Routes to indirect fitness in cooperatively breeding vertebrates: kin discrimination and limited dispersal

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Abstract

Hamilton demonstrated that the evolution of cooperative behaviour is favoured by high relatedness, which can arise through kin discrimination or limited dispersal (population viscosity). These two processes are likely to operate with limited overlap: kin discrimination is beneficial when variation in relatedness is higher, whereas limited dispersal results in less variable and higher average relatedness, reducing selection for kin discrimination. However, most empirical work on eukaryotes has focused on kin discrimination. To address this bias, we analysed how kin discrimination and limited dispersal interact to shape helping behaviour across cooperatively breeding vertebrates. We show that kin discrimination is greater in species where the: (i) average relatedness in groups is lower and more variable; (ii) effect of helpers on breeders reproductive success is greater; and (iii) probability of helping was measured, rather than the amount of help provided. There was also an interaction between these effects with the correlation between the benefits of helping and kin discrimination being stronger in species with higher variance in relatedness. Overall, our results suggest that kin discrimination provides a route to indirect benefits when relatedness is too variable within groups to favour indiscriminate cooperation.

Introduction

A major problem for evolutionary biology is explaining how selection favours cooperative behaviours that benefit other individuals (reviewed by Sachs *et al.*, 2004; Lehmann & Keller, 2006; West *et al.*, 2007a,b). Hamilton's (1964a,b, 1970) theory of inclusive fitness provides a potential solution to this problem by showing that individuals can increase their indirect fitness by helping relatives. In his original papers, Hamilton (1964a,b, 1971, 1972, 1975) pointed out that the degree of relatedness required to generate indirect benefits could arise via two routes: individuals preferentially interacting with closer relatives (kin discrimination), or through limited dispersal (population viscosity) which increases the probability that individuals will interact with relatives. However, there has been little overlap between the theoretical and empirical research on these processes,

with the theoretical literature focusing on limited dispersal and the empirical literature focusing on kin discrimination (West *et al.*, 2002; see discussion for microbial exceptions).

In cooperatively breeding vertebrates, a dominant pair usually produces the majority of the offspring, while the cost of caring for offspring is shared with nonbreeding subordinate helpers (Jennions & Macdonald, 1994; Cockburn, 1998; Hatchwell & Komdeur, 2000; Clutton-Brock, 2002; Griffin & West, 2003; Koenig & Dickinson, 2004). Empirical research on the importance of indirect fitness benefits in explaining such helping behaviour has focused on kin discrimination. However, if relatedness between interacting individuals within groups is high, then it is still possible that indirect fitness benefits will be important, even with indiscriminate helping. Griffin & West (2003) and Boomsma (2007) have argued that one way to test this hypothesis is to examine whether kin discrimination is weaker in species where within group relatedness is higher and/or shows less variation.

We test this prediction with a meta-analysis across cooperative breeding birds and mammals. Griffin & West (2003) have previously shown that the extent of kin

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discrimination is positively correlated with the benefits of helping behaviour. This is predicted by inclusive fitness theory: when helping provides greater benefits, indirect fitness from preferentially helping closer relatives will be greater. Consequently, our major aim here is to test the prediction that the level of kin discrimination across species should be correlated with within group relatedness as well as the benefits of helping. Furthermore, we test the prediction that kin discrimination will be stronger in studies measuring the probability of, rather than, the amount of help provided. This is because the amount of help may depend on other factors, such as the helper's physical condition, which can influence the cost of helping (Emlen & Wrege, 1988; Griffin & West, 2003). We test this prediction by examining differences in the strength of kin discrimination between species where the probability or amount of help provided has been measured. A comparative test of the relative importance of these different possible explanatory variables has only just become possible, thanks to: (i) developments in meta-analysis methodology that allow multivariate and formal phylogentic analyses (J.D. Hadfield & S. Nakagawa, unpublished; Nakagawa *et al.*, 2007; Adams, 2008; unpublished *et al.*, 2009; Knowles *et al.*, 2009; Lajeunese, 2009) and (ii) recently published data that expands the number of species studied sufficiently to allow meaningful multivariate analyses.

Materials and methods

Data collection

We have previously presented data collected on the strength of kin discrimination, rKin (the effect of relatedness on the probability of becoming a helper either in natal group or as immigrant, or amount of help provided by helpers), and the effect of helpers, rHelp (the effect of help on fledgling success or, where possible, survival of offspring to the following year) in Griffin & West (2003) and Griffin *et al.* (2005). All studies used in these previous analyses were included in the present analysis. The dataset was updated to include all studies published since 2005 presenting data that could be used to obtain values for rKin and rHelp. We located relevant papers through keyword searches on Web of Science and forward and backward citation searches on key papers. We also contacted researchers to obtain unpublished data. Full, updated datasets used in analyses are given in Appendix Tables A1–A3. We have been able to add five species to the dataset used to calculate the correlation between rKin and rHelp presented in Griffin & West (2003): *Aegithalos caudatus* (long-tailed tit), *Picoides borealis* (red-cockaded woodpecker), *Corvus c. corone* (carrion crow), *Nesomimus parvula* (Galapagos mockingbird) and the *Manorina melanophrys* (Australian bell miner). The studies used to obtain values of rhelp vary in whether they controlled for potential confounding factors such as

territory and breeder quality. However, we do not expect this to drive relationships between variables, but instead create variation in the data.

In addition to the relationship between rKin and rHelp we measured the relationship between the strength of kin discrimination (rKin) and the mean and variance in relatedness between helpers and offspring that could potentially be helped, and whether helpers in a species were typically natal to the group in which they helped or immigrants (Appendix, Tables A1–A3). In species where helpers are typically retained natals, it is predicted that helping will be indiscriminate because average relatedness is high and that discrimination will be stronger in species with nonnatal helpers because of increased variation in relatedness. Species were categorized as either 'mainly natal' or 'nonnatal' from descriptions of their breeding system from the literature (T.H. Clutton-Brock & Sharp, personal communication). For example, *Suricata suricatta* (meerkats) were categorized as 'mainly natal' as helpers are mainly offspring from previous litters that have not dispersed from the natal territory (even though there are also immigrant helpers present) (Clutton-Brock *et al.*, 2001). *Ceryle rudis* (Pied kingfisher) was categorized as 'nonnatal' as helpers are not the offspring of the breeding pair, and may breed with the breeding female (Reyer, 1984).

When measuring the mean and variance in relatedness we aimed to capture relatedness between offspring and *potential* helpers, but it is often not specified whether studies included nonhelpers in their analyses. This potential bias is likely to result in variance in relatedness being underestimated and mean relatedness overestimated. However, any bias is expected to be equally likely in species with limited dispersal as those with high dispersal, and reduce the ability to detect an effect of mean and variance in relatedness on kin discrimination rather than drive relationships. Furthermore, most of the studies we used to extract this data were examining the effect of kinship on helping (the strength of kin discrimination) and so would be expected to include individuals that did not help as well as those that contributed to help. The methods used to measure relatedness also varied across studies (genealogical vs. molecular genetic, see appendix), but we found no evidence that this significantly affected relatedness estimates (mean relatedness: GLM with binomial error distribution, $F_{1, 13} = 0.18$, $P = 0.68$. Variance in relatedness: GLM with normal error distribution, relatedness method $F_{1, 13} = 0.97$, $P = 0.34$) or kin discrimination when entered into the model outlined in Table 1 ($F_{1, 5} = 0.25$, $P = 0.64$).

Meta-analysis

We conducted a meta-analysis on studies examining kin discrimination (rKin) across vertebrate species using a multivariate linear mixed effects model with restricted maximum likelihood estimation (REML) conducted in

Table 1 Linear mixed model of predictors of kin discrimination (Zr-kin) across cooperatively breeding vertebrates.

Fixed terms	Parameter estimate (β)		SE	95% LCL	95% UCL	DF	F	P
Zr-help†						1, 10	3.66	0.09
Mean relatedness†		−2.62	0.94	−4.68	−0.55	1, 10	7.80	**0.02**
Variance in relatedness†						1, 9	1.27	0.30
Probability vs. amount of help†	Amount	0.10	0.09	−0.11	0.31	1, 10	10.24	**0.01**
	Probability	0.45	0.09	0.26	0.64			
Natal helpers						1, 3	3.50	0.17
Zr-help*Mean relatedness						1, 6	2.24	0.18
Zr-help*Variance in relatedness†		56.15	25.08	0.75	119.93	1, 9	5.01	**0.05**
Zr-help*retained natals						1, 4	0.31	0.61
Zr-help*probability vs. amount of help						1, 8	1.43	0.27
Random terms	Variance Component		SE	95% LCL	95% UCL	DF	LRT	P
Class†	0.00		0.00	0.00	0.00	1	0.00	1.00
Order (class)†	0.00		0.00	0.00	0.00	1	0.00	1.00
Species (order class)†	0.05		0.03	0.02	0.30	1	13.48	**0.0002**

Effect sizes of rkin and rhelp were Z transformed prior to analysis and the parameters estimates are presented on the Z scale. The response variable Zr-kin was weighted by the inverse variance. Significant values are shown in boldface type. LRT, log-likelihood ratio test, LCL, lower confidence limit, UCL, upper confidence limit.
†Denotes terms included in final model. $N_{species} = 14$, $N_{genera} = 14$, $N_{families} = 14$, $N_{orders} = 4$, $N_{classes} = 2$.

SAS version 9.2 (Littell *et al.*, 2006). Prior to the analysis, effect sizes were Z-transformed

$$Zr = \frac{1}{2}\log e\left[\frac{1+r}{1-r}\right]$$

ZrKin was weighted by the inverse variance to account for variation in sample sizes between studies. The variance was calculated by the reciprocal of the sum of the conditional variance,

$$\text{Variance} = \frac{1}{n-3}$$

where n is the sample size of the study (Raudenbush, 1994; Nakagawa *et al.*, 2007). We analysed variation in ZrKin in relation to the following fixed effects: (1) the benefits of helping behaviour (ZrHelp, covariate); (2) the probability of helping ($n_{species} = 13$) vs. the amount of help provided ($n_{species} = 13$. For three species, measures of both amount and probability were available) (two level factor), (3) mean relatedness within groups (covariate), (4) variance in relatedness within groups (covariate), and (5) whether helpers were mainly natal ($n_{species} = 4$) to the group or nonnatal ($n_{species} = 17$) (two level factor; Clutton-Brock & Sharp, personal communication). We checked whether the sample size of the studies used to calculate ZrHelp had an effect on our results by entering the inverse variance of ZrHelp as a covariate in our analyses and in all cases this was nonsignificant ($P > 0.30$).

The published studies on kin discrimination represent a diverse range of bird and mammal species and for some species there were multiple studies that examined both the probability and amount of help directed towards related and unrelated individuals. Nonindependence of data has been dealt with in the past by taking species averages and calculating independent contrasts across phylogenies (Felsenstein, 1985; Harvey & Pagel, 1991; West & Sheldon, 2002; West *et al.*, 2005; Nakagawa *et al.*, 2007; Adams, 2008). However, mixed model meta-analysis can deal with the nonindependence of data through random effects that account for intra-group correlations, avoiding data averaging and allowing the full dataset to be utilized (Hadfield & Nakagawa, submitted; Nakagawa *et al.*, 2007; Adams, 2008; Chapman *et al.*, 2009; Knowles *et al.*, 2009; Lajeunese, 2009). We therefore took into account the nonindependence of data arising from multiple studies on the same species, and from the phylogenetic relationships between species by defining a nested random effects structure whereby species were nested within order and order was nested within class. Only order and class were entered into the model because in our dataset genera and families only contained single species and therefore there were only multiple species at the taxonomic levels of order and class. The significance of fixed effects (factors and covariates) were examined using Wald type adjusted F statistics and the effect with the highest P value was sequentially dropped until only significant terms ($P < 0.05$) remained (Crawley, 2002). The Kenward & Roger (1997) method for estimating standard errors for parameter estimates and denominator degrees of freedom was used as it is specifically designed for models with multiple random effects and unbalanced data, increasing the accuracy of significance tests (Kenward & Roger, 1997; Littell *et al.*, 2006; Bolker *et al.*, 2009). The significance of random effects was assessed using log-likelihood ratio tests (LRTs) (Self & Liang, 1987). Details of all analyses are provided as electronic supplementary material (Tables S1–S4).

Results

We found that variation in kin discrimination was explained by three different effects. First, kin discrimination was weaker when mean relatedness between individuals was higher (mean relatedness: $F_{1, 10} = 7.80$, $P = 0.02$; Table 1; Fig. 1a). This suggests that individuals are less likely to discriminate between kin and nonkin in species that live in groups with closer relatives. Second, kin discrimination was stronger when the probability rather than amount of helping was measured (amount vs. probability of help: $F_{1, 10} = 10.24$, $P = 0.01$; Table 1; Fig. 1b). Third, consistent with Griffin & West (2003), we found a positive relationship between kin discrimination and the benefits of helping (Table 1; Table S1; Fig. 1c). However, in the present study there was additional complexity with the relationship between kin discrimination and the benefits of helping being dependent upon variance in relatedness (ZrHelp*variance in relatedness: $F_{1, 8} = 5.01$, $P = 0.05$; Table 1, Fig. 2). As predicted by inclusive fitness theory, the relationship between kin discrimination and the benefits of helping was stronger when variance in relatedness between group members was higher (Table 1; Fig. 2). Finally, after taking into account mean and variance in relatedness between individuals, kin discrimination did not significantly differ
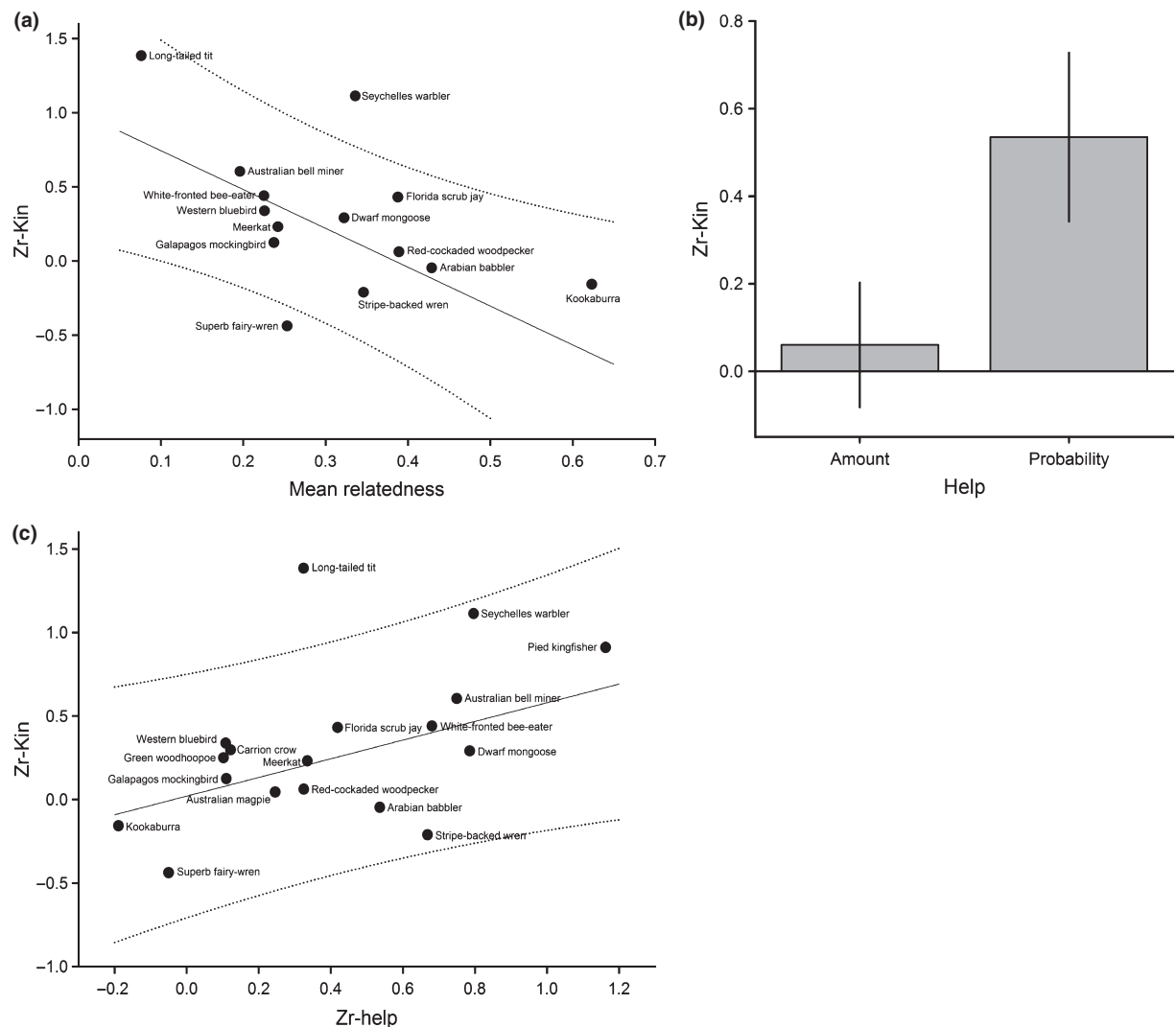
Fig. 1 Kin discrimination (ZrKin) across cooperatively breeding vertebrates. (a) Kin discrimination in relation to average relatedness between individuals. Solid line represents predicted relationship from the linear mixed model (Table 1) with 95% confidence intervals (dotted lines). (b) The difference in kin discrimination when the probability of helping and the amount of help provided were measured. Bars represent means ± SE. (c) The relationship between the benefits to offspring of helping (ZrHelp), and kin discrimination. Solid line represents predicted relationship from the linear mixed model (Table S1) with 95% confidence intervals (dotted lines).
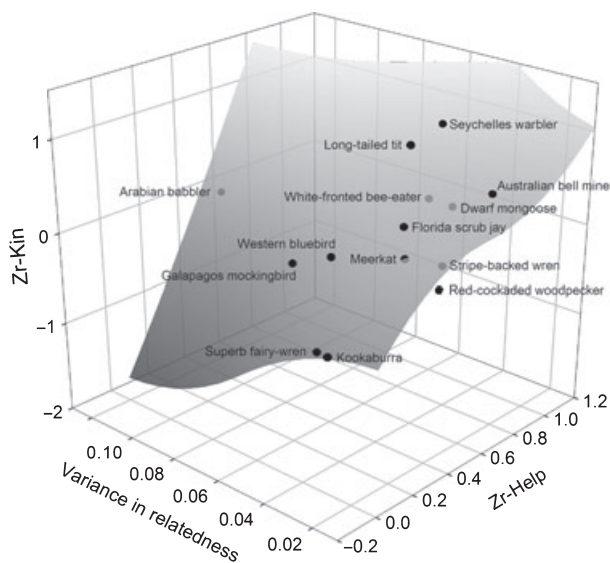
Fig. 2 The effect of the interaction between variance in relatedness and the benefits to offspring of helping (ZrHelp) on kin discrimination (ZrKin). Surface of relationship is visualized using a loess smoothing procedure. The grey circles indicate data points below the line whereas black data points are above the line.

between species with and without natal helpers (natal helpers: $F_{1, 3} = 3.50$, $P = 0.17$).

We tested the robustness of our results in three ways. First, data on mean and variance in relatedness was only available for 14 species ($N_{genera} = 14$, $N_{families} = 14$, $N_{orders} = 4$, $N_{classes} = 2$). We therefore re-ran our analysis removing measures of relatedness from the analysis to use all data on the other explanatory variables (18 species, $N_{genera} = 18$, $N_{families} = 16$, $N_{orders} = 4$, $N_{classes = 2)}$. Variation in kin discrimination was once again explained by the benefits of helping, and whether the probability or amount of helping was measured (ZrHelp: $F_{1, 11} = 5.69$, $P = 0.04$. Amount vs. probability of helping: $F_{1, 16} = 6.63$, $P = 0.02$; Table S1). However, we found that species where helpers are mainly natals had significantly lower kin discrimination (mean ± SE ZrKin = 0.18 ± 0.07) than species with nonnatals (mean ± SE ZrKin = 0.57 ± 0.15. $F_{1, 11} = 5.68$, $P = 0.04$; Table S1). This is perhaps unsurprising given that the presence of natal helpers is likely to be a crude indicator of mean relatedness between individuals when direct measures of relatedness were not entered into this analysis. Second, the number of species in our dataset is small relative to the number of explanatory variables and this may give spurious results. We therefore analysed the effect of each explanatory variable on kin discrimination separately, which also allowed us to utilize all data available for each explanatory variable. Once again the significance of results did not change (ZrHelp: $F_{1, 17} = 5.13$, $P = 0.04$; mean relatedness: $F_{1, 13} = 5.42$, $P = 0.04$; amount vs. probability of helping: $F_{1, 22} = 6.77$, $P = 0.02$; natal helpers:

$F_{1, 20} = 9.25$, $P = 0.007$; Table S2). Finally, we re-ran our analysis after removing *Dacelo novaeguineae* (kookaburra) and *Phoeniculus purpureus* (green woodhoopoe) in turn. We removed *D. novaeguineae* because relatedness was given as band-sharing co-efficients from DNA fingerprinting (Legge & Cockburn, 2000), which relates less directly to the *r* in Hamilton's rule. We removed *P. purpureus* because it could be argued that the experimental approach used to assess helping behaviour by Du Plessis (1993) does not measure the selected response to differences in relatedness. However, removing *D. novaeguineae* and *P. purpureus* from our analyses did not change the significance of any main effects (Tables S3 and S4).

Discussion

As predicted by inclusive fitness theory, we found that kin discrimination was: (i) weaker in species where the average relatedness within a group was higher and less variable (Fig. 1a; Fig. 2), and (ii) stronger in species where the benefit of helping was greater (Fig. 1b). Indiscriminate helping can lead to substantial indirect fitness benefits when within-group relatedness is high and shows little variation, reducing selection for kin discrimination (Griffin & West, 2003; Boomsma, 2007). This can occur, either through dispersal patterns (specifically, strong philopatry) or low extra-pair mating by the breeding pair and/or low breeder turnover. We also found that the interaction between variation in relatedness and benefit of helping was key – the benefits of helping were correlated more strongly with kin discrimination in species with higher variance in relatedness between individuals. This demonstrates that selection for kin discrimination is greatest when high indirect benefits from helping combine with high variance in relatedness, which renders indiscriminate helping an unreliable way of directing help towards kin. Finally, we found that kin discrimination is greater when the probability rather than the amount of help provided is measured. The amount of help given may be influenced by a greater number of factors, such as the condition of helpers, that vary the costs to individuals of helping (Emlen & Wrege, 1988; Griffin & West, 2003) and so is a potentially less reliable indicator of kin discrimination.

These results build on previous work by Griffin & West (2003), demonstrating that variation in the importance of indirect fitness benefits can be explained across cooperatively breeding species by the reproductive benefits helpers provide and by population structure: relatedness between offspring and potential helpers. We tried to capture population structure both by categorizing species according to their dispersal patterns (natal vs. nonnatal helpers) and by measuring mean and variance in relatedness directly. There are pros and cons of these different approaches. Categorizing species as natal and nonnatal is likely to capture cues that animals use to assess likely relatedness to offspring in their group. That

said much information is lost in this broad-brush approach. For example, in white-fronted bee-eaters and western bluebirds helpers that may be classified as nonnatals are often failed breeders that return to their natal nest after dispersal to help their parents (Emlen & Wrege, 1988; Dickinson *et al.*, 1996). Furthermore, helpers that remain in their natal territory may make assessments of their relatedness to offspring based on other cues such as breeder turnover. However, what is key to assessing the role of indirect fitness benefits in the evolution of cooperation is the mean and variance in relatedness. In many cases this can measured directly, thanks to detailed long-term studies (Koenig & Dickinson, 2004). As we have shown this provides greater resolution in explaining kin discrimination across species in comparison to categorizing species according to their dispersal patterns.

Hamilton (1964a,b, 1971, 1972, 1975) demonstrated that limited dispersal leads to high within group relatedness, and hence favours cooperation. However, a potential problem with this idea is that limited dispersal can also lead to increased competition between relatives, which can reduce or even completely remove any effect of relatedness on selection for cooperation (Hamilton, 1971, 1975; Queller, 1992; Taylor, 1992a,b; West *et al.*, 2002; Griffin *et al.*, 2004). One way around this problem is if individuals disperse in groups of relatives (budding dispersal), which maintains relatedness within groups, but reduces competition between social partners (Gardner & West, 2006; Lehmann *et al.*, 2006; Kummerli *et al.*, 2009). This pattern of dispersal has been observed in several cooperative breeding vertebrates and may be an important factor in maintaining the indirect fitness benefits that individuals gain (Haldane, 1932; Clutton-Brock, 2002; Sharp *et al.*, 2008; Williams & Rabenold, 2005; Bradley *et al.*, 2007; Metheny *et al.*, 2008).

Care should be taken to not over-interpret our results. We have investigated the two different routes by which cooperative breeders can gain indirect benefits from helping – population viscosity and kin discrimination. In contrast, we have not investigated the importance of direct fitness benefits, and so our results do not measure the relative importance of indirect and direct fitness in favouring helping behaviours (Griffin & West, 2003). Related to this, previous work has argued the importance of direct fitness benefits by demonstrating that levels of helping are adjusted in response to the cost of helping (e.g. Clutton-Brock *et al.*, 1999, 2000). However, adjustments in cooperative behaviour in response to changes in the cost of helping, correspond to the *c* term of Hamilton's rule (1963, 1964a,b), and so are predicted if the benefits of cooperation are either direct or indirect (e.g. Cant *et al.*, 1996; Field *et al.*, 2006).

To conclude, Hamilton (1964a,b, 1971, 1972, 1975) originally suggested that high relatedness could arise as a result of kin discrimination or limited dispersal. While

the role of limited dispersal has gained much attention in microbes, where it has been shown to influence both cooperation and parasite virulence (Griffin *et al.*, 2004; Kerr *et al.*, 2006; MacLean & Gudelj, 2006; West *et al.*, 2006; Boots & Mealor, 2007; Diggle *et al.*, 2007; Gilbert *et al.*, 2007; Ross-Gillespie *et al.*, 2007; Kummerli *et al.*, 2009; Wild *et al.*, 2009), it has attracted less attention with respect to other taxa (West *et al.*, 2002). Our results suggest that both kin discrimination and limited dispersal are important in cooperatively breeding vertebrates, and that they interact (see Rousset & Roze, 2007 for a general overview of theoretical work on kin discrimination). Specifically, kin discrimination increases indirect benefits when relatedness is too variable within groups to favour indiscriminate cooperation. A major future task is to link determinants of within group relatedness, such as the mating system, to the extent and form of cooperation (Boomsma, 2007).

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Supporting information

Additional Supporting Information may be found in the online version of this article:

Table S1 Linear mixed model of predictors of kin discrimination (Zr-kin) with the mean and variance in relatedness excluded from the model to utilize data from all species.

Table S2 Linear mixed model of kin discrimination (Zr-kin) entering each explanatory variables on their own.

Table S3 Linear mixed model of predictors of kin discrimination (Zr-kin) removing data on the kookaburra, *Dacelo novaeguineae.*

Table S4 Linear mixed model of predictors of kin discrimination (Zr-kin) removing data on the green woodhoopoe, *Phoeniculus purpureus.*

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Appendix

Table A1 List of studies providing data that were used to measure the effect of kinship on the amount or probability of help (rKin). Full details of how *r*-values were converted from test statistics can be found in Table S1 of Griffin & West (2003) unless provided below.

Common name	Species	Reference	n	Probability or amount of help measured?	rKin	Notes
Arabian babbler	*Turdoides squamiceps*	Wright *et al.* (1999)	92	Amount	−0.047	1
Australian bell miner	*Manorina melanophyrus*	Clarke (1984); Wright *et al.* (in press)	7	Amount	0.376	
Australian magpie	*Gymnorhina tibicen*	Finn & Hughes (2001)	72	Probability	0.045	
Brown hyaena	*Hyaena brunnea*	Owens & Owens (1984)	159	Amount	0.185	
Carrion crow	*Corvus c. corone*	Canestrari *et al.* (2005)	28	Amount	0.289	2
Dwarf mongoose	*Helogale parvula*	Creel *et al.* (1991)	181	Probability	0.283	
Florida scrub jay	*Aphelocoma c. coerulescens*	Mumme (1992)	49	Probability	0.406	3
Galapagos mockingbird	*Nesomimus parvulus*	Curry (1988)	292	Probability	0.124	
Green woodhoopoe	*Phoeniculus purpureus*	Du Plessis (1993)	4	Amount	0.245	
Grey-capped social weaver	*Pseudonigrita arnaudi*	Bennun (1989)	8	Probability	0.66	
Grey-capped social weaver	*Pseudonigrita arnaudi*	Bennun (1994)	19	Amount	0.279	4
Kookaburra	*Dacelo novaeguineae*	Legge (2000)	94	Amount	−0.156	
Lion	*Panthero leo*	Grinnel *et al.* (1995)	23	Probability	0.219	
Long-tailed tit	*Aegithalos caudatus*	Russell & Hatchwell (2001)	17	Probability	0.882	
Meerkat	*Suricata suricatta*	Clutton-Brock *et al.* (2001)	43	Amount	0.227	5
Pied kingfisher	*Ceryle rudis*	Reyer (1984)	17	Amount	0.721	6
Red-cockaded woodpecker	*Picoides borealis*	Khan and Walters (2000)	1184	Probability	0.062	
Seychelles warbler	*Acrocephalus sechellensis*	Komdeur (1994)	112	Probability	0.633	
Seychelles warbler	*Acrocephalus sechellensis*	Komdeur (1994)	6	Amount	0.901	
Spotted hyaena	*Crocuta crocuta*	Mills (1985)	262	Probability	0.173	
Stripe-backed wren	*Campylorhynchus nuchalis*	Rabenold (1985)	97	Amount	−0.208	
Superb fairy-wren	*Malurus cyaneus*	Dunn *et al.* (1995)	23	Amount	−0.288	
Western bluebird	*Sialia mexicana*	Dickinson *et al.* (1996)	321	Probability	0.326	
White-browed scrubwren	*Sericornis frontalis*	Magrath & Whittingham (1997)	68	Probability	−0.069	7
White-fronted bee-eater	*Merops bullockoides*	Emlen & Wrege (1988)	59	Amount	0.200	
White-fronted bee-eater	*Merops bullockoides*	Emlen & Wrege (1988)	203	Probability	0.590	8

1) There is a typo in the supplementary information table of Griffin & West (2003): the sample size associated with the *P*-value 0.128 is 75 and not 92 as stated. (The authors thank Stuart Sharp and Tim Clutton-Brock for bringing this error to our attention.)

2) Conversion to rKin using $\chi^2 = 8.08$, rather than $P = 0.02$ (as used by Griffin & West (2003)) and revised sample size of 36. (The authors thank Stuart Sharp and Tim Clutton-Brock for bringing appropriate sample size to our attention.)

3) Average rKin value for study was obtained from statistics measuring the effect of relatedness on the relative contribution to feeding (measured as feeding visits per hour) between 'nonbreeders and nestlings', $F_{(1, 18)} = 1.62$, giving effect size of relatedness on feeding, rKin = 0.287, and between 'nonbreeders and failed breeders', $F_{(1,26)} = 2.38$, giving effect size of relatedness on feeding, rKin = 0.290.

4) Average rKin value (probability and amount combined) revised to 0.428 from 0.386 as published in Griffin & West (2003). Revised value does not alter any conclusions of previous analyses.

5) *r*-Value used in previous analyses ($r = 0.346$, Griffin & West, 2003) was converted from *P*-value ($P = 0.33$) assuming one-tailed test. Corrected *r*-value assumes two-tailed test. (The authors thank Stuart Sharp and Tim Clutton-Brock for bringing this error to our attention.)

6) Average rKin value (probability and amount combined) revised to 0.721 from 0.756 as published in Griffin & West (2003). Revised value does not alter any conclusions of previous analyses.

7) The following chi-sqaure values were converted to give rKin measurements for the white-browed scrubwren: $\chi^2 = 7$, $n = 68$ gives $r = −0.321$; $\chi^2 = 1.5$, $n = 63$ gives $r = 0.15$; $\chi^2 = 0.8$, $n = 63$ gives $r = 0.11$; $\chi^2 = 6$, $n = 63$ gives $r = −0.309$; $\chi^2 = 0.9$, $n = 63$ gives $r = 0.069$. These were averaged to give rKin for study as a whole.

8) Average rKin value (probability and amount combined) revised to 0.563 from 0.545 as published in Griffin & West (2003). Revised value does not alter any conclusions of previous analyses.

Table A2 List of studies providing data that were used to measure the effect of helpers on raising offspring to independence (rHelp). Full details of how *r*-values were converted from test statistics can be found in Table S2 of Griffin & West (2003) unless provided below.

Common Name	Species	Reference	*n*	rHelp	Notes
Arabian babbler	*Turdoides squamiceps*	Wright (1998)	27	0.490	
Australian bell miner	*Manorina melanophyrus*	Clarke (1989)	12	0.635	1
Australian magpie	*Gymnorina tibicen*	P. Finn (Pers. Comm.)	8	0.241	
Carrion crow	*Corvus c. corone*	Canestrari *et al.* (2008)	453	0.121	2
Dwarf mongoose	*Helogale parvula*	Creel *et al.* (1991)	19	0.656	
Florida scrub jay	*Aphelocoma c. coerulescens*	Mumme (1992)	37	0.396	
Galapagos mockingbird	*Nesomimus parvulus*	Curry & Grant (1989)	450	0.110	3
Green woodhoope	*Phoeniculus purpureus*	Du Plessis (1993)	144	0.102	
Kookaburra	*Dacelo novaeguineae*	Legge (2000)	24	−0.187	
Long-tailed tit	*Aegithalos caudatus*	Hatchwell *et al.* (2004)	87	0.314	4
Meerkat	*Suricata suricatta*	A. Russell (Pers. comm.); Clutton-Brock *et al.* (2001)	139	0.323	
Pied kingfisher	*Ceryle rudis*	Reyer (1984)	25	0.822	
Red-cockaded woodpecker	*Picoides borealis*	Lennartz (1987)	93	0.314	1
Seychelles warbler	*Acrocephalus sechellensis*	Komdeur (1994)	15	0.662	
Sociable weaver	*Philetairus socius*	Doutrelant *et al.* (2004)	77	0.268	1
Stripe-backed wren	*Campylorhynchus nuchalis*	Rabenold (1984)	104	0.584	
Superb fairy-wren	*Malurus cyaneus*	Dunn *et al.* (1995)	92	−0.035	5
Western bluebird	*Sialia mexicana*	Dickenson *et al.* (1996)	613	0.108	
White-fronted bee-eater	*Merops bullockoides*	Emlen & Wrege (1988)	104	0.592	

1) Details of how *r*-values were converted from test statistics can be found in Table 1 of Griffin *et al.* (2005).

2) Wald statistic = 6.45 (*n* = 453) on effect of helpers on the probability of producing a fledgling gives effect size of *r* = 0.119; Wald = 6.85 (*n* = 453) on effect of helpers on number of fledglings produced gives effect size of 0.123. *R*-values were averaged to give overall rHelp value for study.

3) R-help calculated from effect of helpers on fledgling success: $F = 5.4$, $P = 0.02$. Sample size was not given in text but was assumed to be 450 from Table 2 of Curry & Grant (1989).

4) R-help calculated from effect of helpers on recruitment: $F = 9.56$, $n = 87$.

5) R-help was given as $r = −0.05$ in Griffin & West (2003), has been corrected, treating *P*-value as two-tailed. The authors thank Stuart Sharp and Tim Clutton-Brock for bringing this error to our attention.

Table A3 List of studies providing data on mean and variance in relatedness between helpers/potential helpers and beneficiaries. Relatedness measures are based on molecular genetic data, unless otherwise stated.

Common name	Species	Reference	n	Mean relatedness	Var. relatedness	Notes on data used in relatedness calculations
Arabian babbler	*Turdoides squamiceps*	Wright *et al.* (1999)	96	0.429	0.121	Relatedness between adults and offspring in 'family' and 'nonfamily' groups merged, using pedigree data confirmed by DNA fingerprinting; see text and Table 1 from ref.
Australian bell miner	*Manorina melanophrys*	Wright *et al.* (in press)	201	0.196	0.020	From Fig. 1 of unpublished manuscript
Dwarf mongoose	*Helogale parvula*	Creel & Waser (1994)	360	0.322	0.038	Relatedness measured between helpers and breeders (Fig. 1 in ref.)
Florida scrub jay	*Aphelocoma c. coerulescens*	Mumme (1992)	49	0.388	0.031	Relatedness measured between helper and nonhelping adults and offspring (Fig. 7a in ref.). Genealogical data used to assess relatedness, assuming monogamy as confirmed by genetic analysis.
Galapagos mockingbird	*Nesomimus parvulus*	Curry (1988)	290	0.237	0.053	Calculated from Table 3 in ref., including only those categories where identity of both parents confirmed.
Kookaburra	*Dacelo novaguineae*	Legge & Cockburn (2000)	268	0.623	0.149	Calculated from Fig. 2b of ref. Relatedness value is band-sharing co-efficient and therefore not comparable with measures of relatedness derived from other studies.
Long-tailed tit	*Aegeithalos caudatus*	Hatchwell *et al.* (2002)	261	0.076	0.023	Relatedness between males (potential helpers) and potential beneficiaries (males in nests within 900m radius) calculated from Fig. 2b from ref.
Meerkat	*Suricata suricatta*	Griffin (1998)	264	0.242	0.025	See Tables 5.2, 6.1 and 6.2 from ref.
Red-cockaded woodpecker	*Picoides borealis*	Khan & Walters (2000)	1184	0.389	0.011	See Table 3 from ref. Based on genealogical data.
Seychelles warbler	*Acrocephalus seychellensis*	Komdeur (1994)	102	0.336	0.043	Relatedness measure based on genealogical data assuming that breeding pair are parents of offspring at nests with only one egg laid, Table 1 from ref.
Stripe-backed wren	*Campylorynchus nuchalis*	Rabenold (1985)	151	0.346	0.033	See Table 1a from ref. Based on genealogical data.
Superb fairy-wren	*Malarus cyaenus*	Dunn (1995)	271	0.253	0.031	See Fig. 1 and Table 1 from ref.
Western bluebird	*Sialia mexicana*	Dickinson (1996)	321	0.226	0.037	See Fig. 2 and Table 4 from ref. Mainly genealogical, subset of relationships confirmed with DNA fingerprinting.
White-fronted bee eater	*Merops bulockoides*	Emlen (1988)	302	0.225	0.040	See Fig. 1 from ref. Based on genealogical data.

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Supplementary material

Table S1: Linear mixed model of predictors of kin discrimination (Zr-kin) with the mean and variance in relatedness excluded from the model to utilize data from all species.

Fixed Terms		Parameter Estimate (β)	SE	95%LCL	95% UCL	DF	F	P
Zr-help†		0.46	0.21	-0.01	0.92	1, 11	4.56	**0.05**
Probability vs. amount of help†	Amount	0.23	0.11	0.00	0.46	1, 16	6.60	**0.03**
	Probability	0.50	0.09	0.30	0.70			
Natal helpers†	Yes	0.16	0.08	-0.01	0.33	1, 10	5.87	**0.04**
	No	0.57	0.15	0.24	0.90			
Zr-help*Natal helpers						1, 11	0.03	0.86
Zr-help*Probability vs. amount of help						1, 11	0.30	0.59

Random Terms	Variance Component	SE	95%LCL	95% UCL	DF	LRT	P
Class†	0.00	0.00	0.00	0.00	1	0.00	1.00
Order (class)†	0.00	0.00	0.00	0.00	1	0.00	1.00
Family (order class) †	0.00	0.00	0.00	0.00	1	0.00	1.00
Species (family order class)†	0.06	0.03	0.03	0.26	1	25.61	**<0.0001**

Note: Effect sizes of rkin and rhelp were Z transformed prior to analysis and the parameters estimates are presented on the Z scale. The response variable Zr-kin was weighted by the inverse variance. Significant values are shown in boldface type. LRT = log-likelihood ratio test. LCL = lower confidence limit, UCL = upper confidence limit. † denotes terms included in final model. $N_{species}=18$, $N_{genera}=18$, $N_{families}=16$, $N_{orders}=4$, $N_{classes}=2$.

Table S2: Linear mixed model of kin discrimination (Zr-kin) entering each explanatory variables on their own.

Fixed Terms		Parameter Estimate (β)	SE	95%LCL	95% UCL	DF	F	P
Zr-help†		0.59	0.26	-0.02	1.16	1, 17	5.03	**0.04**
Mean relatedness		-1.83	0.80	-3.52	-0.20	1, 13	5.19	**0.04**
Variance in relatedness		-2.05	4.51	-12.21	8.11	1, 13	0.21	0.66
Probability vs. amount of help†	Amount	0.09	0.10	-0.11	0.30	1, 22	7.33	**0.01**
	Probability	0.39	0.09	0.19	0.59			
Natal helpers†	Yes	0.14	0.08	-0.02	0.31	1, 20	9.40	**0.007**
	No	0.70	0.16	0.35	1.05			

Note: Effect sizes of rkin and rhelp were Z transformed prior to analysis and the parameters estimates are presented on the Z scale. The response variable Zr-kin was weighted by the inverse variance. LRT = log-likelihood ratio test. LCL = lower confidence limit, UCL = upper confidence limit. † denotes terms included in final model. Significant values are shown in boldface type. Each model was fitted with a nested taxonomic random effects structure: class, order(class), family(order class)(not entered for mean and variance in relatedness terms), species(family order class). Number of species included in each analysis: Zr-help ($N_{species}$=18, N_{genera}=18, $N_{families}$=16, N_{orders}=4, $N_{classes}$=2), mean relatedness ($N_{species}$=14, N_{genera}=14, $N_{families}$=14, N_{orders}=4, $N_{classes}$=2), variance in relatedness ($N_{species}$=14, N_{genera}=14, $N_{families}$=14, N_{orders}=4, $N_{classes}$=2), probability vs. amount of help ($N_{species}$=23, N_{genera}=23, $N_{families}$=20, N_{orders}=4, $N_{classes}$=2), natal helpers ($N_{species}$=21, N_{genera}=21, $N_{families}$=19, N_{orders}=4, $N_{classes}$=2).

Table S3: Linear mixed model of predictors of kin discrimination (Zr-kin) removing data on the kookaburra, *Dacelo novaeguineae.*

Fixed Terms		Parameter Estimate (β)	SE	95%LCL	95% UCL	DF	F	P
Zr-help†		0.74	0.29	0.08	1.41	1, 8	6.78	**0.03**
Mean relatedness		-2.62	0.91	-4.64	-0.60	1, 10	8.25	**0.02**
Variance in relatedness						1, 7	0.20	0.67
Probability vs. amount of help†	Amount	0.11	0.11	-0.13	0.34	1, 11	10.29	**0.008**
	Probability	0.47	0.08	0.28	0.65			
Natal helpers†						1, 3	4.85	0.14
Zr-help*Mean relatedness						1, 6	0.02	0.89
Zr-help*Variance in relatedness						1, 6	2.18	0.19
Zr-help*Natal helpers						1, 5	0.07	0.80
Zr-help*Probability vs. amount of help						1, 8	2.16	0.18

Random Terms	Variance Component	SE	95%LCL	95% UCL	DF	LRT	P
Class†	0.00	0.00	0.00	0.00	1	0.00	1.00
Order (class)†	0.00	0.00	0.00	0.00	1	0.00	1.00
Species (order class)†	0.05	0.03	0.02	0.29	1	19.32	**<0.0001**

Note: Effect sizes of rkin and rhelp were Z transformed prior to analysis and the parameters estimates are presented on the Z scale. The response variable Zr-kin was weighted by the inverse variance. Significant values are shown in boldface type. LRT = log-likelihood ratio test. LCL = lower confidence limit, UCL = upper confidence limit. † denotes terms included in final model. $N_{species}$=13, N_{genera}=13, $N_{families}$=13, N_{orders}=4, $N_{classes}$=2.

Table S4: Linear mixed model of predictors of kin discrimination (Zr-kin) removing data on the green woodhoopoe, *Phoeniculus purpureus.*

Fixed Terms		Parameter Estimate (β)	SE	95%LCL	95% UCL	DF	F	P
Zr-help†		0.46	0.21	-0.01	0.93	1, 11	4.61	**0.05**
Probability vs. amount of help†	Amount	0.23	0.11	0.01	0.46	1, 15	6.65	**0.02**
	Probability	0.51	0.09	0.31	0.71			
Natal helpers†	Yes	0.17	0.08	-0.01	0.35	1, 10	5.87	**0.04**
	No	0.58	0.15	0.25	0.91			
Zr-help*Natal helpers						1, 11	0.03	0.86
Zr-help*Probability vs. amount of help						1, 11	0.27	0.61

Random Terms	Variance Component	SE	95%LCL	95% UCL	DF	LRT	P
Class†	0.00	0.00	0.00	0.00	1	0.00	1.00
Order (class)†	0.00	0.00	0.00	0.00	1	0.00	1.00
Family (order class) †	0.00	0.00	0.00	0.00	1	0.00	1.00
Species (family order class)†	0.06	0.03	0.03	0.26	1	25.66	**<0.0001**

Note: Effect sizes of rkin and rhelp were Z transformed prior to analysis and the parameters estimates are presented on the Z scale. The response variable Zr-kin was weighted by the inverse variance. Significant values are shown in boldface type. LRT = log-likelihood ratio test. LCL = lower confidence limit, UCL = upper confidence limit. † denotes terms included in final model. $N_{species}$=13, N_{genera}=13, $N_{families}$=13, N_{orders}=4, $N_{classes}$=2. Data on mean and variance in relatedness are not available for the green woodhoopoe and therefore was not included in models containing these variables. Consequently this table gives details of a re-analysis of table S1.