Supplementary Material

In the supplementary material, we provide further details on some issues discussed in the main text.

Adaptation and Natural Selection

The duality of process and purpose in evolution is captured in Darwin's suggestion that "natural selection can act only through and for the good of each being" (Darwin, 1859).

Fisher's fundamental theorem of natural selection

Fisher's theorem was frequently misunderstood in the population genetics literature prior to the late 1980's (reviewed by (Grafen, 2003; Grafen, 2007b), and this confusion also occurs in the social sciences (e.g. (Weibull, 1995). The first misunderstanding was the that fundamental theorem purports to describe total evolutionary change – it does not, and instead focuses upon the partial change in mean fitness, due to changes in gene frequency, that can be ascribed to the direct action of natural selection, neglecting other non-selective effects that are collectively termed 'deterioration of the environment' (Edwards, 1994; Ewens, 1989; Fisher, 1930; Frank and Slatkin, 1992; Grafen, 2003; Grafen, 2007b; Lessard, 1997; Price, 1972). The second misunderstanding was that the fundamental theorem concerns population fitness – it does not, and instead describes changes in individual fitness, which is expressed relative to the rest of the population (Fisher, 1941; Grafen, 2003; Grafen, 2007b).

Social Traits

The definition of cooperation does not require that a behaviour initially evolved because of its benefit to others, or that it is completely explained by its benefit to others. A behaviour could initially be selected for because it provides a direct benefit, with the effects on others coming later. For example, many bacteria release factors that benefit both themselves and their neighbouring cells (West et al., 2006). In order to be defined as cooperative traits, all that is required is that the rate at which these factors are produced is maintained at least partially by the social fitness consequences. This can be shown experimentally, without recourse to evolutionary history – for example, by showing that cells that do not produce these factors are able to exploit cells that do, and hence increase in frequency within populations (Diggle et al., 2007a; Griffin et al., 2004). This does not rule out the possibility that the factor originally evolved purely for the direct benefit of the cell that produces it – it just demonstrates the importance of social interactions for the current level at which it is maintained.

The major evolutionary transitions

Explaining the apparent paradox of cooperation is one of the central problems of biology. Although most attention on the problem of cooperation has focused on animals, such as insects, birds and mammals, it is increasingly being realised that cooperation is important

throughout the tree of life (Sachs et al., 2004; West et al., 2007a). For example, the growth and survival of microorganisms, such as bacteria, appears to depend upon the cooperative excretion of products (public goods) that perform a variety of functions, such as scavenging nutrients, communication, defence and movement (Crespi, 2001; West et al., 2006). Furthermore, the same problem occurs at all levels of biological organization (Leigh, 1991; Maynard Smith and Szathmary, 1995). The very existence of multicellular organisms depends upon stable cooperation between the eukaryotic cells that make up their tissues. Likewise, the mitochondria or chloroplasts upon which these eukaryotic cells depend for energy production were once free-living bacterial prokaryotic cells but are now cooperative organelles within these larger cells. The genes that make up the genome of every cell also cooperate with each other, in what has been termed the 'parliament of the genes' (Leigh, 1971). The general point here is that almost all of these major evolutionary transitions from replicating molecules to complex animal societies have relied upon solving the problem of cooperation (Table S1). This illustrates that not only is the problem of cooperation solvable, but it is fundamental to our understanding of evolution (Queller, 2000). Evolutionary biology has discovered multiple mechanisms that can explain cooperation and the repression of selfish behaviour, and hence we have a relatively good understanding of how the major transitions occurred (Queller, 2000).

Replicating molecules	⇒	Populations of molecules in compartments
Independent replicators	⇒	Chromosomes
RNA as gene and enzyme	⇒	DNA & protein (genetic code)
Prokaryotes	⇒	Eukaryotes (cell nucleus & organelles)
Asexual clones	⇒	Sexual populations
Protists	⇒	Multicelled animals, plants & fungi (with cell differentiation, i.e. organs)
Solitary individuals	⇒	Colonies (with non-reproductive worker castes)
Primate societies	⇒	Human societies (language)

Table S1. The major evolutionary transitions. It is generally accepted that there have been eight major evolutionary transitions, each of which has led to a new level of organismal complexity (Maynard Smith and Szathmary, 1995). Whilst major transitions can lead to a marked reduction in within-group competition, there can still be potential for conflicts, such as between genes in a genome or individuals in a society. The problem (of cooperation) in most of these transitions, is why did selection on entities to maximize their fitness at the lower level not prevent integration at the higher levels? The potential solutions are discussed in sections 5 and 6, and the care needed with defining adaptation at a group level is discussed in detail elsewhere (Gardner and Grafen, 2009). Cultural evolution is not included in the table, because it is a separate evolutionary process not a new biological transition.

The solutions to the problem of cooperation

Evolutionary research in this area provides a unified body of work that can explain cooperation at all levels of biological complexity. There has been a huge amount of theoretical research, directed at both developing models for specific systems, and

working out how these models relate to each other. Vast progress has been made in this area over the last 40 years, since Hamilton's groundbreaking work, with overviews of the area produced by different researchers showing relatively general agreement (Bergmüller et al., 2007; Bshary and Bergmüller, 2008; Clutton-Brock, 2002; Foster and Wenseleers, 2006; Frank, 1995; Frank, 1998; Frank, 2003; Grafen, 1984; Grafen, 1985; Grafen, 2006; Queller, 1992; Rousset, 2004; Sachs et al., 2004; Taylor, 1996; West et al., 2007a; West et al., 2006). An exciting feature of research in this area is that we have a single body of theory that can be applied to explain cooperation in everything, from the simplest replicating molecules to complex human societies. The overall aim is to see how the relative importance of the various mechanisms varies across different organisms (Bergmüller et al., 2007; Clutton-Brock, 2002; Maynard Smith and Szathmary, 1995; Sachs et al., 2004; West et al., 2007a). An additional possibility, cultural evolution, will be discussed in section 6.8.

Kin discrimination

Kin discrimination can occur through the use of environmental or genetic cues (Helanterä and Sundström, 2007; Lieberman et al., 2003). Environmental cues, such as prior association or shared environment, appears to be the most common mechanism of kin discrimination, as demonstrated in a range of organisms from ants to humans (Helanterä and Sundström, 2007; Lieberman et al., 2003).

This is also the case with long-tailed tits, where individuals distinguish between relatives and non-relatives on the basis of vocal contact cues, which are learned from related adults during the nesting period (associative learning) (Sharp et al., 2005). Another possible mechanism for kin discrimination is via some cue that is genetically determined, such as the odour produced by scent glands in a mammal (Grafen, 1990); also termed 'genetic similarity detection', 'matching' or 'tags'). This has been demonstrated in a range of organisms, including ants and mammals (Boomsma et al., 2003; Mateo, 2002). In Belding's ground squirrels, individuals discriminate kin on the basis of odours from oral and dorsal glands (Mateo, 2002), and use alarm calls to preferentially warn closer relatives of the approach of predators, despite the fact that this increases their own visibility to predators (Sherman, 1977).

There are a number of studies on potential mechanisms for kin discrimination in humans. Considering environmental cues, individuals are treated as closer relatives if there was a longer period of association during their childhood, which would provide a reasonable rule of thumb for family relationships (Porter and Cernoch, 1983; Russel et al., 1983). A role for odour cues has been supported by the observations that they allow mothers to recognise their newborns newborns to recognise their mothers (Cernoch and Porter, 1985; Russel, 1976) , and adult siblings to recognize each other (Porter et al., 1986). The use of kin discriminatory cues is important for fathers, if attempting to overcome paternity uncertainty. Paternal investment towards a child is determined not only by perceived mate fidelity (Apicella and Marlowe, 2004), but also by physical and psychological similarities between him and the child (Hauber and Sherman, 2001; Lieberman et al., 2007). Furthermore, (Platek et al., 2005; Platek et al., 2004) have shown

the brain area involved in the detection of child facial resemblance is more active in men than women. In order to reinforce the father's paternity belief, the mother and maternal relatives are more inclined to publicly ascribe facial resemblance of a newborn to the father (Alvergne et al., 2007; Daly and Wilson, 1982a; McLain et al., 2000; Regalski and Gaulin, 1993). Patterns of financial investment in children reflects relatedness certainty, with maternal grandmothers investing most in grandchildren, followed by maternal grandfathers, paternal grandmothers and then paternal grandfathers (Eisenberg, 1988; Kahana and Kahana, 1970; Pollet et al., 2007; Rossi and Rossi, 1990). This pattern is also reflected by aunts and uncles, who invest more in the matriline (McBurney et al., 2002). Infanticide data follow similar patterns (Daly and Wilson, 1982b).

Kin selection and limited dispersal

The potential role of limited dispersal has recently been much discussed in work on cooperation in bacteria and other microorganisms, where clonal reproduction means that neighbouring cells can be highly related (Diggle et al., 2007a; Gilbert et al., 2007; Griffin et al., 2004). Experimental support for the role of limited dispersal was provided by an experimental evolution study on how bacteria release siderophore molecules to scavenge for iron. These siderophores represent a cooperative public good: they are costly to the individual to produce, but iron bound to siderophores can be taken up by any cell, providing a benefit to other individuals in the locality. When populations of the bacterium *Pseudomonas aeruginosa* containing a mixture of a wild-type strain that produces siderophores and a cheater mutant that does not were maintained in conditions that led to relatively high or low relatedness, the cooperative wild-type strain outcompeted the cheater mutant strain under conditions of relatively high relatedness, but not under conditions of relatively low relatedness (Griffin et al., 2004). More generally, bacteria release a huge range of extracellular products that appear to be public goods (West et al., 2007c), and a high relatedness also favours signaling between bacterial cells to coordinate the production of these products (Brown and Johnstone, 2001; Diggle et al., 2007b).

As discussed in the main text, there is a huge industry of papers reinventing limited dispersal as an explanation for cooperation (Table 4). The mistakes in these areas seem to stem from the incorrect assumption that kin selection or indirect fitness benefits require kin discrimination (misconception 5), despite the fact that Hamilton pointed out the potential role of limited dispersal in his earliest papers on inclusive fitness theory (Hamilton, 1964; Hamilton, 1971; Hamilton, 1972; Hamilton, 1975); misconceptions 5 & 6). The level of confusion that this reinvention problem can create is illustrated by a recent review which suggested five mechanisms for the evolution of cooperation (Nowak, 2006), but where it turns out that three of those are just the same thing – 'network reciprocity' and group selection are just different ways of analyzing special cases of kin selection (Grafen, 2007a; Grafen and Archetti, 2008; Lehmann et al., 2007a; Lehmann et al., 2007b; Taylor et al., 2007b; West et al., 2007a).

Mechanisms for enforcing cooperation

Within the game theory literature, the possibility for reciprocity or punishment (as well as many other strategies) to solve the problem of cooperation in repeated interactions is sometimes referred to as the 'Folk Theorem'. It was termed this, because everyone seemed to already appreciate this possibility, when it was formalized in the 1950's by(Aumann, 1959).

This idea of reciprocity dates back to Hume (1739) and has been analysed in detail in the economics literature (reviewed by (Aumann, 1981; Aumann and Maschler, 1995; Binmore, 1994; Binmore, 1998; Binmore, 2005; Binmore, 2007; Fudenberg and Maskin, 1986; Kandori, 1992; Luce and Raiffa, 1957; Mailah and Samuelson, 2006) (Binmore, 2007; Mailah and Samuelson, 2006).

One example of punishment is found in meerkats, where the dominant female suppresses reproduction in her subordinates. If a subordinate female becomes pregnant when the dominant is also pregnant, then the dominant is likely to subject the subordinate to aggressive attack and temporarily evict her from the group, which usually leads to abortion of the subordinate's litter. Another example is provided by Superb Fairy Wrens, where subordinates are punished if they are removed (so cannot help) during the breeding season, but not outside it (Mulder and Langmore, 1993). Punishment may also be important in humans, as we shall discuss below.

Enforcement mechanisms have been suggested to be important in explaining cooperation between species. An elegant example is provided on coral reefs where the cleaner fish *Labroides dimidiatus* removes and eats ectoparasites from its 'clients', which refrain from consuming this potential prey while it performs the service. Although parasite removal and food acquisition are clearly beneficial to the client and cleaner, respectively, there is a conflict, because the cleaners would prefer to eat the tissue or mucus of their hosts, which is costly to the host (Bshary and Grutter, 2002a; Bshary and Grutter, 2002b). The clients use three mechanisms to suppress this conflict and enforce cooperative feeding on ectoparasites only: avoiding cleaners that they have observed cheating (reputation effects or partner choice), leaving for another cleaner (partner switching), and aggressively chasing the cleaner (punishment) (Bshary, 2002; Bshary and Grutter, 2002a; Bshary and Grutter, 2002b; Bshary and Schäffer, 2002). Observational and experimental data suggest that cleaner fish are more cooperative and less likely to feed on mucus after punishment (Bshary and Grutter, 2005).

Conditional enforcement may be extremely important in explaining cooperation between species, where kin selection cannot be cannot be the driving force. Other examples include: (a) how Yucca plants, *Glochidion* trees and fig trees selectively abort flowers which have been over exploited by their pollinators (Goto et al., 2010; Jander and Herre, 2010; Pellmyr and Huth, 1994) ; and (b) how legume plants (beans and peas) cut off the O_2 supply to (sanction) the rhizobia bacteria that live in nodules in their roots, if they do not provide them with nitrogen (needed for plant growth) at a sufficiently high rate (Kiers et al., 2006; Kiers et al., 2003).

Enforcement could also be favoured if it provides an indirect fitness benefit (Frank, 1995;

Gardner and West, 2004; Lehmann et al., 2007c; Ratnieks, 1988). The simplest way this could occur is by reducing the fitness of individuals who are competing with relatives and hence freeing up resources for relatives. This occurs in some ants, bees and wasps where a fraction of the workers lay their own eggs (Ratnieks and Visscher, 1989; Ratnieks et al., 2006). Other workers frequently do not tolerate such behaviour and selectively cannibalise or 'police' eggs laid by workers. This behaviour is selected for because the policing workers can be more related to the sons of the queen than to the sons of the other workers and because cheating workers raising their own sons can reduce the colony's overall productivity (Ratnieks, 1988; Wenseleers et al., 2004). Across species, it has been shown that there are higher levels of worker cooperation in species where policing is more common and effective. Specifically, the proportion of workers who lay eggs is negatively correlated with the probability of worker laid eggs being killed (Wenseleers and Ratnieks, 2006). One way of conceptualizing this is that policing reduces the fitness gains of cheating, which is the same as reducing the cost (c) of cooperating in Hamilton's rule

Misconception 1

We are not suggesting that models of cooperation in humans never consider situations that are altruistic. Instead, cooperation can be mutually beneficial or altruistic, depending upon the values of parameters such as the dispersal rate, group size, cost and effect of punishment etc, all of which influence the local competition for resources (Lehmann et al., 2007c). The potential for the evolution of altruistic cooperation, as defined by Hamilton (1964), arises because many models assume limited dispersal, which leads to a significant relatedness between the individuals interacting within a group, and hence indirect fitness benefits. Cooperation can therefore provide both direct fitness benefits and indirect benefits via cooperating with relatives (Lehmann et al., 2007c).

The Prisoners' Dilemma and Tit-For-Tat

The Prisoner's Dilemma (PD) and tit-for-tat have led to much confusion in the biological literature. Whilst we cannot go into detail on this huge literature here, we would like to briefly raise two issues: (1) things are not as simple as is often assumed; (2) what are the major uses of stylized games such as the PD.

<u>Things are not as simple as often assumed</u>

Following Axelrod's (Axelrod, 1984; Axelrod and Hamilton, 1981) hugely influential work in this area, it has commonly been assumed that the strategy 'tit-for-tat' (cooperate, but then punish non-cooperation by also not cooperating) is the evolutionary stable strategy (ESS) in the iterated PD game, and that it is disadvantageous to be the first player to defect (e.g. (Axelrod, 1984; Maynard Smith, 1982; Poundstone, 1988); reviewed by (Binmore, 1994), pp. 173-175, 194-203; (Binmore, 1998), pp. 186, 313-319). This is especially true in the biological literature, where researchers appear to be generally unaware of the huge literature on reciprocity in the fields of game theory and economics (Binmore, 1998). However, the folk theorem has long shown that tit-for-tat is

only one of an enormous number of strategies (Nash equilibria) that can be favoured, and that there are many more ways of supporting cooperation in repeated interactions than by naive pairwise reciprocation (Binmore, 1994; Binmore, 1998; Boyd and Lorberaum, 1987).

A number of studies have supported the folk theorem by showing that a mixed Nash equilibrium is selected for, in which multiple strategies are maintained, with tit-for-tat not even at a particularly high frequency (Binmore, 1994; Binmore, 1998; Boyd and Lorberaum, 1987). Axelrod (Axelrod, 1984) carried out computer simulations that competed different strategies against each other, and whilst tit-for-tat was the most common strategy after competition, the 'best' strategy was actually a mixed strategy that performs tit-for-tat only approximately $1/6^{th}$ of the time. Since then, it has been shown that the results are extremely dependent upon the different strategies that are competed, their initial starting frequencies, and how long the simulations are run for (Binmore, 1994; Binmore, 1998; Young and Foster, 1991). For example, in some cases, a greater success is enjoyed by the more nasty reciprocator 'tat-for-tit' (see also 'Pavlov' in (Nowak and Sigmund, 1993), which starts by not cooperating, and only switches to cooperating in response to the cooperation of others. Furthermore, many of the famous anecdotes of tit-for-tat in humans, such as ceasefire arrangements between soldiers in the trenches during the First World War, are at least as consistent with 'nastier' strategies such as tat-for-tit (Binmore, 1994; Binmore, 1998). Although, the point here, is not that we should argue over what is the best strategy, just that lots of strategies can be maintained at equilibrium, results depend hugely upon starting conditions, and that tit-for-tat won't even necessarily be the most common.

What are the major uses of the PD and other stylised games?

It is sometimes assumed that the evolution of cooperation is usually studied with the PD (Bergstrom, 2002; Nowak et al., 2004). To put this another way: "A whole generation of scholars swallowed the line that the Prisoners' Dilemma embodies the essence of the problem of human cooperation" (Binmore, 2007), p. 18). In the early days of modern biological social evolution research (1960's-80's), it was relatively hard to convince people that altruism and cooperation were problematic, and needed a solution (Hamilton, 1996). The beauty of the PD was that it allowed a clear abstraction of the problem of cooperation, with a 2×2 payoff matrix, and a quick back-story, to help visualisation. The main use of the PD was therefore in convincing people that cooperation was a problem, rather than actually giving general insights into how this problem is solved. This is because it represents the situation in which selection against cooperation is as strong as possible (Binmore, 2007). In the economics literature, this problem has been addressed with elegant extended analyses of the iterated PD (Benoit and Krishna, 1985; Binmore, 1994; Binmore, 1998; Fudenberg and Maskin, 1986; Fudenberg and Maskin, 1990; Fudenberg et al., 1994; Kandori, 1992), but also by looking at a range of other games, for situations that may be particularly appropriate in humans, such as bargaining (Binmore, 1994; Binmore, 1998).

In contrast, in the biological literature, the focus on the PD, and reciprocity, has hindered

progress (Bergmüller et al., 2007; Boyd and Lorberaum, 1987; Clutton-Brock, 2002; Clutton-Brock, 2009; Hammerstein, 2003; Leimar and Hammerstein, 2006; Stevens and Hauser, 2004; Stevens et al., 2005; West et al., 2007a). The PD makes a large number of extremely specific and often unrealistic assumptions, which are rarely stated or justified, such as discrete strategies (cooperation is all or nothing), confounding cooperation with punishment (Axelrod (1984, p. 120-121) argued that this is why complex strategies don't do well), no partner choice (interactions at random), a limited payoff structure, simultaneous moves, etc. Whilst abstraction can be useful for ease of analysis or tractability, the various assumptions of games such as the PD often make analysis more complicated, leading to highly technical mathematics or heavy reliance upon numerical simulations. From an empirical perspective, a focus on the PD has led to the common assumption that reciprocity is important in animals (see any animal behaviour textbook), whereas in reality, there is a lack of evidence that it is important in any non-human animal (Clutton-Brock, 2009; Hammerstein, 2003).

In the biology literature, there is a huge literature on the PD and related games (e.g. the snow drift game), examining consequences such as playing the games in a spatial setting as provided by lattices of graphs. These models are clearly of interest from a mathematical and aesthetic perspective ((Nowak and May, 1992), p. 829; (Nowak and May, 1993), p. 77; (Nowak et al., 1994), p. 4879). However, because these approaches lack transparency, it can be hard to determine the underlying processes, or see how the results of different studies relate to each other, and to theory more generally (Lehmann and Keller, 2006), let alone determine the biological implications. This has led to: (a) repeated reinvention of the 'wheel' – apparently novel solutions to the problem of cooperation that simply turn out to be new names for old ideas (Lehmann and Keller, 2006; West et al., 2007a); (b) a lack of attention to all the other ways in which direct fitness benefits can favour cooperation (see figure 2 and misconception 2), but which cannot be analysed with the PD; (c) empirical workers making things seem more complicated, in an attempt to contort real systems into the assumption of the PD (Brown, 2001; West et al., 2007a). A general point here is that theory should facilitate predictions and empirical testing of these predictions - if empiricists have to bend-over-backwards to get the real world to fit the theory, then something has gone badly wrong. The kin selection theory approach, and especially its 'direct' or neighbour-modulated fitness implementation (Frank, 1998; Taylor and Frank, 1996; Taylor et al., 2007a) provides a solution to these problems, because it allows the biology to lead the mathematics, and hence facilitates the empirical application and testing of theory. It is for this reason that the kin selection methods dominate the empirically driven theoretical work, whilst the study of stylized games such as the PD remains a more purely mathematical pursuit.

The central problem of sociobiology

EO Wilson's (Wilson, 1975), p.31) stated that: "the central theoretical problem of sociobiology [is]: how can altruism, which by definition reduces personal fitness, possibly evolve by natural selection?" (Becker, 1974a; Becker, 1974b). This is misleading, because it is actually cooperation that is the central problem of sociobiology: how can behaviours which benefit others evolve by natural selection? As discussed in

section 4, understanding cooperation is one of the central problems of the whole field of evolutionary biology, because of its role in the major evolutionary transitions. In some cases these transitions have involved mutually beneficial cooperation, and in others, altruistic cooperation (Queller, 2000). A general problem here is that secondary sources aimed at a less specialist audience can give an incorrect impression of the primary literature. For example, Wilson's (1975) book gave a weak representation of social evolutionary theory, even at the time, and is accepted to be misleading on several accounts including incorrect descriptions of inclusive fitness, kin selection, group selection and altruism and spite (Dawkins, 1979; Foster et al., 2006; Grafen, 1982; Helanterä and Bargum, 2007; West et al., 2007b).

Misconception 4: Proximate and Ultimate explanations of cooperation

A general issue here is that care must be taken to not over interpret proximate patterns from an ultimate perspective. Ultimate and proximate factors can operate at different time scales. Natural selection works over evolutionary time, with time steps of generations compared to economic settings where the time step can be a few seconds and the expectation is that utility will be maximised on that time frame. Natural selection will not result in behaviours that are perfect in every conceivable situation - instead it favours proximate mechanisms that maximise fitness in the situations that are encountered (the 'selective regime'). Consequently, if we try to assign ultimate explanations to proximate patterns, outside of the context of the selective regime in which they were favoured, we run the risk of adaptationist story telling. We stress that the possible limits to adaptation is not an idea invented to explain patterns in humans - it has long been accepted in the field of animal behaviour (Herre, 1987; Krebs and McCleery, 1984; Wehner, 1987). To give a specific example in the case of humans, it is often argued that indirect benefits of cooperation can be ruled out from the start in humans, because cooperation still occurs when we "know the players are not relatives". However, the key point here is not the present situation, but whether relatedness was significant when the underlying proximate mechanisms evolved (Binmore, 1998; Seabright, 2004). Note that, we are not necessarily saying that relatedness was important, just that proximate mechanisms (or observations that cooperation occurs between non-relatives) do not necessarily rule it out. We return to the general issue of over interpreting proximate patterns in misconception 14.

Misconception 6: Relatedness in structured populations

Wright's (1931) F_{ST} measures the degree of genetic homogeneity within a group relative to the whole population. For haploids, $F_{ST} = (1-m)^2 / (N - (N-1)(1-m)^2)$, where m is the individual rate of dispersal (proportion of individuals that disperse from their natal patch before breeding) and N is the group size, and this is exactly the kin selection coefficient of relatedness for an individual to its group in this case. For example, if $m = 0.01$ and $N = 100$, then the average relatedness of group mates is approximately 1/3; hence, the relatedness between first cousins will be >1/3, and not the commonly assumed 1/8. For diploids, $F_{ST} = (1-m)^2 / (2N - (2N-1)(1-m)^2)$, which for small m and large N is well approximated by $F_{ST} = 1/(1+4Nm)$, representing one of the most famous equations

of population genetics theory, and relatedness is given by $2F_{ST}/(1+F_{IT})$, where F_{IT} is a measure of genetic homogeneity within a individual (inbredness; (Hamilton, 1970; Rousset, 2004) p. 141). These equations also show that it is incorrect to assume that kin selection cannot be important in large populations. Clear quantitative support for these predictions has been provided by experimental evolution studies on how population structure influences selection for cooperation in bacteria (Brockhurst et al., 2007; Diggle et al., 2007a; Griffin et al., 2004; Kümmerli et al., 2009).

Misconceptions 7-9: relatedness and kin selection

The four misconceptions given above emphasise how the generality of inclusive fitness theory and Hamilton's rule are often underappreciated. Hamilton's rule provides an encapsulation of inclusive fitness theory that can be applied to all forms of social behaviour, and not just altruism: r, b and c can each be positive or negative. Furthermore, it clarifies that the coefficient of relatedness is a measure of the correlation between two individuals in their genetic predisposition for a trait of interest, rather than a measure of their genome-wide similarity or genealogical closeness per se. However, in many scenarios the coefficient of relatedness will (on average) be the same over most of the genome, and will tend to coincide with the genealogical relationship of the two individuals – justifying J.B.S. Haldane's famous quip that he would give his life "for two brothers, or eight cousins".

A possible source of confusion here is the term 'kin selection'. Maynard Smith (1964) coined the term 'kin selection' to describe how indirect fitness benefits arise from helping relatives reproduce. Since then, the phrase kin selection has been used in multiple ways (West et al., 2007b). The narrower use of kin selection works upon interactions between individuals who are genetically related due to common ancestry – i.e. indirect benefits due to limited dispersal or kin discrimination. The broader use of kin selection works upon interactions between individuals who are genetically correlated at the loci of interest, regardless of whether this is due to coancestry or some other mechanism – i.e. this also includes greenbeard effects. The difference between these usages is therefore whether kinship and relatedness are defined on the basis of average genetic similarity over most of the genome (narrow definition), or at the particular locus of the behaviour being examined (broad definition). However, the possibility for confusion is mainly theoretical, because kinship is by far the most common reason for indirect fitness benefits, with greenbeards being incredibly rare. In addition, the use of the phrase "inclusive fitness" should avoid confusion, because it has been defined broadly since its inception (Hamilton, 1964; Hamilton, 1970; Hamilton, 1971; Hamilton, 1975).

Misconceptions 9-13: Group selection

The lack of a formal theory of group selection contrasts clearly with the large literature formalizing inclusive fitness theory, examining the different ways in which it can be modeled mathematically, how this links to population and quantitative genetic theory, and showing that natural selection will produce individuals that maximize their inclusive fitness (see section 2). The idea that individuals strive to maximise their inclusive fitness

holds irrespective of the intensity of selection between-groups; in contrast, group fitness is only maximised in trivial extreme cases or complete repression of competition within groups (Gardner and Grafen, 2009).

To some extent, any debate about whether selection is at the individual or group level (Bergstrom, 2002; Burnham and Johnson, 2005) is not very useful. Selection always operates at the level of inclusive fitness, and the extent to which this is dependent upon within-group versus between-group selection will vary hugely, depending upon model details and parameter values (Gardner and Grafen, 2009; Grafen, 2006).

All the major developments in social evolution theory have been pioneered and led by the inclusive fitness approach, and not group selection. For example, worker policing in social insects, kin discrimination in organisms ranging from slime moulds to cooperative breeding vertebrates, alarm calls, parent offspring conflict, sibling conflict, split sex ratios in social insects, selfish genetic elements, parasite virulence, sex ratios in structured populations (local mate competition), queuing for reproduction in societies, and genomic imprinting (West et al., 2008).

Misconception 14, and human behaviour in economic games

There are three issues here. First, the discussion of possible explanations for cooperation focuses on kin selection and reciprocity, and hence ignores the majority of the direct fitness explanations for cooperation that have been developed (misconception 2). Second, as we shall discuss in misconception 15 (see also misconceptions 5-8), the strong reciprocity theoretical explanations actually rely on standard direct and indirect benefits (Lehmann et al., 2007c), and so do not predict cooperation in one-shot encounters (unless you allow for behaviours misfiring – see below). It is simply that this has not been acknowledged. Third, there are a number of alternative explanations for the data. In the main text of misconception 14 we discuss three non-exclusive possibilities.

One of the simplest explanation for cooperating and punishing in one-shot encounters is that it is a byproduct of selection for cooperation in other conditions. This is analogous to the examples discussed above, such as why a female gorilla protects human children that fall into their pen, dolphins help exhausted swimmers to safety, and enslaved ants rear the broods of their captors. Specifically, humans have evolved a behaviour for cooperation and punishment, that works in the environment usually encountered, but which may lead to suboptimal performance in artificial laboratory games (Bateson et al., 2006; Binmore, 2006; Burnham and Johnson, 2005; Hagen and Hammerstein, 2006; Haley and Fessler, 2005; Nowak et al., 2000; Trivers, 2004; West et al., 2007b).

This is analogous to the discussion in the evolutionary and behavioural literature of limits to adaptation and how they may result in 'rules-of-thumb'. Natural selection produces behaviours that work in the environments in which they evolve, not behaviours that will be perfect in any artificial situation - individuals perform less well in situations that they encounter less frequently (Davies, 1992; Herre, 1987; Herre et al., 2001; Krebs

and McCleery, 1984; Pompilio et al., 2006; Wehner, 1987). This also relates to the discussion of rationality versus saneness in (Ursprung, 1988).

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