Animal Behaviour 92 (2014) 291–304

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

Special Issue: Kin Selection

Hamilton's legacy: kinship, cooperation and social tolerance in mammalian groups

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ARTICLE INFO

Article history:
Received 16 October 2013
Initial acceptance 3 January 2014
Final acceptance 18 February 2014
Available online 1 April 2014
MS. number: ASI-13-00886

Keywords:
cooperation
direct benefit
inclusive fitness
indirect benefit
kin selection

In 1964, W. D. Hamilton proposed a novel solution to the long-standing evolutionary puzzle: why do individuals cooperate? Hamilton predicted that, if individuals possess the ability to discriminate on the basis of kinship, then they should gain inclusive fitness benefits by biasing helpful behaviour towards relatives and harmful behaviour away from them. The possibility that kin selection might favour social evolution has now inspired five decades of active research. Here, I synthesize this evidence for social mammals. First, I report on the methodological advances that allow for pedigree construction, and review the evidence for maternal and paternal kin discrimination. Second, I recognize that a substantial body of evidence for the evolution of cooperative breeding via kin selection exists, and then focus on the potential for kin selection to favour less well understood, yet equally salient, targets of selection: social partner choice, coalition formation and social tolerance (withholding aggression). I find that kin selection favours remarkably similar patterns of nepotism in primate and nonprimates with respect to these short-lived social acts. Although social alliances among maternal and paternal kin are common in mammalian societies, kinship largely fails to protect individuals from aggression. Thus, an individual's closest associates and allies, many of whom are kin, are most often an individual's closest competitors within mammalian social groups. Taken together, these findings highlight the value of Hamilton's holistic approach in simultaneously considering the direct benefits of competition and the indirect fitness benefits of cooperation. Despite major empirical advances since the inception of kin selection theory, future tests using newly available molecular and statistical methods in combination with longitudinal behavioural data are required to partition the relative contributions of direct and indirect fitness on the lifetime inclusive fitness. Such approaches will elucidate the relative influences of evolutionary and ecological forces favouring social evolution across the mammalian lineage of social mammals.

Understanding the evolutionary origins and mechanisms involved in the maintenance of cooperation is a central problem in biology. Specifically, it is unclear why an individual (donor) should help another individual (beneficiary) if doing so is costly (Darwin, 1859). In light of this evolutionary puzzle, the theoretical constructs of kin selection (Hamilton, 1964), reciprocal altruism (Trivers, 1971), direct benefits (also called by-product mutualisms: Brown, 1983; Connor, 1995; West-Eberhard, 1975) and group selection (Wilson, 1975; Wilson & Wilson, 2007) have surfaced as potential explanations (reviewed by: Clutton-Brock, 2009; Dugatkin, 2002; Noë, 2006; Nowak, 2006; Queller, 1985; Sachs, Mueller, Wilcox, & Bull, 2004; West, Griffin, & Gardner, 2007a, 2007b). In particular, the concept that cooperative traits may spread via kin selection is now a central paradigm in evolutionary biology (Abbot et al., 2011; Foster, Wenseleers, & Ratnieks, 2006; Herbers, 2013; Silk, 2002; West et al., 2007a, 2007b).

Although Robert A. Fisher (1930), John B. S. Haldane (1932) and Charles Darwin (1859) independently raised the notion that kinship might explain social evolution, it was William D. Hamilton (1964) who revolutionized evolutionary theory with his elegant inequality: $b \times r > c$. Now widely referred to as Hamilton's rule, this influential inequality predicts the spread of helpful behaviours via kin selection when the net fitness benefits (b) to the beneficiary multiplied by the coefficient of relatedness between the donor and beneficiary (r) are greater than the costs (c) to the donor. Hamilton's seminal contribution has now inspired scholars for half of a century, giving rise to a large body of empirical evidence.

Here, I evaluate the predictive value of kin selection theory in social mammals. First, I identify new methodological tools available for testing the predictions of kin selection theory in free-living mammals, and evaluate our understanding of how mammals

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http://dx.doi.org/10.1016/j.anbehav.2014.02.029
0003-3472/

discriminate on the basis of maternal and paternal kinship given these recent advances. Second, after recognizing the overwhelming evidence for the evolution of cooperative breeding via kin selection, I focus primarily on evaluating the evidence for kin selection favouring three less well understood, yet equally salient, targets of selection: social partner choice, coalition formation and social tolerance (withholding aggression). Evaluating these largely ignored domains is important because Hamilton (1964) originally proposed that kin selection might promote cooperation in viscous populations composed mostly of close relatives. Limited dispersal may indeed act as a cohesive force to promote cooperation among closely related neighbours, but may also expose relatives to intense local competition. In such cases, the direct costs of competition among kin may counteract the benefits of cooperation (Queller, 1994; West, Murray, Machado, Griffin, & Herre, 2001; Wilson, Pollock, & Dugatkin, 1992). Theoretical work attempts to clarify the selective forces shaping the tensions between competition and cooperation among relatives, and identifies the need for a synthesis of the empirical evidence on this topic (e.g. West, Pen, & Griffin, 2002). Thus, a major goal of this review is to quantify the extent to which kinship promotes cooperation and protects against competition in mammals. Because females of most mammalian species are philopatric, remaining at home throughout their entire lives (Greenwood, 1980; Smale, Nunes, & Holekamp, 1997), cooperation is expected to evolve more often via kin selection in female than in male mammals (e.g. Sterck, Watts, & van Schaik, 1997; Wrangham, 1980). Given this, I focus primarily on the social acts of adult females and include some data on species for which males are the philopatric sex.

MOLECULAR MEASURES OF RELATEDNESS IN ECOLOGICAL SETTINGS

Hamilton (1964) proposed that genes coding for cooperative phenotypes may be passed on directly (through personal reproduction by an individual) and/or indirectly (through the reproduction by a relative with whom an individual shares genes). However, molecular techniques to test these predictions in natural populations were largely unavailable in 1964 when Hamilton proposed his seminal theory. In particular, although most social mammals have opportunities to interact with maternal and paternal kin, pioneering studies testing kin selection theory were based only on knowledge of maternal lineages constructed from field observations of nursing and/or spatial associations (reviewed by Widdig, 2007). Scholars of animal behaviour now possess valuable tools for assessing genetic relationships for natural populations.

Pedigree construction now allows for the evaluation of the extent to which individuals cooperate with their direct paternal and maternal descendants (e.g. offspring: $r=0.5$ and grand-offspring: $r=0.25$) and collateral kin (e.g. $r=0.5$ for full siblings, $r=0.25$ for half siblings, $r=0.125$ for aunts or uncles) based on coefficients of relatedness, r, which ranges from 0 to 1. Genetic estimators are useful in cases for which full pedigrees are unavailable. For example, Queller and Goodnight's (1989) R reflects how similar two individuals are at a specific genetic locus relative to other individuals in the same population. R values range from −1 to 1, and are highly variable across mammalian species (for examples, see Table 1). Positive R values indicate that two individuals are more related than expected by chance. In large populations, the R value between any pair of individuals typically reflects the true coefficient of relatedness (r), and is therefore a useful alternative to coefficients of relatedness for testing kin selection theory.

Microsatellites, segments of DNA with very short repeated sequence motifs, have proved invaluable in alleviating many of the historical constraints of kin selection studies (reviewed by: Pemberton, 2008; Queller, Strassmann, & Hughes, 1993; Selkoe & Toonen, 2006). Microsatellites allow for the straightforward segregation of genetic marker loci and are reliable even when DNA is somewhat degraded and gels are run at different times. DNA extracted from samples during field conditions may therefore be straightforwardly amplified using polymerase chain reactions for a modest cost. Microsatellites allow for pedigree construction and are widely available for numerous species of mammals (for examples, see Table 2). Tissue ($N=21$ species), blood ($N=12$ species) and hair ($N=12$ species) are the most common sources of DNA for studies on mammals. DNA may also be extracted from faeces ($N=6$ species), bone ($N=3$ species) and mucous ($N=1$ species). The combination of long-term behavioural observations and pedigree construction based on minimally invasive sampling techniques offers new insights into kin selection theory.

Table 1
Examples of R values for mammalian species

Species	R (mean±SE)	Source
Crocuta crocuta (spotted hyaenas)	−0.05±0.007	Van Horn, Engh, Scribner, Funk, and Holekamp (2004)
Potos flavus (kinkajous, females)	−0.02±0.31	Kays, Gittleman, and Wayne (2000)
Eptesicus fuscus (big brown bats)	−0.01*	Metheny, Kalcounis-Rueppell, Willis, Kolar, and Brigham (2008)
Procyon lotor (raccoons)	0.01±0.02	Hirsch, Prange, Hauver, and Gehrt (2013)
Odocoileus virginianus (white-tailed deer)	0.03±0.01	Ernest, Hoar, Well, and O'Rourke (2010)
Marmota monax (woodchucks)	0.05±0.05	Maher (2009)
Physeter macrocephalus (sperm whales)	0.05±0.05	Ortega-Ortiz, Engelhaupt, Winsor, Mate, and Rus Hoelzel (2012)
Lontra canadensis (river otters)	0.09±0.03	Blundell, Ben-David, Groves, Bowyer, and Geffen (2004)
Potos flavus (kinkajous, males)	0.12±0.25	Kays et al. (2000)
Octodon degus (degu, females)	0.14±0.05	Quirici, Faugeron, Hayes, and Ebensperger (2011)
Octodon degus (degu, males)	0.21±0.12	Quirici et al. (2011)

* Based on a single measure for one social group of bats.

MECHANISMS OF KIN SELECTION

Hamilton (1964) predicted that, if individuals possess the ability to discriminate on the basis of kinship, then they should gain inclusive fitness benefits by biasing helpful behaviour towards relatives, and harmful behaviour away from them. Kin selection therefore requires that animals either recognize specific individuals as genetic relatives ('kin recognition') or be able to discriminate between genetically related and genetically unrelated individuals ('kin discrimination'). Indeed, kin discrimination is widely documented for mammals and operates largely via two major mechanisms: familiarity and phenotypic matching (reviewed by Tang-Martinez, 2001). Kin discrimination based on familiarity, or shared associations, involves learning during a critical period of development during which relatives interact within contexts that vary with relatedness (Kareem & Barnard, 1982). For example, spatial overlap is common when family members share a burrow or den location. Individuals born at different times might also recognize each other as kin based on shared associations with a common parent. For instance, Belding's ground squirrels, *Urocitellus beldingi*, discriminate between siblings and nonsiblings based on shared

Table 2
Examples of mammalian species for which microsatellite markers allow for genotyping

Species	Sample size	Loci	Source of DNA	Reference
Primates				
Pan troglodytes verus (chimpanzee)	41	9	Faeces, hair, bone	Vigilant, Hofreiter, Siedel, and Boesch (2001)
Papio cynocephalus (savannah baboon)	76	12	Blood, faeces	Smith et al. (2000)
Macaca mulatta (rhesus macaque)	141	15	Blood	Langos, Kulik, Mundry, and Widdig (2013)
Cebus capucinus (white-faced capuchin)	172	18	Faeces	Perry, Manson, Muniz, Gros-Louis, and Vigilant (2008)
Callithrix jacchus (common marmoset)	40	11	Hair	Nievergelt, Digby, Ramakrishnan, and Woodruff (2000)
Ungulates				
Loxodonta africana (African elephant)	545	11	Tissue, faeces	Archie et al. (2007)
Ovis canadensis (bighorn sheep)	100	8	Tissue, blood	Forbes, Hogg, Buchanan, Crawford, and Allendorf (1995)
Sus scrofa (European wild boar)	167	14	Tissue	Costa et al. (2012)
Odocoileus virginianus (white-tailed deer)	135	38	Tissue	Ernest et al. (2010)
Giraffa camelopardalis (giraffe)	535	10	Tissue	Carter et al. (2013)
Equus ferus caballus (feral horse)	312	14	Hair	Lee and Cho (2006)
Cetaceans				
Orcinus orca (killer whale)	78	26	Tissue, faeces, mucous	Ford et al. (2011)
Physeter macrocephalus (sperm whale)	51	13	Tissue	Ortega-Ortiz et al. (2012)
Tursiops aduncus (bottlenose dolphin)	46	12	Tissue	Frère, Krützen, Mann, Connor, et al. (2010); Frère, Krützen, Mann, Watson-Capps, et al. (2010)
Carnivores				
Zalophus wollebaeki (Galapagos sea lion)	380	22	Tissue	Wolf and Trillmich (2008)
Crocuta crocuta (spotted hyaena)	201	10	Blood, hair	Van Horn, Engh, et al. (2004)
Panthera leo (African lion)	141	15	Tissue	Spong, Stone, Creel, and Björklund (2002)
Martes americana (American marten)	88	12	Hair	Mowat and Paetkau (2002)
Meles meles (European badger)	66	7	Hair	Frantz et al. (2004)
Potos flavus (kinkajou)	25	11	Blood	Kays et al. (2000)
Procyon lotor (raccoon)	30	15	Blood	Hirsch et al. (2013)
Nasua nasua (ringtailed coatis)	65	15	Tissue	Hirsch et al. (2012)
Ursus arctos (brown bear)	930	8	Hair, bone	Cronin and MacNeil (2012)
Ursus maritimus (polar bear)	473	8	Hair, bone	Cronin and MacNeil (2012)
Lynx rufus (bobcat)	22	12	Blood, hair	Janecka et al. (2006)
Canis lupus (wolves)	163	32	Tissue, blood, faeces	Liberg et al. (2005)
Lontra canadensis (river otter)	110	9	Blood	Blundell et al. (2004)
Suricata suricatta (meerkat)	1494	18	Tissue	Nielsen (2013)
Marsupials				
Trichosurus cunninghami (brushtail possum)	104	7	Tissue, blood	Banks et al. (2011)
Lasiorhinus krefftii (hairy-nosed wombat)	59	8–9	Blood	Taylor, Horsup, Johnson, Sunnucks, and Sherwin (1997)
Cingulates				
Dasypus novemcinctus (nine-banded armadillo)	290	7	Tissue	Prodöhl, Loughry, McDonough, Nelson, and Thompson (1998)
Rodents				
Mus domesticus (house mouse)	54	20	Tissue	Blouin, Parsons, Lacaille, and Lotz (1996)
Peromyscus spp. (deer mouse)	20	60	Tissue	Dewsbury (1990)
Marmota monax (woodchuck)	48	7	Hair	Maher (2009)
M. flaviventris (yellow-bellied marmot)	997	12	Hair	Olson, Blumstein, Pollinger, and Wayne (2012)
M. marmota (alpine marmot)	214	14	Hair	Goossens et al. (1998)
Spermophilus columbianus (Columbian ground squirrel)	42	9–13	Tissue, blood	Stevens, Coffin, and Strobeck (1997)
S. brunneus (Idaho ground squirrel)	10	13	Tissue, blood	May, Gavin, Sherman, and Korves (1997)
Tamiasciurus hudsonicus (North American red squirrel)	7086	16	Tissue	Taylor et al. (2012)
Octodon degus (degu)	48	6	Tissue	Quirici et al. (2011)
Bats				
Eptesicus fuscus (big brown bat)	48	9	Tissue	Metheny et al. (2008)

associations with their mother (Holmes & Sherman, 1983; Mateo, 2003). Cross-fostering experiments in house mice, *Mus musculus domesticus*, suggest that familiarity is an important mechanism for promoting cooperation among sisters (König, 1994). Mothers may also mediate familiarity among paternal half siblings by fostering close relationships with their offspring's father after the infant is born. Specifically, familiarity among paternal half siblings may be based on age proximity when a single dominant male monopolizes reproduction over discrete periods of time (Widdig, 2007).

Kin discrimination via phenotypic matching occurs when phenotypic similarity and genetic similarity are highly correlated. In such circumstances, an individual assesses its relationships to others on the basis of one or more shared traits. This phenomenon is often referred to as the 'arm-pit effect' (Mateo & Johnston, 2000) or 'referential phenotype matching' (Hauber & Sherman, 2001; Mateo, 2010) because some individuals make inferences about relatedness based on the smell (e.g. smelling their own 'arm-pits'). Odour-based discrimination is often associated with genetic variation in the major histocompatibility complex (MHC), a phenomenon that occurs in rodents (e.g. laboratory mice: Yamazaki, Beauchamp, Curran, Bard, & Boyse, 2000; Belding's ground squirrels: Mateo, 2003), carnivores (e.g. spotted hyaenas, *Crocuta crocuta*: Wahaj et al., 2004) and primates (e.g. ringtailed lemurs, *Lemur catta*: Charpentier, Boulet, & Drea, 2008; owl monkeys, *Aotus nancymaae*: MacDonald, Fernandez-duque, Evans, & Hagey, 2008; humans, *Homo sapiens*: Wedekind & Füri, 1997). Recognition may also be based on visual (e.g. chimpanzees, *Pan troglodytes*: Parr & de Waal, 1999), vocal (e.g. spotted hyaenas: Holekamp et al., 1999), or both modes of information (rhesus macaques, *Macaca mulatta*: Kazem & Widdig, 2013; Rendall, Rodman, & Emond, 1996).

Recent tests of kin discrimination revealed two new domains for assessing kin selection in social mammals. First, studies now consider the role of paternal kinship in addition to maternal kinship in mammalian social evolution. This is important because nepotism is expected to occur to similar extents for both maternal and paternal kin. Paternal kin discrimination has been shown for house mice (Kareem & Barnard, 1982), golden hamsters, *Mesocricetus auratus* (Todrank, Heth, & Johnston, 1998), Belding's ground squirrels (Holmes, 1986), mountain gorillas, *Gorilla gorilla beringei* (Watts, 1997), baboons, *Papio cynocephalus* (Alberts, 1999; Buchan, Alberts, Silk, & Altmann, 2003), rhesus macaques (Pfefferle, Ruiz-Lambides, & Widdig, 2014; Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2001), spotted hyaenas (Smith et al., 2010; Van Horn, Wahaj, & Holekamp, 2004; Wahaj et al., 2004) and grey mouse lemurs, *Microcebus murinus* (Kessler, Scheumann, Nash, & Zimmermann, 2012). Second, workers now recognize that individual animals possess knowledge of third-party kin relationships, defined as an understanding of the kin-biased social bonds that exist among other individuals within their groups. That is, individuals who have just been involved in an aggressive interaction are most likely to redirect aggression towards the close relatives of their former opponent or avoid groupmates that were heard fighting with the close relative of a higher-ranking female. Pigtailed macaques, *Macaca nemestrina* (Judge, 1991), spotted hyaenas (Engh, Siebert, Greenberg, & Holekamp, 2005; Holekamp et al., 1999), baboons, *Papio hamadryas ursinus* (Cheney & Seyfarth, 1999; Wittig, Crockford, Wikberg, Seyfarth, & Cheney, 2007) and vervet monkeys, *Chlorocebus aethiops* (Cheney, 2011) all recognize third-party kin relationships. These data importantly extend historical perspectives because they indicate that paternal and extradyadic kin relationships are important, yet largely overlooked, targets of selection.

COOPERATION AND COMPETITION AMONG RELATIVES

The inclusive fitness benefits of cooperative breeding are widely recognized for social insects (e.g. West-Eberhard, 1975; Queller & Strassmann, 1998; Strassmann, Page, Robinson, & Seeley, 2011), birds (e.g. Cockburn, 1998; Emlen, 1984; Griffin & West, 2003; Stacey & Koenig, 1990) and mammals (e.g. Clutton-Brock, 2002; Creel & Creel, 1991; Jennions & Macdonald, 1994; Smith, Swanson, Reed, & Holekamp, 2012; Solomon & French, 1997). Novel tests of Hamilton's rule based on long-term behavioural and molecular data continue to offer exciting new insights. For example, kin selection explains cooperative courtship in free-living turkeys, *Meleagris gallopavo* (Krakauer, 2005); male helpers forgo reproduction to support their brothers. Natural adoptions in red squirrels, *Tamiasciurus hudsonicus*, are also consistent with Hamilton's rule (Gorrell, McAdam, Coltman, Humphries, & Boutin, 2010); squirrels only adopt genetic relatives when the benefits to the adopted juvenile (*b*), discounted by the degree of relatedness between the surrogate and the orphan (*r*), exceed the direct fitness costs of a female adding an extra juvenile to her litter (*c*). Given that the evidence for cooperative breeding via kin selection is so compelling, and given the extensive coverage of this topic elsewhere, the remainder of this review focuses on evaluating the extent to which kin selection favours the evolution of short-lived social acts, such as the maintenance of spatial proximity, agonistic aiding via coalitionary interventions during ongoing fights and social tolerance (withholding aggression). This is important because these factors have been largely overlooked in previous reviews, and any previous treatment of this topic has largely been restricted to primates. Here I focus on the best-studied species of nonhuman mammals for which there are sufficient data on genetic relatedness and the short-lived social behaviours identified here. In doing so, I also evaluate the notion that, because of their social complexity, nepotistic patterns in nonhuman primates might be unique among mammals (reviewed in Kappeler, van Schaik, & van Schaik, 2005; Langergraber, 2012). Although grooming represents another short-lived social commodity in primates, grooming has been reviewed extensively elsewhere for primates (e.g. Schino & Aureli, 2010), and comparable grooming data are sparse for nonprimates.

Kin-biased Spatial Associations

Hamilton's rule predicts that individuals should generally direct helpful behaviour towards relatives. Overall, patterns of association, proximity maintenance and spatial associations within social networks generally indicate that individuals prefer kin over nonkin as social partners (Table 3). In contrast to commonly held perceptions, primates are no more or less likely than nonprimates to show a kinship bias with respect to spatial proximity (chi-square with Yates correction: $\chi^2_1 = 1.307$, $N = 44$ species, $P = 0.253$; Fig. 1). Across mammals tested, the proportion of species (84%) showing at least some degree of preference towards maintaining spatial associations with genetic kin over nonkin was greater than that expected by chance (binomial test: $N = 44$ species, $P < 0.0001$). As predicted by kin selection theory, mammals therefore typically bias affiliative behaviour towards genetic relatives, preferentially selecting for genetic kin as social partners with whom to associate.

Although evidence for kin-biased proximity is overwhelming, the advantages of sharing space with kin can vary based on the current ecological circumstances, such as population demography and resource competition. For example, ecological monitoring of four populations of red howler monkeys, *Alouatta seniculus*, for 5 years suggested that the costs and benefits of nepotism are density dependent (Pope, 1998). Genetic data indicate that the reproductive success of these monkeys, attributed primarily to the recruitment of daughters, increases with the degree of relatedness within groups at high population densities. When population density is approaching or at carrying capacity, monkeys are likely to belong to kin groups and, thus, nepotism is greater than when population densities are low. Long-term ecological monitoring of spotted hyaenas suggests that resource competition also shapes kin-biased patterns of space use in social carnivores. That is, although social bonds among both kin and nonkin are weakest when resource competition is most intense for all groupmates, hyaenas sustain the strongest associations with kin throughout the year despite variation in food abundance associated with annual prey migrations (Holekamp, Smith, Strelioff, Van Horn, & Watts, 2012). Additional inquiries are necessary to understand the extent to which variation in local demography and resource abundance might similarly explain patterns of kin-biased associations across dynamic social networks in other mammalian species. Such an approach would allow us to understand whether kinship structures respond flexibly to changes in local demographics within most mammalian species.

Agonistic Aiding and Coalition Formation

Agonistic aiding, also called intervention or coalition formation, represents a cooperative act; intervening in a fight is potentially costly to the donor, who risks physical injury, expends energy fighting and allocates time to this behaviour that might otherwise be devoted to other activities (reviewed by Smith et al., 2010). Agonistic aiding is beneficial to the recipient because it increases the recipient's likelihood of winning the fight.

Given this, Hamilton's rule makes straightforward predictions about coalition formation when the cost–benefit ratio is held constant (e.g. within a specific ecological circumstance). That is, individuals should intervene more often on behalf of kin than nonkin. As expected, all available evidence is consistent with the notion that kin generally bias coalitionary support towards their genetic relatives. Intragroup coalitions are generally favoured by the combined evolutionary forces of indirect and direct benefits in birds and mammals (Smith et al., 2010). For the 31 species of social

Table 3
Relationships between kinship and patterns of social behaviour in mammalian groups

	Spatial proximity			Social tolerance			Coalition formation		
	Kinship-based analysis	Evidence in predicted direction?	Source	Kinship-based analysis	Evidence in predicted direction?	Source	Kinship-based analysis	Evidence in predicted direction?	Source
Primates									
Pan troglodytes (chimpanzee)	M, P	M=Yes; P=No (males)	Morin et al. (1994)	M, P	M=Yes; P=No	Morin et al. (1994)	M	Yes	de Waal and van Hooff (1981); de Waal and Luttrell (1988)
	M, P	No (females)	Goldberg and Wrangham (1997); Langergraber, Mitani, and Vigilant (2009)	—	—		M	No	Mitani, Merriwether, and Zhang (2000); Mitani, Watts, Pepper, and Merriwether (2002); Watts (2002)
P. paniscus (bonobo)	M, P	Yes	Hohmann, Gerloff, Tautz, and Fruth (1999)	—	—		—	—	
Gorilla g. beringei (mountain gorilla)	—	—		—	—		M, P	Yes	Watts (1997)
Papio cynocephalus (yellow baboon)	M, P	Yes (prefer M over P kin)	Silk, Alberts, and Altmann (2006); Silk, Altmann, et al. (2006)	P	No	Alberts (1999); Silk et al. (2004)	M, P	Yes	Charpentier, Van Horn, Altmann, and Alberts (2008)
Theropithecus gelada (gelada baboon)	M	Yes	Dunbar (1979)	M	No	Dunbar (1984)	M	Yes	Dunbar (1980)
Mandrillus sphinx (mandrill)	M, P	Yes	Charpentier, Peignot, Hossaert-McKey, and Wickings (2007)	M	No	Bernstein (1975)	—	—	
Macaca arctoides (stumptailed macaque)	M, P	Yes	MacKenzie, McGrew, and Chamove (1985)				—	—	
M. fascicularis (longtailed macaque)	—	—		—	—		M	Yes	Hemelrijk (1994)
M. fuscata (Japanese macaque)	M, P	Yes	Chapais, Savard, and Gauthier (2001); Langos et al. (2013)	M, P	Yes	Belisle and Chapais (2001); Langos et al. (2013)	M	Yes	Chapais (1988); Chapais, Girard, and Primi (1991); Schino, di Sorrentino, and Tiddi (2007); Schino, Tiddi, and Polizzi di Sorrentino (2007); Ventura, Majolo, Koyama, Hardie, and Schino (2006)
M. mulatta (rhesus macaque)	M, P	Yes	de Waal and Luttrell (1986); Widdig et al. (2002)	M, P	No	Bernstein and Ehardt (1986); Widdig et al. (2002)	M, P	Yes	de Waal and Luttrell (1986, 1988); Kapsalis and Berman (1996); Kulik et al. (2012); Matheson and Bernstein (2000)
M. nemestrina (pigtailed macaque)	M	Yes	Fredrickson and Sackett (1984); Wu, Holmes, Medina, and Sackett (1980)	—	—		M	Yes	Massey (1977)
M. radiata (bonnet macaque)	M	Yes	Silk et al. (1981)	M	No	Silk et al. (1981)	M	Yes	Silk (1982, 1992, 1993)
M. sylvanus (barbary macaque)	M	Yes	Silk et al. (1981)	M	No	Silk et al. (1981)	M	Yes	Prudhomme and Chapais (1993); Widdig, Streich, and Tembrock (2000)
M. tonkeana (Tonkean macaque)	—	—		—	—		M	Yes	Petit and Thierry (1994)
Presbytis entellus (Hanuman langur)	—	—		—	—		M	Yes	Borries (1993)
Cercopithecus aethiops (vervet monkey)	M	Yes	Fairbanks (1980)	—	—		M, P	Yes	Hunte and Horrocks (1987)

(*continued on next page*)

Table 3 (*continued*)

	Spatial proximity			Social tolerance			Coalition formation		
	Kinship-based analysis	Evidence in predicted direction?	Source	Kinship-based analysis	Evidence in predicted direction?	Source	Kinship-based analysis	Evidence in predicted direction?	Source
C. solatus (suntailed monkey)	M, P	M=Yes; P=No (males)	Charpentier Deubel, and Peignot (2008)	M, P	M=Yes; P=No (males)	Charpentier, Deubel, et al. (2008)	—	—	
Cercocebus torquatus atys (sooty mangabey)	—	—		—	—		M	Yes	Range (2006); Range and Noë (2002)
Lemur catta (ringtailed lemur)	M	Yes	Kappeler (1993)	M	No	Kappeler (1993)	M	Yes	Pereira and Kappeler (1997)
Eulemur fulvus rufus (red-fronted lemur)	M	No	Kappeler (1993)	M	No	Kappeler (1993)	M	Yes	Pereira and Kappeler (1997)
Saimiri oerstedii (squirrel monkeys)	—	—		—	—		M	Yes	Baldwin and Baldwin (1972)
S. boliviensis (squirrel monkey)	—	—		—	—		M	Yes	Boinski, Kauffman, Ehmke, Schet, and Vreedzaam (2005)
Cebus apella (brown/tufted capuchin)	—	—		—	—		M	Yes	Schino, di Giuseppe, and Visalberghi (2009)
C. capucinus (white-faced capuchin)	M, P	M=Yes; P=No (males)	Perry (1996); Perry et al. (2008)	M, P	No	Perry et al. (2008)	M	Yes	Perry et al. (2008)
Alouatta palliate (mantled howler monkey)	—	—		—	—		M	Yes	Jones (1980)
A. seniculus (red howler monkey)	M, P	Density dependent	Pope (1998)	M, P	No	Pope (2000)	M	Yes	Crockett and Pope (1993)
Callithrix jacchus (common marmoset)	M, P	Yes	Nievergelt et al. (2000)	M	No	McGrew and McLuckie (1986)			
Ungulates									
Loxodonta africana (African elephant)	M, P	Yes	Archie, Morrison, et al. (2006)	M	No	Archie, Moss, and Alberts (2006)	M	Yes	Lee (1987)
Equus quagga (plains zebra)	—	—		—	—		M	Yes	Schilder (1990)
E. caballus (wild horse)	—	—		—	—		M, P	No	Feh (1999)
Giraffa camelopardalis (giraffe)	M, P	Yes	Carter, Seddon, Frère, Carter, and Goldizen (2013)						
Ovis canadensis (bighorn sheep)	M	No	Festa-Bianchet (1991)	M	No	Festa-Bianchet (1991)	M, P	Yes	Pelchat (2008)
O. aries (Dorset sheep)	M, P	No	Nituch, Schaefer, and Maxwell (2008)	—	—		—	—	
Cetaceans									
Physeter macrocephalus (sperm whale)	M, P	Yes	Gero, Engelhaupt, and Whitehead (2008); Ortega-Ortiz et al. (2012)	—	—		—	—	
Tursiops aduncus (bottlenose dolphin)	M, P	Yes	Frère, Krützen, Mann, Watson-Capps, et al. (2010); Möller, Beheregaray, Allen, and Harcourt (2006)	M	No	Scott, Mann, Watson-Capps, Sargeant, and Connor (2005)	M, P	Yes	Connor, Smolker, and Richards (1992)

(*continued on next page*)

Table 3 (*continued*)

	Spatial proximity			Social tolerance			Coalition formation		
	Kinship-based analysis	Evidence in predicted direction?	Source	Kinship-based analysis	Evidence in predicted direction?	Source	Kinship-based analysis	Evidence in predicted direction?	Source
Carnivores									
Zalophus wollebaeki (Galápagos sea lion)	M, P	Yes	Hanggi and Schusterman (1990); Wolf and Trillmich (2008)	M, P	Yes	Hanggi and Schusterman (1990)	—	—	
Crocuta crocuta (spotted hyaena)	M, P	Yes	Holekamp et al. (2012); Wahaj et al. (2004)	M, P	No	Smith et al. (2010); Wahaj et al. (2004)	M, P	Yes	Engh et al. (2000); Smith et al. (2010); Wahaj et al. (2004)
Hyaena brunnea (brown hyaenas)	M	Yes	Owens and Owens (1984)						
Panthera leo (African lion)	M, P	Yes	Matoba, Kutsukake, and Hasegawa (2013)	M, P	No	Packer and Pusey (1982)	M	Yes	Schaller (1972)
Ursus americanus (black bear)	M	Yes	Rogers (1987)	M	Yes	Rogers (1987)	—	—	
Nasua nasua (ringtailed coati)	M, P	Yes	Hirsch et al. (2012)	M, P	No	Hirsch et al. (2012)	—	—	
N. narica (white-nosed coati)	M, P	Yes	Gompper, Gittleman, and Wayne (1997)	M, P	Yes	Gompper et al. (1997)	M, P	Yes	Gompper et al. (1997)
Procyon lotor (raccoon)	M, P	Yes	Hirsch et al. (2012); Robert et al. (2013)	M, P	No	Hauver, Hirsch, Prange, Dubach, and Gehrt (2013)	M, P	No	Hauver et al. (2013)
Lontra canadensis (river otter)	M, P	No	Blundell et al. (2004)	M, P	No	Hansen, McDonald, Groves, Maier, and Ben-David (2009)	—	—	
Meles meles (European badger)				M, P	No	Hewitt et al. (2009)	—	—	
Suricata suricatta (meerkat)	M, P	No	Madden et al. (2012)	M, P	No	Madden et al. (2012)	—	—	
Marsupials									
Lasiorhinus krefftii (hairy-nosed wombat)	M, P	Yes	Taylor et al. (1997)	—	—		—	—	
Macropus giganteus (eastern grey kangaroo)	M, P	Yes	Best, Dwyer, Seddon, and Goldizen (2014)	—	—		—	—	
Trichosurus cunninghami (brushtail possum)	M, P	Yes	Banks et al. (2011)	M, P	Yes	Banks et al. (2011)	—	—	
Rodents									
Marmota flaviventris (yellow-bellied marmot)	M, P	Yes	Smith et al. (2013); Wey and Blumstein (2010)	M, P	No	Smith et al. (2013); Wey and Blumstein (2012)	—	—	
M. monax (woodchuck)	M, P	Yes	Maher (2009)	—	—		—	—	
Neotoma macrotis (woodrats)	M, P	Yes	Matocq and Lacey (2004)	—	—		—	—	
Mus domesticus (house mouse)	M, P	Yes	König (1994)	M, P	Yes	Hurst and Barnard (1995); Kareem and Barnard (1982)	—	—	
Octodon degus (degu)	M, P	No	Quirici et al. (2011)	—	—		—	—	
Rhombomys opimus (great gerbil)	M, P	Yes	Randall, Rogovin, Parker, and Eimes (2005)	—	—		—	—	
Urocitellus beldingi (Belding's ground squirrel)	M, P	Yes	Holmes (1986); Mateo (2003)	M, P	No	Holmes (1986)	—	—	Mateo (2003)
Bats									
Eptesicus fuscus (big brown bat)	M, P	No	Metheny et al. (2008)	—	—		—	—	

Analysis was based on maternal (M) and/or paternal (P) kinship. Evidence for kin-biased behaviour was (Yes) or was not (No) in the predicted direction. In cases where results differed between the sexes, results for males and females are reported separately.

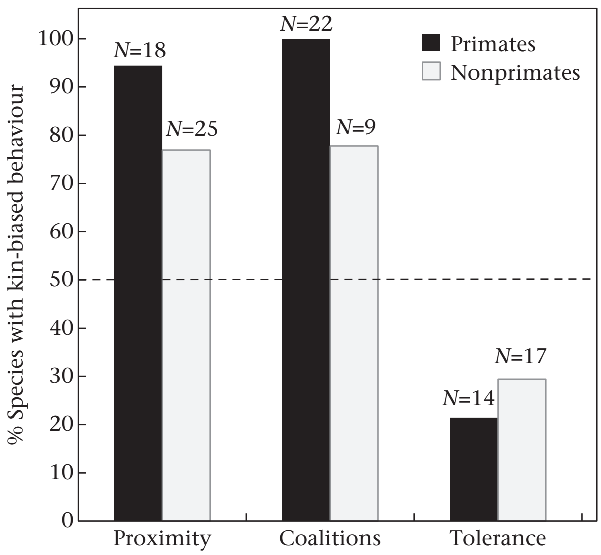

Figure 1. Percentage of mammalian species for which members of at least one sex engage in kin-biased behaviour with respect to social partner choice (spatial proximity), coalition formation or social tolerance (withholding aggression). Dashed line represents expected null hypothesis that mammalian species were equally likely to bias (or not to bias) affiliative behaviours towards their closest genetic relatives. No significant differences were detected between primates and nonprimates ($P \geq 0.139$ for all three behavioural categories).

mammals known to form intragroup coalitions, patterns of kin-biased coalition formation were similar for primates and nonprimates ($\chi^2_1 = 2.193$, $N = 31$ species, $P = 0.139$; Fig. 1, Table 3). The vast majority (94%) of species biased coalitionary support towards their closest relatives, a bias that was statistically different from random (binomial test: $N = 31$ species, $P < 0.0001$).

To my knowledge, the relationships between paternity and coalition formation are currently available for only 10 species of mammals. Paternal kinship explains patterns of coalition formation in some, but not all of these species (Table 3). For example, adult female spotted hyaenas tend to support mothers, daughters and full siblings ($r = 0.5$) more often per opportunity than they support maternal or paternal half sisters ($r = 0.25$) in fights. Interestingly, however, maternal and paternal half sisters were supported to similar extents, and both categories of kin were supported more often than were nonkin ($r \sim 0.00$; Smith et al., 2010). Female baboons also bias their support towards full sibs over half sibs (Smith, Alberts, & Altmann, 2003). However, female baboons bias more support towards maternal than towards paternal kin (Silk, Altmann, & Alberts, 2006), a finding that is inconsistent with the predictions of kin selection theory based solely on measures of relatedness. Instead, it suggests that individuals might gain direct fitness benefits from enduring associations with maternal kin in addition to the indirect benefits they gain from helping either maternal or paternal kin. In chimpanzees, philopatric males also prefer to affiliate and cooperate with maternal over paternal brothers (Langergraber, Mitani, & Vigilant, 2007). Because the results of existing studies failing to detect differences between preferences for maternal and paternal kinship might be attributed to limited sample sizes, additional studies with adequately large sample sizes are therefore required to fully evaluate the role of paternal kinship in structuring cooperative decisions in free-living mammals.

The costs of aiding kin in fights often vary with the immediate opportunity costs. For instance, adult female hyaenas make flexible decisions about whether or not to cooperate based on multiple forms of information in addition to their genetic relationship to potential beneficiaries (Smith et al., 2010). As predicted by kin selection theory, hyaenas support close maternal and paternal kin most often, and the density of cooperation networks increases with genetic relatedness. They also base decisions on the immediate costs and benefits of helping. The social lives of spotted hyaenas are characterized by fission–fusion dynamics such that social decisions change dynamically over time because subgroup composition and ecological context change on an hour-to-hour basis (Smith, Kolowski, Graham, Dawes, & Holekamp, 2008). At reunions, hyaenas preferentially greet kin over nonkin and these greetings often promote coalitions to form (Smith et al., 2011). However, the extent to which kin support each other in fights is context dependent. First, hyaenas are least likely to provide support when foraging at kills (Smith et al., 2010). This is because feeding competition is intense in this species and the direct costs of missed feeding opportunities reduce the inclusive fitness benefits of supporting kin in intense feeding contexts. Importantly, the same adult female aided by others during fights is no more effective in displacing competitors from kills than she is when she is not aided by conspecifics during dyadic aggression. This suggests that the added benefit to agonistic support kin is negligible even though the cost to the donor is highest at kills. Second, because the cost of donating support increases as the number of dominant bystanders increases, the immediate composition of groupmates in the ‘audience’ influences the extent to which females provide support to nonkin and distant kin ($r = 0$ to 0.125). Interestingly, however, females still help close kin ($r = 0.5$) regardless of this context-dependent cost. Hyaenas therefore monitor the composition of their current subgroup, assess their relatedness to potential beneficiaries, track the immediate costs of helping a potential beneficiary (number of dominant bystanders in the audience and whether food is immediately present) and modify their level of cooperation based on this knowledge. These data add to our growing appreciation of the central role that social and ecological contexts play in explaining the immediate costs and benefits of mammalian cooperation.

Social Tolerance and Withholding Aggression

Kin selection theory predicts that individuals should direct fewer attacks or lower intensities of aggression (enhanced social tolerance) towards closer kin than towards less related individuals. However, evidence for the protective value of kinship in curtailing rates of aggression, or promoting social tolerance, in free-living mammals is limited (Fig. 1, Table 3). Overall, rates of aggression were reduced among kin for only 8 out of the 31 (26%) species reviewed such that species were significantly *less* likely to be socially tolerant of genetic relatives than expected by chance (binomial test: $N = 31$ species, $P < 0.0001$). That is, most species either directed higher rates of aggression towards kin or failed to preferentially tolerate groupmates on the basis of kinship. Moreover, this lack of nepotistic tolerance was statistically indistinguishable between primates and nonprimates ($\chi^2_1 = 0.009$, $N = 31$ species, $P = 0.926$; Fig. 1, Table 3).

In many species, the overall rates at which adult individuals direct aggression towards kin and nonkin are simply indistinguishable. This is the case for meerkats, *Suricata suricatta* (Madden, Nielsen, & Clutton-Brock, 2012), European badgers, *Meles meles* (Hewitt, Macdonald, & Dugdale, 2009), ringtailed coatis, *Nasua nasua* (Hirsch, Stanton, & Maldonado, 2012), spotted hyaenas (Smith et al., 2010; Wahaj et al., 2004), bonnet macaques, *Macaca radiata* (Silk, Samuels, & Rodman, 1981) and rhesus macaques (Widdig, Nürnberg, Krawczak, Streich, & Bercovitch, 2002). Kinship also fails to curtail aggression in Belding’s ground squirrels (Holmes, 1986; Mateo, 2003) despite strong evidence indicating that kin selection favours alarm calling in this species (Sherman, 1977).

Whereas there are limited data suggesting that kinship reduces rates of aggression, the immediate context and the intensity of aggression influence nepotistic tolerance in some mammalian species. For instance, mothers are often more tolerant of their offspring than of nonrelatives during feeding contexts, such as in the case of Japanese macaques, *Macaca fuscata* (Belisle & Chapais, 2001) and spotted hyaenas (Engh, Esch, Smale, & Holekamp, 2000). Brushtail possums, *Trichosurus cunninghami*, also vary the degree to which they tolerate kin in response to the changing benefits of doing so (Banks et al., 2011). Specifically, possums are most likely to share limited den space with kin when the cost of sharing is low (i.e. when dens are locally abundant). Thus, as predicted by Hamilton's rule, possums dynamically vary the degree to which they associate with kin in response to changes in the costs of tolerating kin. Moreover, intensity, rather than rates, of aggression decreases with genetic relatedness in some species. For example, bonnet macaques (Silk et al., 1981), spotted hyaenas (Van Horn, Wahaj, et al., 2004) and ringtailed lemurs (Sbeglia, Tang-Martinez, & Sussman, 2010) reserve the most severe forms of aggression for unrelated groupmates, but the effects of kinship on the intensity of threats must be addressed more rigorously in the literature.

Kinship also generally fails to protect individuals from becoming victims of coalitionary attacks in mammals with strict linear dominance hierarchies for which social ranks are often established and reinforced within maternal lineages (e.g. baboons: Alberts, 1999; rhesus macaques: Widdig et al., 2001; spotted hyaenas: Smith et al., 2010; Wahaj et al., 2004). This might be surprising at first given that kin selection generally predicts that individuals should direct lower rates of coalitionary aggression towards kin than towards nonkin. In fights for which the potential donor is more related to one potential target than to the other potential target, then individuals often do join to support the more closely related of the aggressors and attack the more distantly related of the two contestants. For most species, however, individuals also simultaneously gain indirect benefits from assisting kin and direct benefits from forming 'conservative coalitions', during which allies join forces to direct attacks towards subordinates, many of whom are lower-ranking kin (Smith et al., 2010). Specifically, donors of support immediately benefit from reinforcing the status quo in low-cost contests during which they direct attacks down the dominance hierarchy. Such findings generally suggest that direct benefits gained through aggression often overwhelm the indirect benefits of withholding aggression directed towards kin. For example, insofar as coalitions help to maintain the status quo, it is just as important to a female's reproductive success that she maintains her dominance over a lower-ranking sister or daughter as she does over unrelated adult females.

Competition among relatives often emerges because kin are in close spatial proximity and depend upon the same limited resources (reviewed by Stockley & Bro-Jorgensen, 2011). Alexander (1974) and West-Eberhard (1975) pointed out this problem many years ago, suggesting that an individual's closest relatives, and by extension his/her closest associates and/or social allies, are often also his/her closest competitors. The results here support these notions that when this is true, as it is among most mammals, competition among kin can reduce, or even negate, the kin-selected indirect benefits of altruism directed towards relatives. Interestingly, in such contexts, the direct benefits gained from outcompeting relatives through forces such as sibling rivalry and parent conflict generally appear to overwhelm the indirect benefits of social tolerance among kin (Cant, 2006; Johnstone, 2000; Mock & Forbes, 1992; Trivers, 1974). In some species, rates of conflict actually increase with levels of genetic relatedness. This is the case for rhesus macaques (Bernstein & Ehardt, 1986), ringtailed lemurs (Kappeler, 1993), African elephants, *Loxodonta africana* (Archie, Morrison, Foley, Moss, & Alberts, 2006), and yellow-bellied marmots, *Marmota flaviventris* (Smith, Chung, & Blumstein, 2013). For example, as predicted by kin selection, rates of affiliation are positively correlated with genetic relatedness in yellow-bellied marmots as pups, yearlings and adults, but rates of conflict are also highest among the closest relatives at all three stages (Smith et al., 2013). Interestingly, outcomes of early affiliative exchanges, most of which are with genetic kin, predict later wins and losses in agonistic interactions that contribute to dominance status (Blumstein, Chung, & Smith, 2013). Thus, exchanges among relatives confer indirect and direct fitness consequences starting early in life.

DIRECT BENEFITS OF COOPERATING WITH KIN

Overall, this review suggests that the effects of kinship are prolific in shaping social acts among mammals, but that the direct and indirect fitness benefits of helping others must be considered together. Indeed, long-term studies on free-living mammals suggest that exchanges of helpful behaviours, most of which occur among kin, have cumulative direct fitness consequences for individuals (reviewed by Silk & House, 2011). The accumulation of social acts, such as grooming and long-term associations, enhances both the longevity and offspring survival for the vast range of mammals. Fitness consequences of sociality have now been documented in mammalian species including humans (House, Landis, & Umberson, 1988), baboons (Silk, Alberts, & Altmann, 2003; Silk et al., 2010), house mice (Weidt, Hofmann, & Konig, 2008), laboratory rats, *Rattus norvegicus* (Yee, Cavigelli, Delgado, & McClintock, 2008), horses, *Equus caballus* (Cameron, Setsaas, & Linklater, 2009), dolphins, *Tursiops aduncus* (Frère, Krützen, Mann, Connor, et al., 2010), rock hyraxes, *Procavia capensis* (Barocas, Ilany, Koren, Kam, & Geffen, 2011) and yellow-bellied marmots (Armitage & Schwartz, 2000; Wey & Blumstein, 2012).

Nonkin of the same species also cooperate when doing so yields direct immediate or delayed benefits. For example, spotted hyaenas withhold aggression from unrelated adult females with whom they exchange other commodities important for survival (Smith, Memenis, & Holekamp, 2007). Vervet monkeys (Seyfarth & Cheney, 1983) and baboons (Cheney, Moscovice, Heesen, Mundry, & Seyfarth, 2010) also solicit cooperation from recent, unrelated grooming partners, presumably because of the direct benefits that donors receive from helping nonkin. Langergraber et al. (2007) used molecular genetics to tease apart the relative effects of direct and indirect benefits in philopatric male chimpanzees at Ngogo in Kibale National Park, Uganda. Interestingly, the majority of highly affiliative and cooperative dyads (e.g. pairs that formed coalitions at the highest hourly rates) were unrelated or distantly related. Perhaps paternal brothers are unable to recognize each other reliably, but this seems unlikely given that there is some evidence for paternal kin discrimination based on phenotypic cues, such as odour and age proximity.

A recent meta-analysis by Schino and Aureli (2010) provided similar insights about allogrooming in nonhuman primates. By comparing the relative effects of kinship and reciprocity, they found that when both factors were evaluated simultaneously, the effects of reciprocity exceeded those of kinship in explaining grooming patterns. Similarly, meerkats gain direct benefits from sentinel behaviour (Clutton-Brock et al., 1999). That is, rather than guarding only being favoured by indirect benefits gained from helping kin, meerkats gain direct benefits from guarding; sentinels guard to reduce their own predation risk if no other animal is on guard and if they have recently eaten. However, quantifying the direct and indirect benefits associated with patterns of spatial proximity, coalition formation and social tolerance in isolation on lifetime fitness in these and other species of mammals remains largely elusive. As more data become available for the less-studied social acts focused on here, meta-analyses should be conducted to tease apart the relative roles of direct and indirect benefits in shaping proximity, coalitions and social tolerance more generally across the mammalian lineage.

EVOLUTIONARY PUZZLE OF COOPERATION AND THE WAY FORWARD

Although great strides have been made in the quest towards solving the evolutionary puzzle of cooperation over the past half of a century, this review emphasizes the continued need for integrative theoretical frameworks that consider the powerful forces of direct and indirect fitness benefits operating in concert to shape social evolution. Although data on paternity still remain somewhat limited for mammals, the application of microsatellites to a growing list of species is allowing for pedigree construction in groups of free-living mammals. This is important because it allows research to move beyond traditional tests based solely on maternal lineages inferred from demographic measures (e.g. births, deaths). As predicted by kin selection theory, social alliances among maternal and paternal kin are common in mammalian societies, but the protective value of kinship with respect to curtailing aggression is surprisingly limited. Moreover, despite previous assumptions about the potential differences that might exist between primates and nonprimates, the synthesis reported here reveals that the forces of kin selection favour remarkably similar patterns of nepotism in primates and nonprimate mammals.

Although Hamilton made specific predictions about the degree to which kinship promotes context-dependent cooperation in dynamic landscapes, researchers still struggle to assess the precise context-dependent costs and benefits of behaviour on lifetime fitness for even the best-studied free-living mammals. In contrast to the currencies (e.g. number of progeny produced by donors and beneficiaries) used by evolutionary biologists to quantify the costs and benefits of cooperative breeding, tracking the precise costs and benefits of short-lived social acts has been historically challenging. For example, helping out your sister when she is involved in an ongoing fight surely entails opportunity costs and puts donors at risk by exposing them to injuries. However, the precise influences on lifetime fitness likely vary across ecological contexts for the studies testing this notion. Moreover, what if under some circumstances you and your sister are directly competing for access to some limited resource? Recent efforts have started to reveal the specific fitness benefits of short-lived social acts, such as those favouring kin-biased coalition formation (e.g. Gilby et al., 2013; Kulik, Muniz, Mundry, & Widdig, 2012), on correlates of lifetime fitness. Hard-earned data of this sort will therefore prove transformative in testing the genetic basis of social evolution. Furthermore, recent application of statistical tools, such as those from social network theory (e.g. Pinter-Wollman et al., 2013; Wey, Blumstein, Shen, & Jordan, 2008) and quantitative genetics (e.g. Kruuk, 2004), to long-term data from natural populations should allow for the partitioning of direct and indirect effects of short-lived social acts on lifetime fitness.

Many mammals make complex decisions based on multiple forms of information, yet examples of context-dependent cooperation in natural contexts continue to be strikingly absent from the literature. This is worrisome given that relatedness is only one variable in Hamilton's inequality, and because animals inheritably live in dynamic social and ecological landscapes. More data on context-dependent cooperation are therefore needed to fill this gap in our knowledge about the extent to which variation in the payoff distributions of helping behaviour explains nepotism. As such data become available, comparative methods that account for shared phylogenetic histories will prove invaluable in elucidating the degree to which Hamilton's framework generalizes across the mammalian lineage.

Taken together this review highlights the value of Hamilton's holistic approach in simultaneously considering the role of direct and indirect fitness benefits in shaping the evolution of cooperation and competition via inclusive fitness in mammalian social groups. This paper underscores the emerging view that studying cooperation and competition using genetic tools in the natural contexts in which sociality evolved will be a fruitful way forward. Future tests that tease apart the relative contributions of direct and indirect benefits on the lifetime fitness of mammals within socially and ecologically dynamic landscapes are therefore necessary. By investigating the relative influences of evolutionary and ecological forces favouring social evolution across the mammalian lineage, these new avenues for research will surely propel the exciting study of social evolution forward for the next 50 years and beyond.

Acknowledgments

I am grateful to Drs Joan Strassmann and David Queller for their invitation to participate in the exciting symposium that led to this paper as well as to the other participants for their useful conversations. I also thank Valeska Denitze Muñoz for her assistance with the literature review on the use of microsatellites in mammals. V. D. Muñoz and J. E. Smith were funded by the Barrett Foundation and Mills College.

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