permissible signalling cost, and it depends on the relatedness between siblings (Fig. 4). In addition, the largest permissible cost does not depend on the efficiency benefit b beyond the mathematical requirement that defines this case. Of course that mathematical requirement, namely $b > (1 - v)/(1 + v)$, can be rearranged as $v > (1 - b)/(1 + b)$, which puts a lower bound on v (Fig. 4).

The second candidate Nash equilibrium we consider is (H_2, L_1, P_8) , which corresponds to yet another situation in which only the offspring destined to die provides the signal. However, in contrast to the analogous situation described for the previous case, this triplet is not guaranteed to be an equilibrium. Efficiency gains are now large enough to provide a parent with an incentive to invest at random when there is no signal to guide its behaviour. This means that a low-quality offspring may be able to increase its pay-off by switching from L_1 to L_2 , that is by turning off its signal. To ensure this kind of gain cannot be made, we must have $r \geq v$, so that the low-quality offspring values its high-quality sibling more than it values itself. In contrast to the previous case, examination of the consequences of other unilateral deviations from (H_2, L_1, P_8) shows that $r \geq v$ is the only condition that needs to be satisfied if the triplet is to be a Nash equilibrium (Table 3).

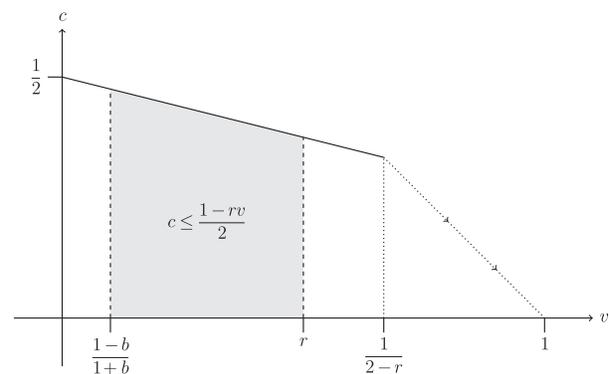


Fig 4 If the efficiency benefit is large, meaning $b > (1 - v)/(1 + v)$ then the strategy profile (H_1, L_2, P_6) is a Nash equilibrium provided v, c parameters remain in the shaded region. The shaded region is bounded by a curve describing maximum permissible cost, $c = (1 - rv)/2$, and the minimum and maximum, respectively, in this case. One can see that the conditions under which (H_1, L_2, P_6) a Nash equilibrium become more restrictive as v increases. By contrast, an increase in r has mixed effects, broadening the range of possible v values on the one hand, but reducing the maximum permissible cost on the other hand (as indicated by the dotted arrows).

Discussion

Broadly speaking, our game-theoretical model results show that natural selection can lead offspring to signal their quality, even if that quality is not cryptic. This agrees with the hypothesis presented in the introduction, but contradicts the common assumption in the field of parent–offspring communication that offspring signals of need or quality must transmit information that cannot be obtained by parents in any other way (e.g. Grafen, 1990; Godfray, 1991; Kilner & Johnstone, 1997; Bergstrom *et al.*, 2002; Johnstone 2004). One implication of our results is that empirical researchers attempting to identify precisely what is encoded in offspring signals should consider the possibility that the biologically relevant aspects of condition may be public. Furthermore, we have focused on the extreme case where cues and signals carry the same information. In reality, signals could have multiple functions, conveying both public information more efficiently, and cryptic information, which could make them even more likely to be favoured. More generally, although we have modelled signals of noncryptic quality in the context of parent–offspring communication, similar outcomes could be expected in other honest signalling scenarios in the fields of biology and economics, such as sexual selection (Grafen, 1990), or even competition in the labour market.

Our analysis considered small and large efficiency benefits separately. In both cases, we identified two distinct instances in which a signal conveyed meaning at equilibrium (Table 4). In the first instance, only the low-quality offspring produced the signal, and the parent used that signal to direct investment towards the signaller's high-quality counterpart. In the second instance, only the high-quality offspring produced the signal that attracted parental investment away from the low-quality offspring. In both instances, the family group can be understood as using the signal for the purpose of making inclusive fitness gains. Aligned interests such as these can contribute to the stability of offspring–parent signals (Maynard Smith, 1991; Rodriguez-Girones, 1999), but it has not been previously shown that efficiency benefits

are able to bring interests into alignment. That said, our results do rely critically on the assumption that offspring differ in quality. As the variation in offspring quality is diminished (i.e. as v increases), the conditions for one and only one signal at equilibrium become more restrictive, and in the limit as v goes to 1, none of the conditions can be met (Table 4).

Signalling models often predict the existence of multiple equilibria (Bergstrom & Lachmann, 1997; Lachmann & Bergstrom, 1998), and ours is no exception. Indeed, the two distinct instances identified above could *simultaneously* be solutions to the game we proposed. It is important to recognize, though, that the mathematical requirements in the first instance (only the high-quality offspring signals) were more restrictive than those in the second (only the low-quality offspring signals). We found that if the high-quality offspring was predicted to signal at equilibrium, then the cost of signalling could not exceed some threshold value. By contrast, no such requirement on cost was made of a low-quality signaller at equilibrium, because, when it signalled at equilibrium, the low-quality offspring did not receive any parental investment, and will therefore die. The actual cost of the signal produced by the low-quality offspring at equilibrium, then, is extremely low. Had we relaxed the assumption that the offspring who does not receive parental investment dies, we would have expected the contrast between equilibrium signalling from the high- and low-quality offspring, respectively, to be weaker. However, it is likely that in order to be maintained at equilibrium, signals provided by the low-quality offspring would have continued to require the costs of signalling to be sufficiently low. Still, we expect that the threshold condition for the maintenance of the signal from the low-quality offspring only would have continued to be more restrictive.

There are some conceptual similarities between our model and a scenario discussed in Lachmann *et al.* (2001). Those authors suggest a verbal model for sparrows in which individuals can produce a relatively cheap signal that indicates aggressiveness, fighting ability or other correlates of their resource-holding potential. In their model, individuals who signal dishonestly are punished by conspecifics, which imposes a cost of dishonest signalling. Similarities between our model and that of Lachmann *et al.* (2001) include: (i) the potential for honest (or meaningful) signalling at equilibrium despite low realized costs of signalling, and (ii) the possibility for individuals to avoid other types of costs, for example agonistic interactions in the sparrow example, by signalling. In the case of (ii), the absence of other types of cost parallels the efficiency benefits introduced here, but the two are distinct – the absence of a cost of dishonesty, on the one hand, and the presence of an efficiency benefit, on the other hand. Differences between the two models

Table 4 Summary of mathematical conditions associated with the two instances of Nash equilibrium solutions at which one, and only one, offspring signals. The marginal case $b = (1 - v)/(1 - v)$ has been neglected.

Case	Only low-quality offspring signals, high-quality offspring receives parental investment	Only high-quality offspring signals, and high-quality offspring receives parental investment
$b < (1 - v)/(1 + v)$	Not applicable (always Nash equil)	$c \leq 1 - 1/(1 + b)$
$b > (1 - v)/(1 + v)$	$r \geq v$	$c \leq (1 - v)/2$ and $r \geq v$

include: (i) the consideration we give to interactions between relatives; (ii) an explicit efficiency benefit from following signals, relative to using cues (our *b* term); (iii) our presentation of explicit conditions for stability of honest signalling; and (iv) our examination of stability against invasion by non-signal-based means of achieving efficiency benefits (i.e. investing at random).

Our model also shares some similarities with models of amplifier signals (Hasson, 1989; Bogaardt & Johnstone, 2016). Amplifiers are traits that magnify differences in cues of quality, and are typically considered in terms of sexual signalling. In both cases, a receiver prefers higher-quality individuals and can use a cue to distinguish between individuals of differing quality, and those cues are linked to a separate trait, which may or may not evolve as a stable signal. The key difference between our models lays in the benefit of the signal: in our model, the benefit is increased efficiency, which increases the amount of parental investment possible, whereas in amplifier models, the benefit is to reduce perceptual errors in the assessment of male cues. Furthermore, amplifiers increase the total amount of information available to receivers, because signallers can vary their level of amplification. In our model, signalling is stable even though receivers never experience an increase in the amount of information they can gain, whether they respond to the cue, the signal, or both.

Empirical applications

Under what conditions would our hypothesis be most likely to apply in the real world? We showed that selection can favour signalling of information that is not cryptic or private, to increase the efficiency with which that 'public' information can be transmitted. Considering offspring soliciting their parents for food, this is more likely to be the case when: (i) it would be relatively difficult for parents to make use of public cues or signals of cryptic condition, due to acoustic interference from the environment, limited visibility or low variability in the public cue, such as in synchronously hatching broods where all nestlings are approximately the same size; (ii) when offspring condition hovers around the viability threshold, so that small increases in the total amount of provisioning could have large impacts on fitness; and/or (iii) when the cost of signalling is relatively low.

How plausible is this set of conditions, where the efficiency benefits from transmitting information with a signal can outweigh the cost of signalling? Consider a common bird species, the great tit (*Parus major*). The efficiency benefit (*b*) of responding to a low cost signal could be relatively high in birds such as the great tit, because: (i) they nest in dark tree holes, where it may be relatively hard to assess cues such as body size

(Wiebe & Slagsvold, 2012); (ii) they frequently experience brood reduction, so slight increases in provisioning rate could have especially large impacts on the fitness of marginal offspring (Bengtsson & Rydén, 1983); and (iii) their breeding period is constrained to the relatively short window when caterpillars are abundant, and so efficiency in distributing food could be important (Hinks *et al.*, 2015). Great tit parents can spend an average of 8 h per day foraging for their brood (Barba *et al.*, 2009; García-Navas *et al.*, 2013). Over a 15-day nestling period, these parents would have approximately 864 000 s of total foraging time. Great tit parents can make approximately 13 provisioning trips per hour, so a parent can return to the nest with prey, such as caterpillars, approximately every 138 s, on average (García-Navas *et al.*, 2013). If the smallest offspring are at a high risk of starvation, parents will be selected to feed the offspring in the best condition (Mock & Parker, 1997; Davis *et al.*, 1999; Caro *et al.*, 2016). Parents could determine condition either by directly assessing body size or by relying on a low cost signal that transmits the same information as body size, such as mouth gape area or begging call volume. For example, assume that parents could realize an efficiency benefit of 5 s per caterpillar by using the signal. In this scenario, parents relying on the signal would be able to bring back an additional 218 caterpillars over the 15-day nestling period. Even if producing the signal costs as much as one caterpillar per day per offspring, parents with a brood of seven offspring would experience a net increase of 113 caterpillars per brood. Those 113 extra caterpillars could be enough to tip the scales between the smallest nestling starving or surviving.

Ultimately, the plausibility of our hypothesis can only be determined with empirical work that explicitly measures the kinds of parameters used in our model. This would require measuring the efficiency of different parental allocation strategies, which could be done experimentally by varying the information available to parents and comparing the amount of time it takes a parent to feed its offspring. For instance, previous researchers have removed parents' ability to distribute food based on begging vocalizations by muting individual nestlings (Glasse & Forbes, 2002). Empirical work must also exclude the possibility that the biologically relevant aspect of condition being signalled is public and not cryptic, which would require measuring the association between signal intensity and various aspects of condition which are more or less public, such as plasma glucose levels as opposed to body mass (e.g. Quillfeldt *et al.*, 2009). Empirical confirmation of our hypothesis would also need to show that parents actively choose which offspring to feed rather than passively allocate food to the most conspicuous signaller (e.g. Heeb *et al.*, 2003; Dugas & Rosenthal, 2009; Wiebe & Slagsvold, 2012). Comparative studies could test whether signals of public information with efficiency benefits are more likely to

evolve when parents would have more difficulty utilizing cues of condition, such as in species that nest in dark cavities or have more synchronous hatching, or when the period of parental care is shorter. Finally, our model predicts that relatedness plays a key role in the establishment of meaningful signals at equilibrium only when efficiency benefits are large; empirical work could also attempt to verify this prediction.

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References

- Barba, E., Atiénzar, F., Marín, M., Monrós, J.S. & Gil Delgado, J.A. 2009. Patterns of nestling provisioning by a single-prey loader bird, great tit *Parus major*. *Bird Study* **56**: 187–197.
- Bengtsson, H. & Rydén, O. 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major*. *Behav. Ecol. Sociobiol.* **12**: 243–251.
- Bergstrom, C.T. & Lachmann, M. 1997. Signalling among relatives. I. Is costly signaling too costly? *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **352**: 609–617.
- Bergstrom, C.T., Szamado, S. & Lachmann, M. 2002. Separating equilibria in continuous signalling games. *Philos. Trans. R. Soc. Lond. B. Biol. Sci.* **357**: 1595–1606.
- Bogaardt, L. & Johnstone, R.A. 2016. Amplifiers and the origin of animal signals. *Proc. Biol. Sci.* **283**: 20160324.
- Bradbury, J.W. & Vehrencamp, S.L. 2011. *Principles of Animal Communication*. Sinauer Associates, Sunderland, MA.
- Caro, S.M., Griffin, A.S., Hinde, C.A. & West, S.A. 2016. Unpredictable environments lead to the evolution of parental neglect in birds. *Nat. Commun.* **7**: 1–10.
- Davis, J.N., Todd, P.M. & Bullock, S. 1999. Environment quality predicts parental provisioning decisions. *Proc. Biol. Sci.* **266**: 1791–1797.
- Drummond, H. & Garcia Chavelas, C. 1989. Food shortage influences sibling aggression in the blue-footed booby. *Anim. Behav.* **37**: 806–819.
- Dugas, M.B. & Rosenthal, G.G. 2009. Carotenoid-rich mouth colors influence the conspicuousness of nestling birds. *Behav. Ecol. Sociobiol.* **64**: 455–462.
- García-Navas, V., Ferrer, E.S. & Sanz, J.J. 2013. Prey choice, provisioning behaviour, and effects of early nutrition on nestling phenotype of titmice. *Ecoscience* **20**: 9–18.
- Glasse, B. & Forbes, S. 2002. Muting individual nestlings reduces parental foraging for the brood. *Anim. Behav.* **63**: 779–786.
- Godfray, H.C.J. 1991. Signalling of need by offspring to their parents. *Nature* **352**: 328–330.
- Grafen, A. 1990. Biological signals as handicaps. *J. Theor. Biol.* **144**: 517–546.
- Hamilton, W.D. 1964. The genetical evolution of social behaviour. I and II. *J. Theor. Biol.* **7**: 1–52.
- Hasson, O. 1989. Amplifiers and the handicap principle in sexual selection: a different emphasis. *Proc. Biol. Sci.* **235**: 383–406.
- Heeb, P., Schwander, T. & Faoro, S. 2003. Nestling detectability affects parental feeding preferences in a cavity-nesting bird. *Anim. Behav.* **66**: 637–642.
- Hinks, A.E., Cole, E.F., Daniels, K.J., Wilkin, T.A., Nakagawa, S. & Sheldon, B.C. 2015. Scale-dependent phenological synchrony between songbirds and their caterpillar food source. *Am. Nat.* **186**: 84–97.
- Johnstone, R.A. 2004. Begging and sibling competition: how should offspring respond to their rivals? *Am. Nat.* **163**: 388–406.
- Kilner, R. & Johnstone, R.A. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol. Evol.* **12**: 11–15.
- Lachmann, M. & Bergstrom, C.T. 1998. Signalling among relatives II. Beyond the tower of Babel. *Theor. Popul. Biol.* **54**: 146–160.
- Lachmann, M., Szamado, S. & Bergstrom, C.T. 2001. Cost of conflict in animal signals and human language. *Proc. Natl. Acad. Sci. USA* **98**: 13189–13194.
- Lack, D. 1954. *The Natural Regulation of Animal Numbers*. Clarendon Press, Oxford.
- Martin-Vivaldi, M., Palomino, J.J., Soler, M. & Soler, J.J. 1999. Determinants of reproductive success in the Hoopoe *Upupa epops*, a hole-nesting non-passerine bird with asynchronous hatching. *Bird Study* **46**: 205–216.
- Maynard Smith, J. 1982. *Evolution and the Theory of Games*. Cambridge University Press, Cambridge.
- Maynard Smith, J. 1991. Honest signalling: the Philip Sidney game. *Anim. Behav.* **42**: 1034–1035.
- Maynard Smith, J. & Harper, D. 2003. *Animal Signals*. Oxford University Press, New York, NY.
- Mock, D.W. & Parker, G.A. 1997. *The Evolution of Sibling Rivalry*. Oxford University Press, Oxford.
- Quillfeldt, P., Everaert, N., Buyse, J., Masello, J.F. & Dridi, S. 2009. General and comparative endocrinology. *Gen. Comp. Endocrinol.* **161**: 171–178.
- Rodriguez-Girones, M.A. 1999. Sibling competition stabilizes resolution models of parent-offspring conflict. *Proc. Biol. Sci.* **266**: 2399–2402.
- Royle, N.J., Hartley, I.R. & Parker, G.A. 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends Ecol. Evol.* **17**: 434–440.
- Searcy, W.A. & Nowicki, S. 2005. *The Evolution of Animal Communication: Reliability and Deception in Signaling Systems*. Princeton University Press, Princeton.
- Wiebe, K.L. & Slagsvold, T. 2012. Parents take both size and conspicuousness into account when feeding nestlings in dark cavity nests. *Anim. Behav.* **84**: 1307–1312.
- Zahavi, A. 1975. Mate selection—a selection for a handicap. *J. Theor. Biol.* **53**: 205–214.

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Table A1. Reference list for within-species meta-analysis (Chapter 3)

Study	Citation
1	Amundsen, T. & Stokland, J. N. 1988. Adaptive Significance of Asynchronous Hatching in the Shag: A Test of the Brood Reduction Hypothesis. <i>The Journal of Animal Ecology</i> , 57, 329–344.
2	Anderson, D. & Ricklefs, R. 1995. Evidence of kin-selected tolerance by nestlings in a siblicidal bird. <i>Behavioral Ecology and Sociobiology</i> , 37, 163–168.
3	Anderson, D. J. & Ricklefs, R. E. 1992. Brood Size and Food Provisioning in Masked and Blue-Footed Boobies (<i>Sula</i> Spp.). <i>Ecology</i> , 73, 1363–1374.
4	Arroyo, B. E., De Cornulier, T. & Bretagnolle, V. 2002. Parental investment and parent–offspring conflicts during the postfledging period in Montagu’s harriers. <i>Animal Behaviour</i> , 63, 235–244.
5	Avilés, J. M., Parejo, D. & Rodríguez, J. 2011. Parental favouritism strategies in the asynchronously hatching European Roller (<i>Coracias garrulus</i>). <i>Behavioral Ecology and Sociobiology</i> , 65, 1549–1557.
6	Beissinger, S. & Waltman, J. 1991. Extraordinary Clutch Size and Hatching Asynchrony of a Neotropical Parrot. <i>Auk</i> , 108, 863–871.
7	Bengtsson, H. & Rydén, O. 1983. Parental Feeding Rate in Relation to Begging Behavior in Asynchronously Hatched Broods of the Great Tit <i>Parus major</i> : An Experimental Study. <i>Behavioral Ecology and Sociobiology</i> , 12, 243–251.
8	Bitton, P.-P., Dawson, R. D. & O’Brien, E. L. 2006. Influence of intraclutch egg-mass variation and hatching asynchrony on relative offspring performance within broods of an altricial bird. <i>Canadian Journal of Zoology</i> , 84, 1721–1726.
9	Blomqvist, D., Johansson, O. & Götmark, F. 1997. Parental quality and egg size affect chick survival in a precocial bird, the lapwing <i>Vanellus vanellus</i> . <i>Oecologia</i> , 110, 18–24.
10	Boland, C. R. J., Heinsohn, R. & Cockburn, A. 1997. Experimental manipulation of brood reduction and parental care in cooperatively breeding white-winged choughs. <i>Journal of Animal Ecology</i> , 66, 683–691.
11	Bollinger, P. B., Bollinger, E. K. & Malecki, R. A. 1990. Tests of Three Hypotheses of Hatching Asynchrony in the Common Tern. <i>The Auk</i> , 107, 696–706.
12	Boncoraglio, G., Caprioli, M., Boncoraglio, S. & Saino, N. 2013. Effect of UV-reflectance of chick flanges on begging behaviour and body condition in Barn Swallow (<i>Hirundo rustica</i> , Aves: Hirundinidae) chicks. <i>Italian Journal of Zoology</i> , 80, 35–45.
13	Boncoraglio, G., Martinelli, R. & Saino, N. 2007. Sex-related asymmetry in competitive ability of sexually monomorphic barn swallow nestlings. <i>Behavioral Ecology and Sociobiology</i> , 62, 729–738.
14	Bowers, E. K., Sakaluk, S. K. & Thompson, C. F. 2011. Adaptive sex allocation in relation to hatching synchrony and offspring quality in house wrens. <i>The American naturalist</i> , 177, 617–29.
15	Braun, B. M. & Hunt, G. L. J. 1983. Brood reduction in black-legged kittiwakes. <i>The Auk</i> , 100, 469–476.
16	Bryant, D. M. & Tatner, P. 1990. Hatching asynchrony, sibling competition and siblicide in nestling birds: studies of swiftlets and bee-eaters. <i>Animal Behaviour</i> , 39, 657–671.
17	Budden, A. E. & Beissinger, S. R. 2009. Resource allocation varies with parental sex and brood size in the asynchronously hatching green-rumped parrotlet (<i>Forpus passerinus</i>). <i>Behavioral Ecology and Sociobiology</i> , 63, 637–647.
18	Clotfelter, E. D., Whittingham, L. A. & Dunn, P. O. 2000. Laying order, hatching asynchrony and nestling body mass in Tree Swallows <i>Tachycineta bicolor</i> . <i>Journal of Avian Biology</i> , 31, 329–334.
19	Cook, M. I., Monaghan, P. & Burns, M. D. 2000. Effects of short-term hunger and competitive asymmetry on facultative aggression in nestling black guillemots <i>Cephus grylle</i> . <i>Behavioral Ecology</i> , 11, 282–287.
20	Custer, T. W. & Peterson, D. W. J. 1991. Growth rates of great egret, snowy egret and black-crowned night-heron chicks. <i>Colonial Waterbirds</i> , 14, 46–50.
21	De Ayala, R. M., Saino, N., Møller, A. P. & Anselmi, C. 2007. Mouth coloration of nestlings covaries with offspring quality and influences parental feeding behavior. <i>Behavioral Ecology</i> , 18, 526–534.
22	Dickens, M. & Hartley, I. R. 2007. Differences in parental food allocation rules: evidence for

Study	Citation
	sexual conflict in the blue tit? <i>Behavioral Ecology</i> , 18, 674–679.
23	Djerdali, S., Tortosa, F. S. & Doumandji, S. 2008. Do white stork (<i>Ciconia ciconia</i>) parents exert control over food distribution when feeding is indirect? <i>Ethology Ecology & Evolution</i> , 20, 361–374.
24	Drummond, H. & Chavelas, C. G. 1989. Food shortage influences sibling aggression in the blue-footed booby. <i>Animal Behaviour</i> , 37, 806–819.
25	Drummond, H., González, E. & Osorno, J. 1986. Parent-offspring cooperation in the blue-footed booby (<i>Sula nebouxii</i>): social roles in infanticidal brood reduction. <i>Behavioral Ecology and Sociobiology</i> , 19, 365–372.
26	Evans, R. M. & McMahon, B. F. 1987. Within-brood variation in growth and condition in relation to brood reduction in the American white pelican. <i>The Wilson Bulletin</i> , 99, 190–201.
27	Fargallo, J. A., Polo, V., De Neve, L., Martín, J., Dávila, J. A. & Soler, M. 2006. Hatching order and size-dependent mortality in relation to brood sex ratio composition in chinstrap penguins. <i>Behavioral Ecology</i> , 17, 772–778.
28	Ferrari, R. P., Martinelli, R. & Saino, N. 2006. Differential effects of egg albumen content on barn swallow nestlings in relation to hatch order. <i>Journal of Evolutionary Biology</i> , 19, 981–93.
29	Fujioka, M. 1985. Food delivery and sibling competition in experimentally even-aged broods of the cattle egret. <i>Behavioral Ecology and Sociobiology</i> , 17, 67–74.
30	Fujioka, M. 1985. Sibling competition and siblicide in asynchronously-hatching broods of the cattle egret <i>Bubulcus ibis</i> . <i>Animal Behaviour</i> , 33, 1228–1242.
31	García-Navas, V., Ferrer, E. S. & Serrano-Davies, E. 2014. Experimental evidence for parental, but not parentally biased, favouritism in relation to offspring size in Blue Tits <i>Cyanistes caeruleus</i> . <i>Ibis</i> , 156, 404–414.
32	Gilby, A. J., Mainwaring, M. C. & Griffith, S. C. 2011. The adaptive benefit of hatching asynchrony in wild zebra finches. <i>Animal Behaviour</i> , 82, 479–484.
33	Gilby, A. J., Sorato, E. & Griffith, S. C. 2012. Maternal effects on begging behaviour: an experimental demonstration of the effects of laying sequence, hatch order, nestling sex and brood size. <i>Behavioral Ecology and Sociobiology</i> , 66, 1519–1529.
34	Gottlander, K. 1987. Parental Feeding Behaviour and Sibling Competition in the Pied Flycatcher <i>Ficedula hypoleuca</i> . <i>Ornis Scandinavica</i> , 18, 269–276.
35	Greig-Smith, P. 1985. Weight differences, brood reduction, and sibling competition among nestling Stonechats <i>Saxicola torquata</i> (Aves: Turdidae). <i>Journal of Zoology</i> , 205, 453–465.
36	Guerra, M. & Drummond, H. 1995. Reversed sexual size dimorphism and parental care: minimal division of labour in the blue-footed booby. <i>Behaviour</i> , 132, 479–496.
37	Hafner, H., Dugan, P. J., Kersten, M., Pineau, O. & Wallace, J. P. 1993. Flock feeding and food intake in Little Egrets <i>Egretta garzetta</i> and their effects on food provisioning and reproductive success. <i>Ibis</i> , 135, 25–32.
38	Hahn, D. C. & Aldwell. 1981. Asynchronous hatching in the laughing gull: Cutting losses and reducing rivalry. <i>Animal Behaviour</i> , 29, 421–427.
39	Haley, K. L. & Rosenberg, D. K. 2013. Influence of Food Limitation on Reproductive Performance of Burrowing Owls. <i>BioOne</i> , 47, 365–376.
40	Harper, R. G., Juliano, S. A. & Thompson, C. F. 1992. Hatching asynchrony in the house wren, <i>Troglodytes aedon</i> : a test of the brood-reduction hypothesis. <i>Behavioral Ecology</i> , 3, 76–83.
41	Heg, D. & van der Velde, M. 2001. Effects of territory quality, food availability and sibling competition on the fledging success of oystercatchers (<i>Haematopus ostralegus</i>). <i>Behavioral Ecology and Sociobiology</i> , 49, 157–169.
42	Hegyi, G., Rosivall, B., Szöllösi, E., Eens, M. & Török, J. 2011. Context-dependent effects of nestling growth trajectories on recruitment probability in the collared flycatcher. <i>Behavioral Ecology and Sociobiology</i> , 65, 1647–1658.
43	Herbert, P. N. & Barclay, R. M. R. 1986. Asynchronous and synchronous hatching: Effect on early growth and survivorship. <i>Canadian Journal of Zoology</i> , 64, 2357–2362.
44	Hillström, L., Kilpi, M. & Lindström, K. 2000. Is Asynchronous Hatching Adaptive in Herring Gulls (<i>Larus argentatus</i>)? <i>Behavioral Ecology and Sociobiology</i> , 47, 304–311.
45	Howe, H. 1976. Egg Size, Hatching Asynchrony, Sex, and Brood Reduction in the Common Grackle. <i>Ecology</i> , 57, 1195–1207.
46	Howe, H. F. 1978. Initial Investment, Clutch Size, and Brood Reduction in the Common

Study	Citation
	Grackle (<i>Quiscalus Quiscula</i> L.). <i>Ecology</i> , 59, 1109–1122.
47	Inoue, Y. 1985. The Process of Asynchronous Hatching and Sibling Competition in the Little Egret <i>Egretta garzetta</i> . <i>Colonial Waterbirds</i> , 8, 1–12.
48	Kilner, R. 1995. When do Canary Parents Respond to Nestling Signals of Need? <i>Proceedings of the Royal Society B: Biological Sciences</i> , 260, 343–348.
49	Kilner, R. 1997. Mouth colour is a reliable signal of need in begging canary nestlings. <i>Proceedings of the Royal Society B: Biological Sciences</i> , 264, 963–968.
50	Kilner, R. 2002. Sex differences in canary (<i>Serinus canaria</i>) provisioning rules. <i>Behavioral Ecology and Sociobiology</i> , 52, 400–407.
51	Kim, K.-J., Kang, J.-H. & Rhim. 2013. Influence of begging call playback on behavior of great tit (<i>Parus major</i>) parents. <i>Journal of Animal and Veterinary Advances</i> , 12, 1044–1047.
52	Kim, S. Y. & Monaghan, P. 2006. Sex of the first hatched chick influences survival of the brood in the herring gull (<i>Larus argentatus</i>). <i>Journal of Zoology</i> , 270, 116–121.
53	Klauke, N., Jansen, J., Kramer, J. & Schaefer, H. M. 2014. Food allocation rules vary with age and experience in a cooperatively breeding parrot. <i>Behavioral Ecology and Sociobiology</i> , 68, 1037–1047.
54	Kloskowski, J. 2003. Brood reduction in the Red-necked Grebe <i>Podiceps grisegena</i> . <i>Ibis</i> , 145, 233–243.
55	Kolliker, M., Richner, H., Werner, I. & Heeb, P. 1998. Begging signals and biparental care: nestling choice between parental feeding locations. <i>Animal Behaviour</i> , 55, 215–222.
56	Krebs, E. & Magrath, R. 2000. Food allocation in crimson rosella broods: parents differ in their responses to chick hunger. <i>Animal behaviour</i> , 59, 739–751.
57	Krebs, E. 2001. Begging and food distribution in crimson rosella (<i>Platycercus elegans</i>) broods: why don't hungry chicks beg more? <i>Behavioral Ecology and Sociobiology</i> , 50, 20–30.
58	Krebs, E. A., Cunningham, R. B. & Donnelly, C. F. 1999. Complex patterns of food allocation in asynchronously hatching broods of crimson rosellas. <i>Animal Behaviour</i> , 57, 753–763.
59	Krebs, E., Green, D., Double, M. & Griffiths, R. 2002. Laying date and laying sequence influence the sex ratio of crimson rosella broods. <i>Behavioral Ecology and Sociobiology</i> , 51, 447–454.
60	Krist, M., Remes, V., Uvírová, L., Nádvorník, P. & Bures, S. 2004. Egg size and offspring performance in the collared flycatcher (<i>Ficedula albicollis</i>): a within-clutch approach. <i>Oecologia</i> , 140, 52–60.
61	Lago, K., Johnson, L. S. & Albrecht, D. J. 2000. Growth of late-hatched, competitively disadvantaged nestling house wrens relative to their older, larger nestmates. <i>Journal of Field Ornithology</i> , 71, 676–685.
62	Lee, S.-I., Choi, J. & Choe, J. C. 2012. Hunger is not the Only Determinant of Nestling Begging behavior and Parental Feeding in the Black-Billed Magpie <i>Pica pica</i> . <i>Acta Ornithologica</i> , 47, 10–18.
63	Leedman, A. W. & Magrath, R. D. 2003. Long-term brood division and exclusive parental care in a cooperatively breeding passerine. <i>Animal Behaviour</i> , 65, 1093–1108.
64	Leonard, M. L. & Horn, A. G. 1996. Provisioning rules in tree swallows. <i>Behavioral Ecology and Sociobiology</i> , 38, 341–347.
65	Leonard, M. L. & Horn, A. G. 1998. Need and nestmates affect begging in tree swallows. <i>Behavioral Ecology and Sociobiology</i> , 42, 431–436.
66	Leonard, M. L. & Horn, A. G. 2001. Begging calls and parental feeding decisions in tree swallows (<i>Tachycineta bicolor</i>). <i>Behavioral Ecology and Sociobiology</i> , 49, 170–175.
67	Leonard, M. L., Horn, A. G. & Parks, E. 2003. The role of posturing and calling in the begging display of nestling birds. <i>Behavioral Ecology and Sociobiology</i> , 54, 188–193.
68	Levréro, F., Blanc, A. & Mathevon, N. 2012. Response to begging calls by Zebra Finch parents: “first come, first served” rule may overcome a parental preference between chicks. <i>Comptes Rendus Biologies</i> , 335, 135–41.
69	Lichtenstein, G. & Sealy, S. G. 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests. <i>Proceedings of the Royal Society B: Biological Sciences</i> , 265, 249–254.
70	Lotem, A. 1998. Higher levels of begging behavior by small nestlings: A case of a negatively correlated handicap. <i>Israel Journal of Zoology</i> , 44, 29–45.

Study	Citation
71	Lyon, B. E. 1993. Conspecific brood parasitism as a flexible female reproductive tactic in American coots. <i>Animal Behaviour</i> , 46, 911–928.
72	Lyon, B. E., Eadie, J. M. & Hamilton, L. D. 1994. Parental choice selects for ornamental plumage in American coot chicks. <i>Nature</i> , 371, 240–243.
73	Machmer, M. M. & Ydenberg, R. C. 1998. The relative roles of hunger and size asymmetry in sibling aggression between nestling ospreys, <i>Pandion haliaetus</i> . <i>Canadian Journal of Zoology</i> , 76, 181–186.
74	Mainwaring, M. C., Dickens, M. & Hartley, I. R. 2010. Environmental and not maternal effects determine variation in offspring phenotypes in a passerine bird. <i>Journal of Evolutionary Biology</i> , 23, 1302–11.
75	Mainwaring, M. C., Dickens, M. & Hartley, I. R. 2012. Sexual dimorphism and offspring growth: smaller female Blue Tit nestlings develop relatively larger gapes. <i>Journal of Ornithology</i> , 153, 1011–1016.
76	Mainwaring, M. C., Lucy, D. & Hartley, I. R. 2011. Parentally biased favouritism in relation to offspring sex in zebra finches. <i>Behavioral Ecology and Sociobiology</i> , 65, 2261–2268.
77	Malacarne, G. & Cucco, M. 1991. Chick mortality and hatching asynchrony in the Pallid swift <i>Apus pallidus</i> . <i>Avocetta</i> , 15, 19–24.
78	Malacarne, G., Cucco, M. & Bertolo, E. 1994. Sibling competition in asynchronously hatched broods of the Pallid swift (<i>Apus pallidus</i>). <i>Ethology Ecology & Evolution</i> , 6, 293–300.
79	Martín-Gálvez, D., De Neve, L., Pérez-Contreras, T., Soler, M., Martínez, J. G. & Soler, J. J. 2012. Manipulation of hunger levels affects great spotted cuckoo and magpie host nestlings differently. <i>Journal of Avian Biology</i> , 43, 531–540.
80	Martín-Gálvez, D., Pérez-Contreras, T., Soler, M. & Soler, J. J. 2011. Benefits associated with escalated begging behaviour of black-billed magpie nestlings overcompensate the associated energetic costs. <i>The Journal of Experimental Biology</i> , 214, 1463–72.
81	Martín-Vivaldi, M., Palomino, J. J., Soler, M. & Soler, J. J. 1999. Determinants of reproductive success in the Hoopoe <i>Upupa epops</i> , a hole-nesting non-passerine bird with asynchronous hatching. <i>Bird Study</i> , 46, 205–216.
82	Mead, P. S. & Morton, M. L. 1985. Hatching asynchrony in the mountain white-crowned sparrow (<i>Zonotrichia leucophrys oriantha</i>): A selected or incidental trait? <i>The Auk</i> , 102, 781–792.
83	Merkling, T., Agdere, L., Albert, E., Durieux, R., Hatch, S. A., Danchin, E. & Blanchard, P. 2013. Is natural hatching asynchrony optimal? An experimental investigation of sibling competition patterns in a facultatively siblicidal seabird. <i>Behavioral Ecology and Sociobiology</i> , 68, 309–319.
84	Mock, D. W. 1985. Siblicidal Brood Reduction: The Prey-Size Hypothesis. <i>The American Naturalist</i> , 125, 327–343.
85	Mock, D. W. 1987. Siblicide, parent-offspring conflict, and unequal parental investment by egrets and herons. <i>Behavioral Ecology and Sociobiology</i> , 20, 247–256.
86	Moncada, A. V. 2008. Sibling Rivalry in Black-legged Kittiwakes (<i>Rissa tridactyla</i>). PhD Dissertation. University of Glasgow: U.K.
87	Mondloch, C. J. 1995. Chick hunger and begging affect parental allocation of feedings in pigeons. <i>Animal Behaviour</i> , 49, 601–613.
88	Moreno-Rueda, G., Soler, M., Soler, J. J., Martínez, J. G. & Pérez-Contreras, T. 2007. Rules of food allocation between nestlings of the black-billed magpie, <i>Pica pica</i> , a species showing brood reduction. <i>Ardeola</i> , 54, 15–25.
89	Morris, L. C. 2012. Breeding Ecology of Arctic Tern (<i>Sterna paradisaea</i>) and Common Tern (<i>Sterna hirundo</i>). PhD dissertation. University of Newcastle upon Tyne: UK.
90	Müllner, A. 2004. Breeding ecology and related life-history traits of the Hoatzin, <i>Opisthocomus hoazin</i> , in a primary rainforest habitat. PhD dissertation. Universität Würzburg: Germany.
91	Nilsson, J.-Å. & Gårdmark, A. 2001. Sibling competition affects individual growth strategies in marsh tit, <i>Parus palustris</i> , nestlings. <i>Animal Behaviour</i> , 61, 357–365.
92	Parejo, D., Silva, N., Avilés, J. M. & Danchin, É. 2010. Developmental plasticity varied with sex and position in hatching hierarchy in nestlings of the asynchronous European roller, <i>Coracias garrulus</i> . <i>Biological Journal of the Linnean Society</i> , 99, 500–511.

Study	Citation
93	Parker, G. A., Mock, D. W. & Lamey, T. C. 1989. How Selfish Should Stronger Sibs Be? <i>American Naturalist</i> , 133, 846–868.
94	Ploger, B. J. & Medeiros, M. J. 2004. Unequal Food Distribution among Great Egret <i>Ardea alba</i> Nestlings: Parental Choice or Sibling aggression? <i>Journal of Avian Biology</i> , 35, 399–404.
95	Price, K. 1998. Benefits of begging for yellow-headed blackbird nestlings. <i>Animal Behaviour</i> , 56, 571–577.
96	Price, K., Harvey, H. & Ydenberg, R. 1996. Begging tactics of nestling yellow-headed blackbirds, <i>Xanthocephalus xanthocephalus</i> , in relation to need. <i>Animal Behaviour</i> , 51, 421–435.
97	Redondo, T. & Castro, F. 1992. Signalling of nutritional need by magpie nestlings. <i>Ethology</i> , 92, 193–204.
98	Rensel, M. A., Wilcoxon, T. E. & Schoech, S. J. 2011. Corticosterone, brood size, and hatch order in free-living Florida scrub-jay (<i>Aphelocoma coerulescens</i>) nestlings. <i>General and Comparative Endocrinology</i> , 171, 197–202.
99	Reynolds, S. J., Schoech, S. J. & Bowman, R. 2003. Diet quality during pre-laying and nestling periods influences growth and survival of Florida scrub-jay (<i>Aphelocoma coerulescens</i>) chicks. <i>Journal of Zoology</i> , 261, 217–226.
100	Richter, W. 1984. Nestling Survival and Growth in the Yellow-Headed Blackbird, <i>Xanthocephalus Xanthocephalus</i> . <i>Ecology</i> , 65, 597–608.
101	Robinson, J. A. & Hamer, K. C. 2000. Brood size and food provisioning in common terns <i>Sterna Hirundo</i> and arctic terns <i>S. paradisaea</i> : consequences for chick growth. <i>Ardea</i> , 88, 51–60.
102	Rosivall, B., Szöllösi, E. & Török, J. 2005. Maternal compensation for hatching asynchrony in the collared flycatcher <i>Ficedula albicollis</i> . <i>Journal of Avian Biology</i> , 36, 531–537.
103	Rosivall, B., Szöllösi, E., Hasselquist, D. & Török, J. 2009. Effects of extrapair paternity and sex on nestling growth and condition in the collared flycatcher, <i>Ficedula albicollis</i> . <i>Animal Behaviour</i> , 77, 611–617.
104	Rosivall, B., Török, J. & Szöllosi, E. 2005. Food allocation in collared flycatcher (<i>Ficedula albicollis</i>) broods: Do rules change with the age of nestlings? <i>The Auk</i> , 122, 1112–1122.
105	Royle, N. & Hamer, K. 1998. Hatching asynchrony and sibling size hierarchies in gulls: effects on parental investment decisions, brood reduction and reproductive success. <i>Journal of Avian Biology</i> , 29, 266–272.
106	Ryser, S. 2012. Prey delivery strategy at nestbox determines differential food allocation to nestlings by male and female Hoopoe parents. Masters Thesis. University of Bern: Germany.
107	Safriel, U. N. 1981. Social hierarchy among siblings in broods of the oystercatcher <i>Haematopus ostralegus</i> . <i>Behavioral Ecology and Sociobiology</i> , 9, 59–63.
108	Saino, N., Ninni, P., Incagli, M., Calza, S., Sacchi, R. & Moller, A. P. 2000. Begging and Parental Care in Relation to Offspring Need and Condition in the Barn Swallow (<i>Hirundo rustica</i>). <i>The American Naturalist</i> , 156, 637–649.
109	Sasvári, L. 1990. Feeding response of mated and widowed bird parents to fledglings: an experimental study. <i>Ornis Scandinavica</i> , 21, 287–292.
110	Sasvári, L., Hegyi, Z. & Péczely, P. 1999. Brood reduction in white storks mediated through asymmetries in plasma testosterone concentrations in chicks. <i>Ethology</i> , 105, 458–471.
111	Sasvári, L., Peczely, P. & Hegyi, Z. 2004. The influence of parental age and weather on testosterone concentration and offspring survival in broods of tawny owl <i>Strix aluco</i> . <i>Behavioral Ecology and Sociobiology</i> , 56, 306–313.
112	Schuster, C. 1996. The role of nonvocal begging behaviour in food allocation in nestling Yellow Warblers (<i>Dendroica petechia</i>). <i>UFS (Delta Marsh) Annual Report</i> , 31, 103–106.
113	Shizuka, D. & Lyon, B. E. 2013. Family dynamics through time: brood reduction followed by parental compensation with aggression and favouritism. <i>Ecology letters</i> , 16, 315–22.
114	Skagen, S. 1988. Asynchronous hatching and food limitation: A test of Lack's hypothesis. <i>The Auk</i> , 105, 78–88.
115	Slagsvold, T. & Wiebe, K. L. 2007. Hatching asynchrony and early nestling mortality: the feeding constraint hypothesis. <i>Animal Behaviour</i> , 73, 691–700.
116	Slagsvold, T. 1997. Is there a sexual conflict over hatching asynchrony in American Robins? <i>The Auk</i> , 114, 593–600.
117	Slagsvold, T., Amundsen, T. & Dale, S. 1995. Costs and benefits of hatching asynchrony in blue tits <i>Parus caeruleus</i> . <i>Journal of Animal Ecology</i> , 64, 563–578.

Study	Citation
118	Smiseth, P. T. & Amundsen, T. 2002. Senior and junior nestlings in asynchronous bluethroat broods differ in their effectiveness of begging. <i>Evolutionary Ecology Research</i> , 4, 1177–1189.
119	Smiseth, P. T., Amundsen, T. & Hansen, L. T. T. 1998. Do males and females differ in the feeding of large and small siblings? An experiment with the bluethroat. <i>Behavioral Ecology and Sociobiology</i> , 42, 321–328.
120	Smiseth, P. T., Bu, R. J., Eikenaes, A. K. & Amundsen, T. 2003. Food limitation in asynchronous bluethroat broods: effects on food distribution, nestling begging, and parental provisioning rules. <i>Behavioral Ecology</i> , 14, 793–801.
121	Smith, T. E., Leonard, M. L. & Smith, B. D. 2005. Provisioning rules and chick competition in asynchronously hatching common terns (<i>Sterna hirundo</i>). <i>Behavioral Ecology and Sociobiology</i> , 58, 456–465.
122	Snow, B. 1960. The breeding biology of the shag <i>Phalacrocorax aristotelis</i> on the island of Lundy, Bristol Channel. <i>Ibis</i> , 102, 554–575.
123	Steidl, R. J. & Griffin, C. R. 1991. Growth and Brood Reduction of Mid-Atlantic Coast Ospreys. <i>The Auk</i> , 108, 363–370.
124	Sternalski, A., Mougeot, F. & Bretagnolle, V. 2012. Carotenoid limitation and allocation priorities in asynchronous raptor nestlings. <i>Biological Journal of the Linnean Society</i> , 105, 13–24.
125	Stoleson, S. H. & Beissinger, S. R. 1997. Hatching Asynchrony, Brood Reduction, and Food Limitation in a Neotropical Parrot. <i>Ecological Monographs</i> , 67, 131–154.
126	Styrsky, J. D., Eckerle, K. P. & Thompson, C. F. 1999. Fitness-related consequences of egg mass in nestling house wrens. <i>Proceedings of the Royal Society B: Biological Sciences</i> , 266, 1253–1258.
127	Surmacki, A. & Kosicki, J. Z. 2009. Condition-dependent leg colour of nestling White Storks <i>Ciconia ciconia</i> . <i>Ibis</i> , 151, 762–765.
128	Szollosi, E., Rosivall, B. & Torok, J. 2007. Is hatching asynchrony beneficial for the brood? <i>Behavioral Ecology</i> , 18, 420–426.
129	Tanner, M., Kölliker, M. & Richner, H. 2008. Differential food allocation by male and female great tit, <i>Parus major</i> , parents: are parents or offspring in control? <i>Animal Behaviour</i> , 75, 1563–1569.
130	Tarwater, C. E. & Brawn, J. D. 2008. Patterns of brood division and an absence of behavioral plasticity in a neotropical passerine. <i>Behavioral Ecology and Sociobiology</i> , 62, 1441–1452.
131	Tarwater, C. E., Kelley, J. P. & Brawn, J. D. 2009. Parental response to elevated begging in a high predation, tropical environment. <i>Animal Behaviour</i> , 78, 1239–1245.
132	Teather, K. & Weatherhead, P. 1989. Sex-Specific Mortality in Nestling Great-Tailed Grackles. <i>Ecology</i> , 70, 1485–1493.
133	Teather, K. 1990. The influence of sibling gender on the growth and survival of Great-tailed Grackle nestlings. <i>Canadian Journal of Zoology</i> , 68, 1925–1930.
134	Vallarino, A., Wingfield, J. & Drummond, H. 2006. Does extra corticosterone elicit increased begging and submissiveness in subordinate booby (<i>Sula neboxii</i>) chicks? <i>General and Comparative Endocrinology</i> , 147, 297–303.
135	Vermeer, K. 1963. The breeding ecology of the glaucous-winged gull (<i>Larus glaucescens</i>) on Mandarte Island, B.C. Masters Dissertation. University of British Columbia.
136	Viñuela, J. & Bustamante, J. 1992. Effect of growth and hatching asynchrony on the fledging age of black and red kites. <i>The Auk</i> , 109, 748–757.
137	Viñuela, J. 2000. Opposing selective pressures on hatching asynchrony: egg viability, brood reduction, and nestling growth. <i>Behavioral Ecology and Sociobiology</i> , 48, 333–343.
138	Weatherhead, P. & McRae, S. 1990. Brood care in American robins: implications for mixed reproductive strategies by females. <i>Animal Behaviour</i> , 39, 1179–1188.
139	White, J., Leclaire, S., Krilloff, M., Mulard, H., Hatch, S. a. & Danchin, E. 2010. Sustained increase in food supplies reduces broodmate aggression in black-legged kittiwakes. <i>Animal Behaviour</i> , 79, 1095–1100.
140	Whittingham, L. A., Dunn, P. O. & Clotfelter, E. D. 2003. Parental allocation of food to nestling tree swallows: the influence of nestling behaviour, sex and paternity. <i>Animal Behaviour</i> , 65, 1203–1210.
141	Wiebe, K. L. & Bortolotti, G. R. 1994. Food Supply and Hatching Spans of Birds: Energy Constraints or Facultative Manipulation? <i>Ecology</i> , 75, 813–823.

Study	Citation
142	Wiebe, K. L. & Slagsvold, T. 2009. Parental Sex Differences in Food Allocation to Junior Brood Members as Mediated by Prey Size. <i>Ethology</i> , 115, 49–58.
143	Wiebe, K. L. & Slagsvold, T. 2012. Parents take both size and conspicuousness into account when feeding nestlings in dark cavity nests. <i>Animal Behaviour</i> , 84, 1307–1312.
144	Wright, J., Hinde, C., Fazey, I. & Both, C. 2002. Begging signals more than just short-term need: cryptic effects of brood size in the pied flycatcher (<i>Ficedula hypoleuca</i>). <i>Behavioral Ecology and Sociobiology</i> , 52, 74–83.
145	Wright, J., Karasov, W. H., Kazem, A. J. N., Gonçalves, I. B. & McSwan, E. 2010. Begging and digestive responses to differences in long-term and short-term need in nestling pied flycatchers. <i>Animal Behaviour</i> , 80, 517–525.

Table A2. Data included in the within-species meta-analysis (Chapter 3)

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and begging	<i>Apus pallidus</i>	78	Normal	0.40	12
Feeding and begging	<i>Apus pallidus</i>	78	Good	0.72	12
Feeding and begging	<i>Bubulcus ibis</i>	29	Normal	0.43	8
Feeding and begging	<i>Bubulcus ibis</i>	29	Normal	0.47	17
Feeding and begging	<i>Bubulcus ibis</i>	29	Normal	0.51	9
Feeding and begging	<i>Bubulcus ibis</i>	29	Normal	0.54	10
Feeding and begging	<i>Bubulcus ibis</i>	29	Poor	0.42	28
Feeding and begging	<i>Bubulcus ibis</i>	29	Poor	0.42	8
Feeding and begging	<i>Bubulcus ibis</i>	29	Poor	0.43	21
Feeding and begging	<i>Bubulcus ibis</i>	29	Poor	0.44	8
Feeding and begging	<i>Bubulcus ibis</i>	30	Poor	0.44	3
Feeding and begging	<i>Bubulcus ibis</i>	30	Poor	0.52	3
Feeding and begging	<i>Bubulcus ibis</i>	30	Normal	0.76	6
Feeding and begging	<i>Bubulcus ibis</i>	30	Normal	0.63	6
Feeding and begging	<i>Columba livia</i>	87	Good	0.39	6
Feeding and begging	<i>Columba livia</i>	87	Good	0.99	6
Feeding and begging	<i>Columba livia</i>	87	Good	0.92	6
Feeding and begging	<i>Columba livia</i>	87	Good	0.96	6
Feeding and begging	<i>Columba livia</i>	87	Normal	0.33	12
Feeding and begging	<i>Columba livia</i>	87	Normal	0.59	12
Feeding and begging	<i>Columba livia</i>	87	Normal	0.82	12
Feeding and begging	<i>Columba livia</i>	87	Normal	0.93	12
Feeding and begging	<i>Columba livia</i>	87	Poor	0.37	6
Feeding and begging	<i>Columba livia</i>	87	Poor	0.42	6
Feeding and begging	<i>Columba livia</i>	87	Poor	0.74	6
Feeding and begging	<i>Columba livia</i>	87	Poor	0.96	6
Feeding and begging	<i>Dendroica petechia</i>	69	Normal	0.34	15
Feeding and begging	<i>Dendroica petechia</i>	69	Normal	0.19	15
Feeding and begging	<i>Dendroica petechia</i>	112	Good	0.55	6
Feeding and begging	<i>Dendroica petechia</i>	112	Good	-0.39	6
Feeding and begging	<i>Dendroica petechia</i>	112	Normal	0.49	7
Feeding and begging	<i>Dendroica petechia</i>	112	Normal	-0.50	7
Feeding and begging	<i>Ficedula albicollis</i>	104	Normal	0.19	9
Feeding and begging	<i>Ficedula albicollis</i>	104	Good	0.20	8
Feeding and begging	<i>Ficedula albicollis</i>	104	Good	0.19	8
Feeding and begging	<i>Ficedula albicollis</i>	104	Good	0.19	8
Feeding and begging	<i>Ficedula hypoleuca</i>	34	Poor	0.34	5
Feeding and begging	<i>Ficedula hypoleuca</i>	34	Poor	0.85	5
Feeding and begging	<i>Ficedula hypoleuca</i>	34	Normal	0.69	6
Feeding and begging	<i>Ficedula hypoleuca</i>	34	Normal	0.84	6
Feeding and begging	<i>Forpus passerinus</i>	17	Poor	0.41	7
Feeding and begging	<i>Forpus passerinus</i>	17	Poor	0.45	4

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and begging	<i>Forpus passerinus</i>	17	Poor	0.68	9
Feeding and begging	<i>Forpus passerinus</i>	17	Good	0.02	8
Feeding and begging	<i>Forpus passerinus</i>	17	Good	0.57	6
Feeding and begging	<i>Forpus passerinus</i>	17	Good	0.68	10
Feeding and begging	<i>Hirundo rustica</i>	12	Normal	0.27	30
Feeding and begging	<i>Hirundo rustica</i>	12	Normal	0.13	33
Feeding and begging	<i>Hirundo rustica</i>	13	Poor	0.58	42
Feeding and begging	<i>Hirundo rustica</i>	13	Normal	0.67	42
Feeding and begging	<i>Hirundo rustica</i>	13	Normal	0.67	42
Feeding and begging	<i>Hirundo rustica</i>	21	Good	0.39	40
Feeding and begging	<i>Hirundo rustica</i>	70	Normal	0.12	11
Feeding and begging	<i>Hirundo rustica</i>	70	Normal	0.49	11
Feeding and begging	<i>Hirundo rustica</i>	108	Good	0.72	24
Feeding and begging	<i>Hirundo rustica</i>	108	Normal	0.54	24
Feeding and begging	<i>Hirundo rustica</i>	108	Normal	0.46	41
Feeding and begging	<i>Hirundo rustica</i>	108	Poor	0.31	27
Feeding and begging	<i>Luscinia svecica</i>	120	Normal	0.07	19
Feeding and begging	<i>Luscinia svecica</i>	120	Normal	0.13	19
Feeding and begging	<i>Luscinia svecica</i>	120	Normal	0.09	19
Feeding and begging	<i>Luscinia svecica</i>	120	Normal	0.05	19
Feeding and begging	<i>Luscinia svecica</i>	120	Normal	0.26	19
Feeding and begging	<i>Luscinia svecica</i>	120	Poor	0.15	19
Feeding and begging	<i>Luscinia svecica</i>	120	Poor	0.16	19
Feeding and begging	<i>Luscinia svecica</i>	120	Poor	0.18	19
Feeding and begging	<i>Luscinia svecica</i>	120	Poor	0.20	19
Feeding and begging	<i>Luscinia svecica</i>	120	Poor	0.49	19
Feeding and begging	<i>Parus major</i>	7	Normal	0.03	2
Feeding and begging	<i>Parus major</i>	7	Normal	-0.03	2
Feeding and begging	<i>Parus major</i>	7	Poor	-0.07	4
Feeding and begging	<i>Parus major</i>	7	Poor	0.08	4
Feeding and begging	<i>Parus major</i>	51	Normal	0.67	15
Feeding and begging	<i>Parus major</i>	55	Normal	0.77	65
Feeding and begging	<i>Parus major</i>	55	Normal	0.83	65
Feeding and begging	<i>Parus major</i>	109	Normal	0.82	20
Feeding and begging	<i>Parus major</i>	109	Normal	0.85	20
Feeding and begging	<i>Parus major</i>	109	Normal	0.91	20
Feeding and begging	<i>Parus major</i>	109	Normal	0.94	20
Feeding and begging	<i>Parus major</i>	129	Normal	0.38	26
Feeding and begging	<i>Parus major</i>	129	Normal	0.15	26
Feeding and begging	<i>Parus major</i>	129	Normal	0.69	26
Feeding and begging	<i>Pica pica</i>	62	Poor	0.26	6
Feeding and begging	<i>Pica pica</i>	62	Poor	0.42	6
Feeding and begging	<i>Pica pica</i>	62	Poor	0.64	6
Feeding and begging	<i>Pica pica</i>	62	Poor	0.92	6
Feeding and begging	<i>Pica pica</i>	62	Good	0.93	6
Feeding and begging	<i>Pica pica</i>	62	Normal	0.83	6
Feeding and begging	<i>Pica pica</i>	62	Good	0.32	6
Feeding and begging	<i>Pica pica</i>	62	Normal	0.74	6
Feeding and begging	<i>Pica pica</i>	62	Good	0.54	6
Feeding and begging	<i>Pica pica</i>	62	Normal	0.59	6
Feeding and begging	<i>Pica pica</i>	62	Good	0.16	6
Feeding and begging	<i>Pica pica</i>	62	Normal	0.83	6
Feeding and begging	<i>Pica pica</i>	79	Normal	0.44	42
Feeding and begging	<i>Pica pica</i>	79	Normal	0.15	42
Feeding and begging	<i>Pica pica</i>	79	Normal	0.28	42
Feeding and begging	<i>Pica pica</i>	80	Normal	0.41	33
Feeding and begging	<i>Pica pica</i>	80	Normal	0.41	33
Feeding and begging	<i>Pica pica</i>	80	Normal	0.91	33
Feeding and begging	<i>Pica pica</i>	80	Normal	0.58	33
Feeding and begging	<i>Pica pica</i>	88	Normal	0.82	11
Feeding and begging	<i>Pica pica</i>	88	Normal	0.93	11
Feeding and begging	<i>Pica pica</i>	88	Normal	0.93	4
Feeding and begging	<i>Pica pica</i>	88	Good	0.94	7
Feeding and begging	<i>Pica pica</i>	97	Normal	0.34	38
Feeding and begging	<i>Pica pica</i>	97	Normal	0.32	38

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and begging	<i>Pica pica</i>	97	Normal	0.26	21
Feeding and begging	<i>Pica pica</i>	97	Normal	0.22	8
Feeding and begging	<i>Platycercus elegans</i>	56	Normal	-0.24	9
Feeding and begging	<i>Platycercus elegans</i>	56	Normal	0.70	9
Feeding and begging	<i>Platycercus elegans</i>	56	Normal	0.59	9
Feeding and begging	<i>Platycercus elegans</i>	56	Normal	-0.10	9
Feeding and begging	<i>Platycercus elegans</i>	57	Poor	0.00	9
Feeding and begging	<i>Platycercus elegans</i>	57	Normal	0.01	9
Feeding and begging	<i>Platycercus elegans</i>	57	Poor	0.09	9
Feeding and begging	<i>Platycercus elegans</i>	57	Normal	0.41	9
Feeding and begging	<i>Rissa tridactyla</i>	15	Poor	0.14	9
Feeding and begging	<i>Rissa tridactyla</i>	86	Poor	0.30	6
Feeding and begging	<i>Rissa tridactyla</i>	86	Poor	0.62	13
Feeding and begging	<i>Rissa tridactyla</i>	86	Good	0.75	22
Feeding and begging	<i>Rissa tridactyla</i>	86	Good	0.69	17
Feeding and begging	<i>Sula neboxii</i>	24	Normal	0.19	8
Feeding and begging	<i>Sula neboxii</i>	24	Normal	0.49	8
Feeding and begging	<i>Sula neboxii</i>	24	Normal	0.53	14
Feeding and begging	<i>Sula neboxii</i>	24	Normal	0.64	17
Feeding and begging	<i>Sula neboxii</i>	24	Good	0.69	11
Feeding and begging	<i>Sula neboxii</i>	24	Poor	0.54	18
Feeding and begging	<i>Sula neboxii</i>	134	Normal	0.59	17
Feeding and begging	<i>Sula neboxii</i>	134	Normal	0.36	17
Feeding and begging	<i>Sula neboxii</i>	134	Normal	0.97	17
Feeding and begging	<i>Sula neboxii</i>	134	Normal	-0.75	17
Feeding and begging	<i>Sula neboxii</i>	134	Poor	-0.98	17
Feeding and begging	<i>Sula neboxii</i>	134	Poor	-0.91	17
Feeding and begging	<i>Sula neboxii</i>	134	Poor	0.98	17
Feeding and begging	<i>Sula neboxii</i>	134	Poor	0.99	17
Feeding and begging	<i>Tachycineta bicolor</i>	64	Normal	0.88	16
Feeding and begging	<i>Tachycineta bicolor</i>	65	Normal	0.74	27
Feeding and begging	<i>Tachycineta bicolor</i>	65	Normal	0.37	29
Feeding and begging	<i>Tachycineta bicolor</i>	65	Normal	-0.04	16
Feeding and begging	<i>Tachycineta bicolor</i>	65	Poor	0.58	13
Feeding and begging	<i>Tachycineta bicolor</i>	66	Normal	0.23	25
Feeding and begging	<i>Tachycineta bicolor</i>	66	Normal	0.40	23
Feeding and begging	<i>Tachycineta bicolor</i>	66	Normal	0.20	12
Feeding and begging	<i>Tachycineta bicolor</i>	66	Normal	0.41	7
Feeding and begging	<i>Tachycineta bicolor</i>	66	Normal	0.65	10
Feeding and begging	<i>Tachycineta bicolor</i>	67	Normal	0.61	31
Feeding and begging	<i>Tachycineta bicolor</i>	67	Normal	0.85	31
Feeding and begging	<i>Tachycineta bicolor</i>	67	Normal	0.19	31
Feeding and begging	<i>Tachycineta bicolor</i>	67	Normal	0.47	31
Feeding and begging	<i>Tachycineta bicolor</i>	140	Normal	0.98	18
Feeding and begging	<i>Tachycineta bicolor</i>	140	Normal	0.99	18
Feeding and begging	<i>Tachycineta bicolor</i>	140	Normal	0.99	18
Feeding and begging	<i>Taeniopygia guttata</i>	32	Normal	0.80	28
Feeding and begging	<i>Taeniopygia guttata</i>	32	Normal	0.15	28
Feeding and begging	<i>Taeniopygia guttata</i>	68	Good	0.62	6
Feeding and begging	<i>Taeniopygia guttata</i>	68	Good	0.78	6
Feeding and begging	<i>Taeniopygia guttata</i>	68	Good	0.94	6
Feeding and begging	<i>Taeniopygia guttata</i>	68	Good	0.97	6
Feeding and begging	<i>Taeniopygia guttata</i>	76	Good	0.95	13
Feeding and begging	<i>Taeniopygia guttata</i>	76	Good	0.95	17
Feeding and begging	<i>Taeniopygia guttata</i>	76	Good	0.95	17
Feeding and begging	<i>Taeniopygia guttata</i>	76	Good	0.97	13
Feeding and begging	<i>Thamnophilus atrinucha</i>	131	Normal	0.76	11
Feeding and begging	<i>Thamnophilus atrinucha</i>	131	Poor	0.72	11
Feeding and body size	<i>Aphelocoma coerulescens</i>	98	Good	0.43	10
Feeding and body size	<i>Aphelocoma coerulescens</i>	98	Normal	0.51	8
Feeding and body size	<i>Aphelocoma</i>	98	Poor	0.60	6

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and body size	<i>coerulescens</i>				
Feeding and body size	<i>Aphelocoma</i>	99	Good	-0.45	9
	<i>coerulescens</i>				
Feeding and body size	<i>Aphelocoma</i>	99	Good	0.07	9
	<i>coerulescens</i>				
Feeding and body size	<i>Aphelocoma</i>	99	Poor	0.13	19
	<i>coerulescens</i>				
Feeding and body size	<i>Aphelocoma</i>	99	Normal	0.19	18
	<i>coerulescens</i>				
Feeding and body size	<i>Apus pallidus</i>	77	Good	0.37	16
Feeding and body size	<i>Apus pallidus</i>	77	Poor	0.54	33
Feeding and body size	<i>Apus pallidus</i>	78	Poor	0.41	14
Feeding and body size	<i>Apus pallidus</i>	78	Good	0.30	11
Feeding and body size	<i>Athene cunicularia</i>	39	Normal	0.29	5
Feeding and body size	<i>Athene cunicularia</i>	39	Normal	0.87	8
Feeding and body size	<i>Athene cunicularia</i>	39	Good	0.38	4
Feeding and body size	<i>Athene cunicularia</i>	39	Good	0.36	7
Feeding and body size	<i>Athene cunicularia</i>	39	Normal	-0.09	3
Feeding and body size	<i>Athene cunicularia</i>	39	Normal	0.78	5
Feeding and body size	<i>Athene cunicularia</i>	39	Good	-0.25	3
Feeding and body size	<i>Athene cunicularia</i>	39	Good	-0.09	7
Feeding and body size	<i>Casmerodius albus</i>	20	Normal	0.42	7
Feeding and body size	<i>Casmerodius albus</i>	84	Normal	0.85	16
Feeding and body size	<i>Casmerodius albus</i>	84	Normal	0.88	16
Feeding and body size	<i>Casmerodius albus</i>	85	Good	0.49	5
Feeding and body size	<i>Casmerodius albus</i>	85	Normal	0.84	6
Feeding and body size	<i>Casmerodius albus</i>	85	Good	0.34	5
Feeding and body size	<i>Casmerodius albus</i>	85	Normal	0.72	6
Feeding and body size	<i>Casmerodius albus</i>	93	Normal	0.64	15
Feeding and body size	<i>Casmerodius albus</i>	94	Normal	0.59	5
Feeding and body size	<i>Casmerodius albus</i>	94	Normal	0.67	5
Feeding and body size	<i>Casmerodius albus</i>	94	Normal	0.76	5
Feeding and body size	<i>Cepphus grylle</i>	19	Normal	0.05	5
Feeding and body size	<i>Cepphus grylle</i>	19	Normal	-0.01	15
Feeding and body size	<i>Cepphus grylle</i>	19	Poor	0.60	15
Feeding and body size	<i>Ciconia ciconia</i>	23	Normal	0.80	9
Feeding and body size	<i>Ciconia ciconia</i>	23	Normal	0.85	7
Feeding and body size	<i>Ciconia ciconia</i>	23	Normal	0.73	11
Feeding and body size	<i>Ciconia ciconia</i>	23	Poor	0.78	34
Feeding and body size	<i>Ciconia ciconia</i>	23	Normal	0.79	35
Feeding and body size	<i>Ciconia ciconia</i>	23	Normal	0.78	40
Feeding and body size	<i>Ciconia ciconia</i>	110	Normal	0.48	14
Feeding and body size	<i>Ciconia ciconia</i>	110	Poor	0.98	8
Feeding and body size	<i>Ciconia ciconia</i>	110	Poor	0.97	8
Feeding and body size	<i>Ciconia ciconia</i>	110	Poor	0.97	8
Feeding and body size	<i>Ciconia ciconia</i>	110	Good	0.85	6
Feeding and body size	<i>Ciconia ciconia</i>	110	Good	0.84	6
Feeding and body size	<i>Ciconia ciconia</i>	110	Good	0.49	6
Feeding and body size	<i>Ciconia ciconia</i>	110	Poor	0.97	12
Feeding and body size	<i>Ciconia ciconia</i>	110	Poor	0.68	3
Feeding and body size	<i>Ciconia ciconia</i>	110	Poor	0.96	9
Feeding and body size	<i>Ciconia ciconia</i>	110	Normal	0.81	9
Feeding and body size	<i>Ciconia ciconia</i>	110	Good	0.89	9
Feeding and body size	<i>Ciconia ciconia</i>	127	Normal	0.00	16
Feeding and body size	<i>Circus pygargus</i>	4	Normal	0.35	22
Feeding and body size	<i>Circus pygargus</i>	4	Good	-0.55	4
Feeding and body size	<i>Circus pygargus</i>	4	Normal	0.61	8
Feeding and body size	<i>Circus pygargus</i>	4	Normal	0.77	9
Feeding and body size	<i>Circus pygargus</i>	4	Poor	0.99	1
Feeding and body size	<i>Circus pygargus</i>	4	Normal	0.28	62
Feeding and body size	<i>Circus pygargus</i>	4	Normal	0.30	62
Feeding and body size	<i>Circus pygargus</i>	4	Normal	0.32	62
Feeding and body size	<i>Circus pygargus</i>	124	Normal	0.27	50
Feeding and body size	<i>Circus pygargus</i>	124	Good	0.12	50
Feeding and body size	<i>Collocalia esculenta</i>	16	Normal	0.31	26

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and body size	<i>Collocalia esculenta</i>	16	Good	0.20	17
Feeding and body size	<i>Collocalia esculenta</i>	16	Normal	0.52	16
Feeding and body size	<i>Collocalia esculenta</i>	16	Good	0.37	5
Feeding and body size	<i>Collocalia esculenta</i>	16	Normal	0.44	7
Feeding and body size	<i>Collocalia esculenta</i>	16	Good	0.00	3
Feeding and body size	<i>Coracias garrulus</i>	5	Normal	0.48	21
Feeding and body size	<i>Coracias garrulus</i>	5	Good	0.01	21
Feeding and body size	<i>Coracias garrulus</i>	5	Normal	0.48	21
Feeding and body size	<i>Coracias garrulus</i>	92	Normal	0.66	26
Feeding and body size	<i>Coracias garrulus</i>	92	Normal	0.32	26
Feeding and body size	<i>Coracias garrulus</i>	92	Normal	0.55	26
Feeding and body size	<i>Coracias garrulus</i>	92	Normal	0.31	26
Feeding and body size	<i>Coracias garrulus</i>	92	Normal	0.26	26
Feeding and body size	<i>Coracias garrulus</i>	92	Normal	0.48	12
Feeding and body size	<i>Coracias garrulus</i>	92	Normal	-0.73	12
Feeding and body size	<i>Coracias garrulus</i>	92	Normal	0.68	12
Feeding and body size	<i>Coracias garrulus</i>	92	Normal	0.38	12
Feeding and body size	<i>Corcorax melanorhamphos</i>	10	Good	-0.15	13
Feeding and body size	<i>Corcorax melanorhamphos</i>	10	Normal	0.34	13
Feeding and body size	<i>Egretta garzetta</i>	37	Good	0.01	39
Feeding and body size	<i>Egretta garzetta</i>	37	Normal	0.06	67
Feeding and body size	<i>Egretta garzetta</i>	47	Normal	0.52	37
Feeding and body size	<i>Egretta garzetta</i>	47	Normal	0.61	3
Feeding and body size	<i>Egretta garzetta</i>	47	Normal	0.31	37
Feeding and body size	<i>Egretta garzetta</i>	47	Poor	0.15	8
Feeding and body size	<i>Egretta garzetta</i>	47	Poor	0.82	8
Feeding and body size	<i>Egretta garzetta</i>	47	Normal	0.81	3
Feeding and body size	<i>Falco sparverius</i>	141	Normal	0.86	206
Feeding and body size	<i>Falco sparverius</i>	141	Good	0.52	49
Feeding and body size	<i>Falco sparverius</i>	141	Good	0.86	51
Feeding and body size	<i>Falco sparverius</i>	141	Normal	0.65	53
Feeding and body size	<i>Ficedula albicollis</i>	42	Good	0.09	57
Feeding and body size	<i>Ficedula albicollis</i>	42	Normal	0.70	57
Feeding and body size	<i>Ficedula albicollis</i>	42	Normal	0.88	57
Feeding and body size	<i>Ficedula albicollis</i>	42	Normal	0.40	57
Feeding and body size	<i>Ficedula albicollis</i>	60	Normal	0.63	22
Feeding and body size	<i>Ficedula albicollis</i>	60	Normal	-0.02	22
Feeding and body size	<i>Ficedula albicollis</i>	60	Normal	0.38	22
Feeding and body size	<i>Ficedula albicollis</i>	60	Normal	0.46	22
Feeding and body size	<i>Ficedula albicollis</i>	102	Normal	0.60	45
Feeding and body size	<i>Ficedula albicollis</i>	102	Normal	0.45	45
Feeding and body size	<i>Ficedula albicollis</i>	102	Normal	0.09	45
Feeding and body size	<i>Ficedula albicollis</i>	102	Normal	0.25	45
Feeding and body size	<i>Ficedula albicollis</i>	103	Normal	0.38	32
Feeding and body size	<i>Ficedula albicollis</i>	103	Normal	0.23	32
Feeding and body size	<i>Ficedula albicollis</i>	104	Good	0.23	8
Feeding and body size	<i>Ficedula albicollis</i>	104	Good	0.36	8
Feeding and body size	<i>Ficedula albicollis</i>	104	Good	0.39	8
Feeding and body size	<i>Ficedula albicollis</i>	104	Normal	-0.14	9
Feeding and body size	<i>Ficedula albicollis</i>	104	Normal	-0.21	9
Feeding and body size	<i>Ficedula albicollis</i>	104	Normal	-0.25	9
Feeding and body size	<i>Ficedula albicollis</i>	128	Normal	0.56	43
Feeding and body size	<i>Ficedula albicollis</i>	128	Normal	0.37	43
Feeding and body size	<i>Ficedula albicollis</i>	128	Normal	0.79	43
Feeding and body size	<i>Ficedula albicollis</i>	128	Normal	0.45	43
Feeding and body size	<i>Ficedula albicollis</i>	128	Normal	0.15	43
Feeding and body size	<i>Ficedula hypoleuca</i>	34	Normal	-0.01	6
Feeding and body size	<i>Ficedula hypoleuca</i>	34	Poor	0.03	5
Feeding and body size	<i>Ficedula hypoleuca</i>	34	Poor	-0.09	5
Feeding and body size	<i>Ficedula hypoleuca</i>	34	Normal	-0.76	5
Feeding and body size	<i>Ficedula hypoleuca</i>	34	Normal	0.24	5
Feeding and body size	<i>Ficedula hypoleuca</i>	34	Poor	0.44	5
Feeding and body size	<i>Ficedula hypoleuca</i>	115	Normal	0.60	24

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and body size	<i>Ficedula hypoleuca</i>	142	Normal	0.23	24
Feeding and body size	<i>Ficedula hypoleuca</i>	142	Normal	0.14	24
Feeding and body size	<i>Ficedula hypoleuca</i>	142	Good	0.12	24
Feeding and body size	<i>Ficedula hypoleuca</i>	142	Good	0.08	24
Feeding and body size	<i>Ficedula hypoleuca</i>	142	Normal	0.47	24
Feeding and body size	<i>Ficedula hypoleuca</i>	142	Normal	0.48	24
Feeding and body size	<i>Ficedula hypoleuca</i>	142	Good	0.50	24
Feeding and body size	<i>Ficedula hypoleuca</i>	142	Normal	0.91	24
Feeding and body size	<i>Ficedula hypoleuca</i>	143	Normal	0.36	48
Feeding and body size	<i>Ficedula hypoleuca</i>	144	Good	0.49	18
Feeding and body size	<i>Ficedula hypoleuca</i>	144	Good	0.66	18
Feeding and body size	<i>Ficedula hypoleuca</i>	144	Good	0.54	18
Feeding and body size	<i>Ficedula hypoleuca</i>	144	Poor	0.75	18
Feeding and body size	<i>Ficedula hypoleuca</i>	144	Poor	0.81	18
Feeding and body size	<i>Ficedula hypoleuca</i>	144	Poor	0.46	18
Feeding and body size	<i>Ficedula hypoleuca</i>	145	Normal	0.50	30
Feeding and body size	<i>Forpus passerinus</i>	6	Normal	0.40	27
Feeding and body size	<i>Forpus passerinus</i>	6	Normal	0.33	25
Feeding and body size	<i>Forpus passerinus</i>	6	Poor	0.58	4
Feeding and body size	<i>Forpus passerinus</i>	6	Normal	0.60	11
Feeding and body size	<i>Forpus passerinus</i>	6	Good	0.32	8
Feeding and body size	<i>Forpus passerinus</i>	6	Poor	0.98	4
Feeding and body size	<i>Forpus passerinus</i>	6	Normal	0.26	11
Feeding and body size	<i>Forpus passerinus</i>	6	Good	-0.01	8
Feeding and body size	<i>Forpus passerinus</i>	17	Good	-0.28	10
Feeding and body size	<i>Forpus passerinus</i>	17	Poor	-0.50	9
Feeding and body size	<i>Forpus passerinus</i>	17	Poor	0.82	9
Feeding and body size	<i>Forpus passerinus</i>	17	Good	0.90	10
Feeding and body size	<i>Forpus passerinus</i>	125	Normal	0.50	61
Feeding and body size	<i>Forpus passerinus</i>	125	Normal	0.21	61
Feeding and body size	<i>Forpus passerinus</i>	125	Good	0.28	7
Feeding and body size	<i>Forpus passerinus</i>	125	Normal	0.43	7
Feeding and body size	<i>Forpus passerinus</i>	125	Poor	0.58	17
Feeding and body size	<i>Forpus passerinus</i>	125	Poor	0.58	17
Feeding and body size	<i>Forpus passerinus</i>	125	Good	-0.33	7
Feeding and body size	<i>Forpus passerinus</i>	125	Normal	0.09	7
Feeding and body size	<i>Forpus passerinus</i>	125	Poor	0.62	17
Feeding and body size	<i>Forpus passerinus</i>	125	Poor	0.17	17
Feeding and body size	<i>Fulica americana</i>	71	Normal	0.29	152
Feeding and body size	<i>Fulica americana</i>	71	Normal	0.99	152
Feeding and body size	<i>Fulica americana</i>	72	Good	-0.03	21
Feeding and body size	<i>Fulica americana</i>	72	Poor	0.39	21
Feeding and body size	<i>Fulica americana</i>	113	Good	-0.24	24
Feeding and body size	<i>Fulica americana</i>	113	Good	-0.18	24
Feeding and body size	<i>Fulica americana</i>	113	Good	-0.36	24
Feeding and body size	<i>Fulica americana</i>	113	Good	0.07	57
Feeding and body size	<i>Fulica americana</i>	113	Normal	0.29	57
Feeding and body size	<i>Fulica americana</i>	113	Good	-0.09	57
Feeding and body size	<i>Fulica americana</i>	113	Normal	0.13	57
Feeding and body size	<i>Fulica americana</i>	113	Good	-0.25	79
Feeding and body size	<i>Fulica americana</i>	113	Normal	0.02	79
Feeding and body size	<i>Haematopus ostralegus</i>	41	Normal	0.19	63
Feeding and body size	<i>Haematopus ostralegus</i>	41	Good	0.16	433
Feeding and body size	<i>Haematopus ostralegus</i>	41	Poor	-0.08	142
Feeding and body size	<i>Haematopus ostralegus</i>	41	Good	0.11	227
Feeding and body size	<i>Haematopus ostralegus</i>	41	Poor	0.04	534
Feeding and body size	<i>Haematopus ostralegus</i>	107	Normal	0.44	10
Feeding and body size	<i>Hirundo rustica</i>	13	Poor	0.47	42
Feeding and body size	<i>Hirundo rustica</i>	13	Normal	-0.13	42

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and body size	<i>Hirundo rustica</i>	13	Poor	-0.29	42
Feeding and body size	<i>Hirundo rustica</i>	28	Normal	0.55	126
Feeding and body size	<i>Hirundo rustica</i>	28	Normal	0.69	126
Feeding and body size	<i>Hirundo rustica</i>	28	Good	0.37	126
Feeding and body size	<i>Hirundo rustica</i>	28	Good	0.50	126
Feeding and body size	<i>Hirundo rustica</i>	28	Normal	0.76	126
Feeding and body size	<i>Hirundo rustica</i>	28	Normal	0.09	126
Feeding and body size	<i>Hirundo rustica</i>	70	Normal	0.13	11
Feeding and body size	<i>Hirundo rustica</i>	70	Normal	0.42	11
Feeding and body size	<i>Hirundo rustica</i>	108	Poor	0.29	27
Feeding and body size	<i>Hirundo rustica</i>	108	Good	0.75	24
Feeding and body size	<i>Hirundo rustica</i>	108	Normal	0.36	41
Feeding and body size	<i>Larus argentatus</i>	43	Normal	0.80	10
Feeding and body size	<i>Larus argentatus</i>	43	Normal	0.57	13
Feeding and body size	<i>Larus argentatus</i>	43	Normal	0.09	18
Feeding and body size	<i>Larus argentatus</i>	43	Normal	0.50	13
Feeding and body size	<i>Larus argentatus</i>	43	Normal	0.59	10
Feeding and body size	<i>Larus argentatus</i>	43	Normal	0.27	12
Feeding and body size	<i>Larus argentatus</i>	43	Normal	0.52	13
Feeding and body size	<i>Larus argentatus</i>	43	Normal	0.76	13
Feeding and body size	<i>Larus argentatus</i>	43	Normal	0.19	16
Feeding and body size	<i>Larus argentatus</i>	43	Normal	0.03	13
Feeding and body size	<i>Larus argentatus</i>	43	Normal	0.00	18
Feeding and body size	<i>Larus argentatus</i>	44	Normal	0.05	18
Feeding and body size	<i>Larus argentatus</i>	44	Normal	0.13	23
Feeding and body size	<i>Larus argentatus</i>	44	Normal	0.36	14
Feeding and body size	<i>Larus argentatus</i>	44	Normal	0.38	18
Feeding and body size	<i>Larus argentatus</i>	52	Poor	0.39	46
Feeding and body size	<i>Larus argentatus</i>	52	Poor	0.23	46
Feeding and body size	<i>Larus argentatus</i>	52	Good	0.36	49
Feeding and body size	<i>Larus argentatus</i>	52	Good	0.47	49
Feeding and body size	<i>Larus atricilla</i>	38	Normal	0.37	48
Feeding and body size	<i>Larus atricilla</i>	38	Normal	0.33	48
Feeding and body size	<i>Larus atricilla</i>	38	Normal	0.32	48
Feeding and body size	<i>Larus atricilla</i>	38	Poor	0.00	13
Feeding and body size	<i>Larus fuscus</i>	105	Poor	0.42	13
Feeding and body size	<i>Larus fuscus</i>	105	Poor	0.41	13
Feeding and body size	<i>Larus fuscus</i>	105	Poor	0.52	13
Feeding and body size	<i>Larus fuscus</i>	105	Normal	-0.14	13
Feeding and body size	<i>Larus fuscus</i>	105	Normal	0.19	13
Feeding and body size	<i>Larus fuscus</i>	105	Normal	0.48	13
Feeding and body size	<i>Larus fuscus</i>	105	Normal	0.98	13
Feeding and body size	<i>Larus fuscus</i>	105	Normal	0.51	13
Feeding and body size	<i>Larus fuscus</i>	105	Normal	0.85	13
Feeding and body size	<i>Larus fuscus</i>	105	Normal	0.46	13
Feeding and body size	<i>Larus fuscus</i>	105	Normal	0.31	13
Feeding and body size	<i>Larus fuscus</i>	105	Normal	0.31	13
Feeding and body size	<i>Larus glaucescens</i>	135	Normal	-0.58	11
Feeding and body size	<i>Larus glaucescens</i>	135	Good	-0.06	25
Feeding and body size	<i>Luscinia svecica</i>	118	Normal	0.57	20
Feeding and body size	<i>Luscinia svecica</i>	118	Normal	0.52	10
Feeding and body size	<i>Luscinia svecica</i>	118	Normal	0.87	10
Feeding and body size	<i>Luscinia svecica</i>	119	Good	0.20	19
Feeding and body size	<i>Luscinia svecica</i>	119	Good	0.57	19
Feeding and body size	<i>Luscinia svecica</i>	119	Good	0.63	20
Feeding and body size	<i>Luscinia svecica</i>	119	Good	0.72	20
Feeding and body size	<i>Luscinia svecica</i>	119	Normal	0.12	23
Feeding and body size	<i>Luscinia svecica</i>	119	Normal	0.13	23
Feeding and body size	<i>Luscinia svecica</i>	119	Normal	0.63	25
Feeding and body size	<i>Luscinia svecica</i>	119	Normal	0.74	25
Feeding and body size	<i>Luscinia svecica</i>	120	Normal	0.72	26
Feeding and body size	<i>Luscinia svecica</i>	120	Poor	0.44	26
Feeding and body size	<i>Luscinia svecica</i>	120	Normal	0.54	26
Feeding and body size	<i>Luscinia svecica</i>	120	Normal	0.68	26
Feeding and body size	<i>Milvus migrans</i>	136	Normal	0.40	31

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and body size	<i>Milvus migrans</i>	136	Normal	0.40	31
Feeding and body size	<i>Milvus migrans</i>	136	Normal	0.58	31
Feeding and body size	<i>Milvus migrans</i>	137	Normal	0.18	15
Feeding and body size	<i>Milvus migrans</i>	137	Normal	0.40	15
Feeding and body size	<i>Milvus migrans</i>	137	Normal	0.22	13
Feeding and body size	<i>Milvus migrans</i>	137	Normal	0.33	13
Feeding and body size	<i>Milvus migrans</i>	137	Normal	0.28	58
Feeding and body size	<i>Milvus migrans</i>	137	Normal	0.31	58
Feeding and body size	<i>Milvus migrans</i>	137	Normal	0.23	38
Feeding and body size	<i>Milvus migrans</i>	137	Poor	0.53	38
Feeding and body size	<i>Opisthocomus hoazin</i>	90	Normal	0.68	27
Feeding and body size	<i>Opisthocomus hoazin</i>	90	Poor	-0.11	10
Feeding and body size	<i>Opisthocomus hoazin</i>	90	Poor	0.14	10
Feeding and body size	<i>Opisthocomus hoazin</i>	90	Poor	-0.18	10
Feeding and body size	<i>Opisthocomus hoazin</i>	90	Normal	0.17	29
Feeding and body size	<i>Pandion haliaetus</i>	73	Good	0.55	9
Feeding and body size	<i>Pandion haliaetus</i>	73	Normal	0.56	9
Feeding and body size	<i>Pandion haliaetus</i>	123	Normal	0.84	13
Feeding and body size	<i>Pandion haliaetus</i>	123	Normal	0.85	14
Feeding and body size	<i>Parus caeruleus</i>	22	Normal	0.07	45
Feeding and body size	<i>Parus caeruleus</i>	22	Normal	0.45	45
Feeding and body size	<i>Parus caeruleus</i>	31	Normal	-0.81	13
Feeding and body size	<i>Parus caeruleus</i>	31	Good	-0.46	7
Feeding and body size	<i>Parus caeruleus</i>	31	Normal	-0.23	16
Feeding and body size	<i>Parus caeruleus</i>	31	Good	0.44	14
Feeding and body size	<i>Parus caeruleus</i>	31	Normal	0.51	13
Feeding and body size	<i>Parus caeruleus</i>	31	Good	0.21	7
Feeding and body size	<i>Parus caeruleus</i>	31	Normal	0.83	16
Feeding and body size	<i>Parus caeruleus</i>	31	Good	-0.64	14
Feeding and body size	<i>Parus caeruleus</i>	31	Good	-0.10	24
Feeding and body size	<i>Parus caeruleus</i>	31	Normal	0.56	24
Feeding and body size	<i>Parus caeruleus</i>	74	Normal	0.32	36
Feeding and body size	<i>Parus caeruleus</i>	74	Normal	0.33	36
Feeding and body size	<i>Parus caeruleus</i>	74	Normal	0.43	36
Feeding and body size	<i>Parus caeruleus</i>	74	Normal	-0.44	36
Feeding and body size	<i>Parus caeruleus</i>	74	Normal	0.19	36
Feeding and body size	<i>Parus caeruleus</i>	74	Normal	-0.22	45
Feeding and body size	<i>Parus caeruleus</i>	74	Normal	0.10	45
Feeding and body size	<i>Parus caeruleus</i>	74	Normal	0.32	45
Feeding and body size	<i>Parus caeruleus</i>	74	Normal	-0.12	45
Feeding and body size	<i>Parus caeruleus</i>	74	Normal	0.14	45
Feeding and body size	<i>Parus caeruleus</i>	75	Normal	0.09	66
Feeding and body size	<i>Parus caeruleus</i>	75	Normal	0.45	66
Feeding and body size	<i>Parus caeruleus</i>	117	Poor	0.56	44
Feeding and body size	<i>Parus caeruleus</i>	117	Good	0.72	53
Feeding and body size	<i>Parus palustris</i>	91	Normal	0.16	5
Feeding and body size	<i>Parus palustris</i>	91	Poor	0.98	7
Feeding and body size	<i>Parus palustris</i>	91	Poor	0.83	7
Feeding and body size	<i>Parus palustris</i>	91	Good	-0.07	8
Feeding and body size	<i>Parus palustris</i>	91	Good	0.24	8
Feeding and body size	<i>Pelecanus erythrorhynchos</i>	26	Normal	0.69	80
Feeding and body size	<i>Pelecanus erythrorhynchos</i>	26	Good	0.38	8
Feeding and body size	<i>Pelecanus erythrorhynchos</i>	26	Good	0.45	8
Feeding and body size	<i>Pelecanus erythrorhynchos</i>	26	Normal	0.65	80
Feeding and body size	<i>Pelecanus erythrorhynchos</i>	26	Normal	0.84	26
Feeding and body size	<i>Pelecanus erythrorhynchos</i>	26	Good	0.50	8
Feeding and body size	<i>Pelecanus erythrorhynchos</i>	26	Normal	0.66	26
Feeding and body size	<i>Pelecanus erythrorhynchos</i>	26	Normal	0.79	26

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and body size	<i>erythrorhynchos</i> <i>Pelecanus</i>	26	Normal	0.73	45
Feeding and body size	<i>erythrorhynchos</i> <i>Phalacrocorax aristotelis</i>	1	Normal	-0.10	16
Feeding and body size	<i>Phalacrocorax aristotelis</i>	1	Normal	0.58	16
Feeding and body size	<i>Phalacrocorax aristotelis</i>	1	Normal	0.12	16
Feeding and body size	<i>Phalacrocorax aristotelis</i>	1	Normal	0.50	16
Feeding and body size	<i>Phalacrocorax aristotelis</i>	1	Normal	0.71	16
Feeding and body size	<i>Phalacrocorax aristotelis</i>	1	Normal	0.00	16
Feeding and body size	<i>Phalacrocorax aristotelis</i>	1	Normal	0.21	16
Feeding and body size	<i>Phalacrocorax aristotelis</i>	1	Normal	-0.06	16
Feeding and body size	<i>Phalacrocorax aristotelis</i>	1	Normal	0.14	16
Feeding and body size	<i>Phalacrocorax aristotelis</i>	1	Normal	0.32	16
Feeding and body size	<i>Phalacrocorax aristotelis</i>	1	Normal	0.44	16
Feeding and body size	<i>Phalacrocorax aristotelis</i>	122	Good	0.11	1
Feeding and body size	<i>Phalacrocorax aristotelis</i>	122	Good	-0.25	1
Feeding and body size	<i>Phalacrocorax aristotelis</i>	122	Good	0.91	9
Feeding and body size	<i>Platycercus elegans</i>	56	Normal	0.80	9
Feeding and body size	<i>Platycercus elegans</i>	56	Normal	-0.54	9
Feeding and body size	<i>Platycercus elegans</i>	56	Normal	0.55	9
Feeding and body size	<i>Platycercus elegans</i>	56	Normal	-0.74	9
Feeding and body size	<i>Platycercus elegans</i>	57	Normal	-0.05	9
Feeding and body size	<i>Platycercus elegans</i>	57	Poor	-0.19	9
Feeding and body size	<i>Platycercus elegans</i>	57	Poor	0.22	9
Feeding and body size	<i>Platycercus elegans</i>	57	Normal	0.32	9
Feeding and body size	<i>Platycercus elegans</i>	57	Normal	0.10	9
Feeding and body size	<i>Platycercus elegans</i>	57	Poor	0.31	9
Feeding and body size	<i>Platycercus elegans</i>	58	Normal	0.07	18
Feeding and body size	<i>Platycercus elegans</i>	58	Normal	0.13	18
Feeding and body size	<i>Platycercus elegans</i>	58	Normal	-0.02	18
Feeding and body size	<i>Platycercus elegans</i>	59	Normal	0.09	42
Feeding and body size	<i>Platycercus elegans</i>	59	Normal	0.32	42
Feeding and body size	<i>Podiceps grisegena</i>	54	Normal	0.87	6
Feeding and body size	<i>Podiceps grisegena</i>	54	Good	0.56	11
Feeding and body size	<i>Pygoscelis antarcticus</i>	27	Poor	0.39	25
Feeding and body size	<i>Pygoscelis antarcticus</i>	27	Normal	0.66	39
Feeding and body size	<i>Pygoscelis antarcticus</i>	27	Normal	0.53	82
Feeding and body size	<i>Pygoscelis antarcticus</i>	27	Good	0.00	18
Feeding and body size	<i>Pyrrhura orcesi</i>	53	Normal	-0.29	16
Feeding and body size	<i>Pyrrhura orcesi</i>	53	Normal	0.38	16
Feeding and body size	<i>Pyrrhura orcesi</i>	53	Normal	-0.57	16
Feeding and body size	<i>Pyrrhura orcesi</i>	53	Normal	-0.32	16
Feeding and body size	<i>Pyrrhura orcesi</i>	53	Normal	0.50	4
Feeding and body size	<i>Pyrrhura orcesi</i>	53	Good	-0.01	4
Feeding and body size	<i>Pyrrhura orcesi</i>	53	Normal	0.32	4
Feeding and body size	<i>Pyrrhura orcesi</i>	53	Good	-0.37	4
Feeding and body size	<i>Pyrrhura orcesi</i>	53	Normal	-0.33	4

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and body size	<i>Pyrrhura orcesi</i>	53	Good	-0.75	4
Feeding and body size	<i>Quiscalus mexicanus</i>	132	Good	0.21	329
Feeding and body size	<i>Quiscalus mexicanus</i>	132	Normal	0.10	329
Feeding and body size	<i>Quiscalus mexicanus</i>	132	Poor	0.28	329
Feeding and body size	<i>Quiscalus mexicanus</i>	132	Good	0.23	189
Feeding and body size	<i>Quiscalus mexicanus</i>	132	Normal	0.36	189
Feeding and body size	<i>Quiscalus mexicanus</i>	132	Poor	0.62	189
Feeding and body size	<i>Quiscalus mexicanus</i>	133	Normal	0.36	43
Feeding and body size	<i>Quiscalus mexicanus</i>	133	Normal	0.52	43
Feeding and body size	<i>Quiscalus mexicanus</i>	133	Normal	0.72	163
Feeding and body size	<i>Quiscalus mexicanus</i>	133	Normal	0.77	163
Feeding and body size	<i>Quiscalus mexicanus</i>	133	Normal	0.71	163
Feeding and body size	<i>Quiscalus mexicanus</i>	133	Normal	0.79	163
Feeding and body size	<i>Quiscalus quiscula</i>	45	Normal	0.92	39
Feeding and body size	<i>Quiscalus quiscula</i>	45	Normal	-0.20	23
Feeding and body size	<i>Quiscalus quiscula</i>	45	Normal	0.26	16
Feeding and body size	<i>Quiscalus quiscula</i>	46	Poor	0.63	14
Feeding and body size	<i>Quiscalus quiscula</i>	46	Normal	0.40	25
Feeding and body size	<i>Rissa tridactyla</i>	15	Poor	0.55	50
Feeding and body size	<i>Rissa tridactyla</i>	15	Normal	0.54	82
Feeding and body size	<i>Rissa tridactyla</i>	15	Poor	0.59	5
Feeding and body size	<i>Rissa tridactyla</i>	15	Good	0.31	2
Feeding and body size	<i>Rissa tridactyla</i>	15	Good	0.42	4
Feeding and body size	<i>Rissa tridactyla</i>	15	Poor	0.98	3
Feeding and body size	<i>Rissa tridactyla</i>	15	Normal	0.58	5
Feeding and body size	<i>Rissa tridactyla</i>	15	Normal	0.93	9
Feeding and body size	<i>Rissa tridactyla</i>	15	Normal	0.64	3
Feeding and body size	<i>Rissa tridactyla</i>	15	Poor	0.95	8
Feeding and body size	<i>Rissa tridactyla</i>	15	Poor	0.64	7
Feeding and body size	<i>Rissa tridactyla</i>	15	Poor	0.55	6
Feeding and body size	<i>Rissa tridactyla</i>	15	Poor	0.54	9
Feeding and body size	<i>Rissa tridactyla</i>	15	Good	0.54	5
Feeding and body size	<i>Rissa tridactyla</i>	83	Normal	0.24	98
Feeding and body size	<i>Rissa tridactyla</i>	83	Normal	0.16	98
Feeding and body size	<i>Rissa tridactyla</i>	83	Normal	0.22	98
Feeding and body size	<i>Rissa tridactyla</i>	83	Normal	0.04	35
Feeding and body size	<i>Rissa tridactyla</i>	83	Normal	0.34	35
Feeding and body size	<i>Rissa tridactyla</i>	83	Normal	0.59	35
Feeding and body size	<i>Rissa tridactyla</i>	86	Good	-0.10	22
Feeding and body size	<i>Rissa tridactyla</i>	86	Poor	-0.44	13
Feeding and body size	<i>Rissa tridactyla</i>	139	Good	0.38	41
Feeding and body size	<i>Rissa tridactyla</i>	139	Normal	0.19	64
Feeding and body size	<i>Saxicola torquatus</i>	35	Good	0.44	17
Feeding and body size	<i>Saxicola torquatus</i>	35	Normal	0.53	42
Feeding and body size	<i>Saxicola torquatus</i>	35	Poor	0.71	10
Feeding and body size	<i>Sericornis frontalis</i>	63	Good	-0.08	8
Feeding and body size	<i>Sericornis frontalis</i>	63	Good	0.12	8
Feeding and body size	<i>Sericornis frontalis</i>	63	Good	-0.14	17
Feeding and body size	<i>Sericornis frontalis</i>	63	Normal	-0.50	9
Feeding and body size	<i>Sericornis frontalis</i>	63	Normal	-0.24	13
Feeding and body size	<i>Sericornis frontalis</i>	63	Normal	0.29	15
Feeding and body size	<i>Serinus canaria</i>	48	Normal	0.28	10
Feeding and body size	<i>Serinus canaria</i>	48	Normal	0.76	10
Feeding and body size	<i>Serinus canaria</i>	48	Normal	0.49	10
Feeding and body size	<i>Serinus canaria</i>	48	Normal	0.65	10
Feeding and body size	<i>Serinus canaria</i>	49	Poor	0.21	8
Feeding and body size	<i>Serinus canaria</i>	49	Normal	0.63	8
Feeding and body size	<i>Serinus canaria</i>	50	Normal	-0.22	10
Feeding and body size	<i>Serinus canaria</i>	50	Normal	-0.24	10
Feeding and body size	<i>Sterna hirundo</i>	11	Good	0.66	16
Feeding and body size	<i>Sterna hirundo</i>	11	Poor	0.73	33
Feeding and body size	<i>Sterna hirundo</i>	11	Poor	0.72	15
Feeding and body size	<i>Sterna hirundo</i>	11	Good	0.83	16
Feeding and body size	<i>Sterna hirundo</i>	11	Poor	0.76	33
Feeding and body size	<i>Sterna hirundo</i>	89	Normal	0.47	144

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and body size	<i>Sterna hirundo</i>	101	Normal	-0.09	15
Feeding and body size	<i>Sterna hirundo</i>	101	Normal	0.41	15
Feeding and body size	<i>Sterna hirundo</i>	101	Normal	0.45	15
Feeding and body size	<i>Sterna hirundo</i>	121	Normal	0.34	26
Feeding and body size	<i>Strix aluco</i>	111	Poor	0.56	14
Feeding and body size	<i>Strix aluco</i>	111	Normal	0.54	17
Feeding and body size	<i>Strix aluco</i>	111	Good	0.22	23
Feeding and body size	<i>Sula neboxii</i>	2	Normal	0.76	17
Feeding and body size	<i>Sula neboxii</i>	3	Normal	0.28	59
Feeding and body size	<i>Sula neboxii</i>	3	Normal	0.94	31
Feeding and body size	<i>Sula neboxii</i>	3	Normal	0.47	29
Feeding and body size	<i>Sula neboxii</i>	24	Good	0.00	15
Feeding and body size	<i>Sula neboxii</i>	24	Normal	-0.30	6
Feeding and body size	<i>Sula neboxii</i>	24	Normal	0.99	15
Feeding and body size	<i>Sula neboxii</i>	24	Poor	0.95	18
Feeding and body size	<i>Sula neboxii</i>	25	Normal	0.35	54
Feeding and body size	<i>Sula neboxii</i>	25	Normal	0.64	6
Feeding and body size	<i>Sula neboxii</i>	36	Normal	0.35	9
Feeding and body size	<i>Sula neboxii</i>	36	Normal	0.50	9
Feeding and body size	<i>Sula neboxii</i>	36	Good	0.03	21
Feeding and body size	<i>Sula neboxii</i>	36	Normal	0.42	21
Feeding and body size	<i>Sula neboxii</i>	36	Normal	0.44	30
Feeding and body size	<i>Sula neboxii</i>	36	Normal	0.36	30
Feeding and body size	<i>Sula neboxii</i>	36	Normal	0.19	30
Feeding and body size	<i>Sula neboxii</i>	36	Normal	0.98	7
Feeding and body size	<i>Sula neboxii</i>	36	Good	0.97	7
Feeding and body size	<i>Sula neboxii</i>	36	Good	0.77	7
Feeding and body size	<i>Sula neboxii</i>	36	Normal	0.90	7
Feeding and body size	<i>Sula neboxii</i>	134	Normal	0.21	17
Feeding and body size	<i>Sula neboxii</i>	134	Normal	0.54	17
Feeding and body size	<i>Sula neboxii</i>	134	Normal	0.69	17
Feeding and body size	<i>Sula neboxii</i>	134	Poor	0.61	17
Feeding and body size	<i>Tachycineta bicolor</i>	8	Poor	-0.21	13
Feeding and body size	<i>Tachycineta bicolor</i>	8	Poor	0.31	13
Feeding and body size	<i>Tachycineta bicolor</i>	8	Poor	0.45	13
Feeding and body size	<i>Tachycineta bicolor</i>	8	Poor	0.15	13
Feeding and body size	<i>Tachycineta bicolor</i>	8	Poor	-0.02	14
Feeding and body size	<i>Tachycineta bicolor</i>	8	Poor	0.55	14
Feeding and body size	<i>Tachycineta bicolor</i>	18	Good	0.19	33
Feeding and body size	<i>Tachycineta bicolor</i>	18	Normal	0.12	58
Feeding and body size	<i>Tachycineta bicolor</i>	18	Normal	0.58	58
Feeding and body size	<i>Tachycineta bicolor</i>	18	Good	0.57	33
Feeding and body size	<i>Tachycineta bicolor</i>	64	Normal	0.01	16
Feeding and body size	<i>Tachycineta bicolor</i>	64	Normal	0.81	16
Feeding and body size	<i>Tachycineta bicolor</i>	64	Normal	-0.77	16
Feeding and body size	<i>Tachycineta bicolor</i>	140	Normal	0.39	39
Feeding and body size	<i>Taeniopygia guttata</i>	32	Good	0.72	7
Feeding and body size	<i>Taeniopygia guttata</i>	32	Normal	0.80	16
Feeding and body size	<i>Taeniopygia guttata</i>	33	Normal	0.64	15
Feeding and body size	<i>Taeniopygia guttata</i>	33	Normal	0.63	13
Feeding and body size	<i>Taeniopygia guttata</i>	33	Normal	0.27	15
Feeding and body size	<i>Taeniopygia guttata</i>	33	Normal	0.21	13
Feeding and body size	<i>Taeniopygia guttata</i>	68	Good	-0.28	6
Feeding and body size	<i>Taeniopygia guttata</i>	68	Good	-0.48	6
Feeding and body size	<i>Taeniopygia guttata</i>	76	Good	0.25	28
Feeding and body size	<i>Taeniopygia guttata</i>	76	Good	0.45	28
Feeding and body size	<i>Taeniopygia guttata</i>	76	Good	0.14	13
Feeding and body size	<i>Taeniopygia guttata</i>	76	Good	0.34	13
Feeding and body size	<i>Taeniopygia guttata</i>	76	Good	0.41	17
Feeding and body size	<i>Taeniopygia guttata</i>	76	Good	0.69	17
Feeding and body size	<i>Taeniopygia guttata</i>	114	Poor	0.13	10
Feeding and body size	<i>Taeniopygia guttata</i>	114	Good	0.32	6
Feeding and body size	<i>Taeniopygia guttata</i>	114	Poor	-0.30	8
Feeding and body size	<i>Taeniopygia guttata</i>	114	Good	0.40	12
Feeding and body size	<i>Taeniopygia guttata</i>	114	Good	-0.35	6

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and body size	<i>Taeniopygia guttata</i>	114	Good	0.39	6
Feeding and body size	<i>Taeniopygia guttata</i>	114	Good	-0.55	6
Feeding and body size	<i>Taeniopygia guttata</i>	114	Poor	0.67	8
Feeding and body size	<i>Taeniopygia guttata</i>	114	Poor	0.79	8
Feeding and body size	<i>Taeniopygia guttata</i>	114	Poor	0.90	8
Feeding and body size	<i>Taeniopygia guttata</i>	114	Poor	0.01	10
Feeding and body size	<i>Taeniopygia guttata</i>	114	Poor	0.06	10
Feeding and body size	<i>Taeniopygia guttata</i>	114	Poor	0.21	10
Feeding and body size	<i>Taeniopygia guttata</i>	114	Good	0.30	10
Feeding and body size	<i>Taeniopygia guttata</i>	114	Good	0.37	10
Feeding and body size	<i>Taeniopygia guttata</i>	114	Good	0.48	10
Feeding and body size	<i>Thamnophilus atrinucha</i>	130	Normal	-0.35	15
Feeding and body size	<i>Thamnophilus atrinucha</i>	130	Normal	0.35	15
Feeding and body size	<i>Thamnophilus atrinucha</i>	130	Normal	-0.47	15
Feeding and body size	<i>Thamnophilus atrinucha</i>	130	Normal	0.47	15
Feeding and body size	<i>Thamnophilus atrinucha</i>	131	Normal	0.50	11
Feeding and body size	<i>Thamnophilus atrinucha</i>	131	Normal	0.68	11
Feeding and body size	<i>Thamnophilus atrinucha</i>	131	Normal	0.04	11
Feeding and body size	<i>Thamnophilus atrinucha</i>	131	Poor	-0.21	11
Feeding and body size	<i>Troglodytes aedon</i>	14	Normal	0.20	27
Feeding and body size	<i>Troglodytes aedon</i>	14	Normal	0.51	20
Feeding and body size	<i>Troglodytes aedon</i>	14	Normal	-0.13	27
Feeding and body size	<i>Troglodytes aedon</i>	14	Normal	0.69	20
Feeding and body size	<i>Troglodytes aedon</i>	40	Good	-0.21	50
Feeding and body size	<i>Troglodytes aedon</i>	40	Poor	0.12	33
Feeding and body size	<i>Troglodytes aedon</i>	40	Normal	0.04	24
Feeding and body size	<i>Troglodytes aedon</i>	40	Good	-0.15	34
Feeding and body size	<i>Troglodytes aedon</i>	61	Good	0.26	12
Feeding and body size	<i>Troglodytes aedon</i>	61	Good	0.61	12
Feeding and body size	<i>Troglodytes aedon</i>	61	Good	0.84	12
Feeding and body size	<i>Troglodytes aedon</i>	126	Poor	0.16	31
Feeding and body size	<i>Troglodytes aedon</i>	126	Good	-0.19	46
Feeding and body size	<i>Troglodytes aedon</i>	126	Poor	0.03	31
Feeding and body size	<i>Troglodytes aedon</i>	126	Good	-0.10	47
Feeding and body size	<i>Turdus migratorius</i>	116	Normal	0.12	14
Feeding and body size	<i>Turdus migratorius</i>	116	Normal	0.03	14
Feeding and body size	<i>Turdus migratorius</i>	116	Normal	0.16	14
Feeding and body size	<i>Turdus migratorius</i>	116	Normal	-0.09	14
Feeding and body size	<i>Turdus migratorius</i>	138	Good	0.04	6
Feeding and body size	<i>Turdus migratorius</i>	138	Good	0.08	6
Feeding and body size	<i>Turdus migratorius</i>	138	Normal	-0.04	7
Feeding and body size	<i>Turdus migratorius</i>	138	Normal	0.08	7
Feeding and body size	<i>Turdus migratorius</i>	138	Poor	-0.11	4
Feeding and body size	<i>Turdus migratorius</i>	138	Poor	0.19	4
Feeding and body size	<i>Upupa epops</i>	81	Normal	0.82	54
Feeding and body size	<i>Upupa epops</i>	81	Normal	0.99	1
Feeding and body size	<i>Upupa epops</i>	106	Normal	0.14	30
Feeding and body size	<i>Upupa epops</i>	106	Normal	0.05	30
Feeding and body size	<i>Upupa epops</i>	106	Normal	0.44	30
Feeding and body size	<i>Upupa epops</i>	106	Normal	0.38	30
Feeding and body size	<i>Upupa epops</i>	106	Normal	0.06	30
Feeding and body size	<i>Upupa epops</i>	106	Normal	0.12	30
Feeding and body size	<i>Upupa epops</i>	106	Poor	0.05	30
Feeding and body size	<i>Upupa epops</i>	106	Poor	0.53	30
Feeding and body size	<i>Upupa epops</i>	106	Normal	0.29	30
Feeding and body size	<i>Vanellus vanellus</i>	9	Poor	0.16	15
Feeding and body size	<i>Vanellus vanellus</i>	9	Normal	0.41	41

Relationship between...	Species	Study	Environmental quality	Correlation coefficient	n
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	95	Normal	0.26	11
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	95	Poor	0.44	11
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	95	Poor	0.05	11
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	95	Normal	0.70	11
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	96	Normal	0.59	10
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	96	Normal	0.85	10
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	100	Normal	0.02	6
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	100	Normal	0.05	14
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	100	Normal	-0.20	10
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	100	Normal	0.18	10
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	100	Normal	0.44	16
Feeding and body size	<i>Xanthocephalus xanthocephalus</i>	100	Normal	0.32	34
Feeding and body size	<i>Zonotrichia leucophrys</i>	82	Poor	0.72	37
Feeding and body size	<i>Zonotrichia leucophrys</i>	82	Normal	0.18	2