SPECIAL ISSUE: KIN SELECTION

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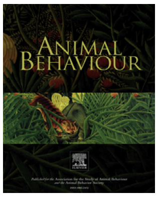

Special Issue: Kin Selection

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

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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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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 grandoffspring: $r = 0.25$) 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.

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.

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.

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

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