

Commentary

The evolution of cooperative breeding; is there cheating?

Joel L. Sachs^{a,*}, Dustin R. Rubenstein^{a,b}

^a Department of Integrative Biology, University of California, Berkeley, USA

^b Museum of Vertebrate Zoology, 3060 Valley Life Sciences Building, Berkeley, CA 94720-3140, USA

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Over the past four decades biologists have developed a body of theory to explain the evolution of cooperative behavior. Three key conditions have been modeled in which the fitness of individuals can be enhanced by their cooperative acts. Cooperation can evolve and be stable when (i) cooperative individuals *share genes* with the recipients (Hamilton, 1964a,b), (ii) when cooperation is a *byproduct* of selfish action (West-Eberhard, 1975; Brown, 1983; Connor, 1986), and (iii) when there is *directed reciprocity* for cooperative acts (Trivers, 1971; Axelrod and Hamilton, 1981; Sachs et al., 2004). Cooperative breeding is a common example of cooperation observed in numerous species of vertebrates and invertebrates; it occurs when some members of a social group delay independent breeding and help others raise young (Brown, 1987). In their struggle to understand why individuals should invest in the offspring of others, biologists have developed an exclusive, and sometimes idiosyncratic, set of models to explain the evolutionary maintenance of cooperative breeding (e.g. Gaston, 1978; Woolfenden and Fitzpatrick, 1978; Wiley and Rabenold, 1984; Jamieson, 1989; Emlen et al., 1991; Connor and Curry, 1995; Zahavi, 1995; Cockburn, 1998; Clutton-Brock, 2002; Kokko et al., 2001, 2002). Despite the wealth of theory to explain the evolution of cooperative breeding, it is not immediately evident how these hypotheses relate to one another or to general theories of cooperation (Axelrod and Hamilton, 1981; Queller, 1985; Bull and Rice, 1991; Connor, 1995; Sachs et al., 2004; Foster and Wenseleers, 2006; Lehmann and Keller, 2006).

Bergmüller et al. (2007) attempted to bridge the theoretical divide between the evolution of cooperation and cooperative breeding. They developed a seven part classification system for cooperation theory and used it to connect hypotheses for the maintenance of cooperative breeding in vertebrates. Here, we review a simpler, tripartite framework for the evolution of

cooperation (Sachs et al., 2004), and show how their structure fits into it (Table 1). Subsequently, we discuss a series of hypotheses to explain the maintenance of cooperative breeding in vertebrates, and describe how these models fit into our framework. A fundamental aspect of the framework we employ is that it predicts cooperative systems to vary in their vulnerability to exploitation (Sachs et al., 2004). We use these predictions to investigate a surprisingly unexplored aspect of cooperative breeding, the potential for cheating. Cheaters are defined as individuals that have evolved to take benefit from others without compensation (Sachs and Simms, 2006). We review previous predictions of cheating (e.g. Connor and Curry, 1995), and speculate on hypothetical types of cheats in cooperative breeding systems.

1. A general framework for cooperation

Cooperation can be defined as any trait that increases the fitness of other individuals (Sachs et al., 2004). Evolutionary theory predicts that cooperative traits can only be maintained under restricted conditions because purely selfish alternatives most often provide superior fitness (Hamilton, 1964a,b; Axelrod and Hamilton, 1981). Sachs et al. (2004) developed a comprehensive framework for the maintenance of cooperation that describes three simple models: shared genes, byproducts, and directed reciprocity. Although these models are not mutually exclusive, they describe different scenarios in which cooperative traits can benefit the bearer. Moreover, each model predicts a different (i) degree of vulnerability to cheating and (ii) type of cheating that is likely to occur. The seven ‘mechanisms’ that Bergmüller et al. describe for the evolution of cooperation (Bergmüller et al., 2007, Box 1) can be easily subsumed within our approach (see Table 1). In contrast to Bergmüller et al. (2007), we include kin selection models in our framework (shared genes) because most cooperatively breeding groups consist primarily of relatives (Brown, 1987; Emlen, 1997; Dickinson

* Corresponding author. Tel.: +1 510 642 0591; fax: +1 510 643 6264.
E-mail address: jlsachs@berkeley.edu (J.L. Sachs).

Table 1
Evolutionary models of cooperation and cooperative breeding

Models of cooperation ¹		Models of cooperative breeding	Type of cheating predicted
General models	Specific models ²		
Shared genes – Cooperation increases the inclusive fitness of cooperative individuals	Kin fidelity – Context-dependent or spatially associated cooperation with kin	Kin association based upon social context (i.e. same nest/burrow) • <i>Limited dispersal favors kin cooperation</i> (Hamilton, 1964a; West et al., 2002)	‘Kin deceit’ – Cheaters inhabit the context where kin normally are found
	Kin Choice – Cooperation with kin based upon phenotypic choice	Kin association based upon choice mechanisms • <i>Assorted encounters with kin via choice</i> (Eshel and Cavalli-Sforza, 1982)	‘Kin mimicry’ – Cheaters mimic kin phenotypically or behaviorally
Byproducts – Cooperation automatically benefits cooperative individuals	Simple Byproducts – Cooperation as a pure byproduct of selfish action – (<i>byproduct mutualism</i>)	Not predicted – <i>Helping involves investment in others and cannot be a simple byproduct</i>	No cheating predicted
	Pseudo-reciprocity – Cooperative investment in others that provides automatic (byproduct) benefit – (<i>Pseudo-reciprocity</i>)	Helpers invest in those that offer automatic benefits (i.e. byproduct) • <i>Passive group augmentation</i> (Kokko et al., 2001) • <i>Enhanced breeding experience</i> (Skutch, 1961)	
Directed reciprocity – Cooperative investments in others are compensated by reciprocated benefits	Partner fidelity – Cooperative investment reciprocated by others with coupled fitness interests – (<i>positive reciprocity-without choice</i>)	Helpers invest in those that reciprocate based upon linked fitness interests • <i>Territory inheritance</i> (Woolfenden and Fitzpatrick, 1978) • <i>Active group augmentation</i> (Kokko et al., 2001).	‘Vagrants’ – Cheaters move from group to group, reaping benefits from them without reciprocation
	Partner choice – Cooperative benefits reciprocated by specifically chosen partners – (<i>Negative pseudo-reciprocity, positive, negative, and indirect reciprocity</i>)	Helpers invest in those that reciprocate based upon choice mechanisms • <i>Pay-to-stay</i> (Gaston, 1978) • <i>Prestige</i> (Zahavi, 1995)	‘Freeloaders’ – Cheaters subvert choice mechanisms and receive benefits without reciprocation

The simplified framework for the evolution of cooperation is on the left. Hypotheses for the maintenance of cooperation breeding, on the right, can be subsumed into the framework. Different types of cheating for each type of model are also predicted.

Models of cooperation are adapted from Sachs et al. (2004). Bergmüller et al. (2007, Box 1) mechanisms of cooperation are listed under ‘specific models’ in *italics*.

and Hatchwell, 2004), and a complete analysis of the evolution of cooperation and cheating in cooperatively breeding species cannot be conducted without considering inclusive fitness benefits.

1.1. Shared genes

Kin selection models predict that cooperation can be maintained among relatives according to (i) their level of relatedness and (ii) the costs and benefits of cooperation (Hamilton, 1964a,b). These models do not require that individuals benefit directly from their cooperation, since the improved fitness of kin leads to indirect or inclusive fitness benefits (Hamilton, 1964a,b). Kin systems exhibit two mechanisms by which individuals can preferentially direct benefits to relatives: *kin choice* and *kin fidelity* (Sachs et al., 2004; Table 1). With kin choice, relatives are actively chosen based on some form of phenotypic recognition. In contrast, recognition does not exist with kin fidelity because relatives are reliably found nearby or in

a particular context, such as on a shared territory or at a nest (Hamilton, 1964a). Thus, kin choice and kin fidelity systems differ primarily in the role that choice plays in cooperative decisions, which ultimately leads to different predictions of cheating.

1.2. Byproducts

Cooperation can be maintained simply because cooperative traits are automatic byproducts of selfish action (West-Eberhard, 1975; Brown, 1983; Connor, 1986). Byproducts differ from other forms of cooperation because benefits are automatic, and thus cheating is not predicted. There are two forms of byproducts cooperation: *simple byproducts* and *pseudo-reciprocity* (Table 1). Simple byproducts involve no costly acts. A common illustration is the case of vultures benefiting from abandoned lion kills; the benefit to vultures is automatic and involves no investment by either party. In contrast, pseudo-reciprocity is a more complex form of byproducts that occurs when individu-

als invest in others that automatically return benefits (Connor, 1986). In this case, the investment is one-sided (which differs from the two-way investment described for directed-reciprocity below). Pseudo-reciprocity often occurs when individuals automatically enhance their fitness by increasing their group size, as in the case when larger groups are better protected from predation or forage more efficiently than smaller groups (Connor, 1986; Kokko et al., 2001).

1.3. Directed reciprocity

Cooperation can be maintained if the cooperative individuals are compensated by returned benefits from others (Trivers, 1971; Axelrod and Hamilton, 1981). Models of directed reciprocity differ from pseudo-reciprocity (as described above) in that (i) both the cooperative act and the reciprocation are potentially costly, and (ii) neither occurs automatically (Trivers, 1971; Axelrod and Hamilton, 1981). Directed reciprocity is vulnerable to cheaters that evolve to receive benefits, but not return them. Two divergent models predict how reciprocated benefits can be selected: *partner choice* and *partner fidelity* (Bull and Rice, 1991) (Table 1). In partner choice, cooperative individuals preferentially receive benefits from others who choose them based on their cooperative traits, whereas in partner fidelity, cooperative investment is reciprocated by others with coupled fitness interests (Bull and Rice, 1991; Sachs et al., 2004). No choice mechanisms are necessary with partner fidelity because a positive fitness feedback, which relies on repeated or long-term interaction, selects for cooperation. Directed reciprocity differs from reciprocal altruism models (Trivers, 1971; Axelrod and Hamilton, 1981) in that (i) the directed reciprocity is not restricted to pairs of interacting individuals and (ii) partner choice and partner fidelity have been dissected into independent mechanisms (Bull and Rice, 1991). Foster and Wenseleers (2006) have explicitly modeled these mechanisms.

1.4. The role of choice in cooperation

Choice can play a critical selective role in cooperative systems, whether they are based on kinship or reciprocation. By offering benefits to individuals according to the level of cooperation they exhibit, whether by rewards or punishment, the choosing individuals select for cooperative traits in others and can curtail cheaters (Sachs et al., 2004; Foster and Wenseleers, 2006). Yet, choice does not evolve in all systems, perhaps because (i) the mechanisms are costly, (ii) there are constraints, (iii) there is no variation from which to choose (Foster and Kokko, 2006), or (iv) fidelity is in place. Choice and fidelity systems differ in their vulnerability to cheating, an aspect which we explore below. Choice systems can be vulnerable to cheaters that exploit and potentially mimic the signals of cooperation, whereas fidelity systems are vulnerable to cheaters that escape the effects of fitness feedbacks, perhaps by transmitting among partners (Bull and Rice, 1991; Sachs and Wilcox, 2006). However, some authors have argued that pure fidelity systems are inherently unstable and unlikely to persist

(Lehmann and Keller, 2006), except in intimate inter-specific interactions such as symbioses (Sachs, 2006). Because individuals of most vertebrate cooperatively breeding species are able to disperse or to remain on the natal territory as a helper, we argue that choice systems, either based on kinship or reciprocation, are most likely to explain the evolution of cooperation in vertebrates.

2. Models for the evolution of cooperative breeding

Since Hamilton (1964a,b) first modeled the evolution of altruism among relatives, studies of cooperative breeding have focused on kin selection to explain alloparental care (when individuals provision the young of others; hereafter, helping behavior) (Brown, 1978; Brown, 1987). However, subsequent empirical progress has revealed that in many cooperatively breeding vertebrates, (i) a significant proportion of the helping is done by non-relatives (Brooke and Hartley, 1995; Dunn et al., 1995; Magrath and Whittingham, 1997; Clutton-Brock, 2002; Dickinson and Hatchwell, 2004; Stiver et al., 2005), and (ii) the direct fitness benefits of helping might have been greatly underestimated (Cockburn, 1998; Heinsohn and Legge, 1999; Clutton-Brock, 2002; Cockburn, 2004). To understand how cooperation is maintained in cooperative breeding systems, it is important to recognize that cooperative breeding is generally seen as a two-step process (Dickinson and Hatchwell, 2004) where individuals first delay dispersal and stay on the natal territory, and secondarily help others (Emlen, 1982; Koenig et al., 1992). Helping clearly qualifies as cooperation, but remaining on a natal territory is not necessarily a cooperative act. The decision to stay on the natal territory and forgo dispersal and independent breeding is often driven by ecological constraints that include a limitation of suitable territories (Woolfenden and Fitzpatrick, 1990; Komdeur, 1992), nest sites (Walters, 1990), mates (Emlen, 1982), or other resources (Dickinson and McGowan, 2005; Baglione et al., 2006). Helping cannot be studied in isolation from these forces because the ecological constraints on dispersal can influence the relative payoffs for cooperating versus leaving a group (Reeve and Shen, 2006). Moreover, there may be fitness benefits to delaying dispersal (e.g. benefits of remaining with parents or on the natal territory) that are independent of any benefits gained from helping (Dickinson and Hatchwell, 2004). Here, we focus on helping behavior, but recognize that (i) ecological constraints may influence levels of cooperation and conflict between breeders and helpers (Rubenstein, 2007) and (ii) helpers may cooperate in ways independent of nest provisioning, such as nest defense from predators (Rubenstein, 2006).

There are many hypotheses to explain the maintenance of helping behavior in cooperative breeding systems (reviewed in Emlen et al., 1991; Cockburn, 1998; Dickinson and Hatchwell, 2004). Bergmüller et al. (2007) focus on three of the dominant hypotheses for the evolution of helping behavior, referred to as ‘pay-to-stay’, ‘prestige’ and ‘group augmentation’. We discuss these three models, but also explore and synthesize other hypotheses as we fit them into our unified framework for cooperation (Table 1).

2.1. Shared genes and helping behavior

Kinship is thought to be central to the evolution of helping behaviors because of the inclusive fitness benefits that can be gained by living with and assisting relatives (Brown, 1978; Brown, 1987; Emlen, 1995; Cockburn, 1998; Dickinson and Hatchwell, 2004). The specific mechanisms that drive kin association have recently received increased attention (e.g. Griffin and West, 2003). Although original kin models suggested that individuals can cooperate with kin as a passive consequence of staying on natal territory (Hamilton, 1964a), recent theoretical work shows how competition with local relatives can negate the benefits of spatially structured relatedness (West et al., 2002), calling into question the importance of kin fidelity. Kin choice models offer an active mechanism of kin association in which benefits can be preferentially delivered to kin irrespective of local structure. There is increasing evidence for kin choice mechanisms in a variety of cooperatively breeding species (i.e. Lessells et al., 1994; Russell and Hatchwell, 2001; Baglione et al., 2003; Sharp et al., 2005; Covas et al., 2006; McDonald et al., 2007).

2.2. Byproducts and helping behavior

Helping cannot be maintained by simple byproducts (or *byproduct mutualism*, Bergmüller et al., 2007) because helping behavior is characterized by an active investment in the recipient. However, pseudo-reciprocity models could potentially explain the evolutionary maintenance of helping (Table 1). According to the ‘group augmentation’ hypothesis (Woolfenden, 1975), which suggests that individuals gain fitness by increasing their group size, helping is an adaptive behavior to expand the social group. Kokko et al. (2001) modeled group augmentation explicitly and found that helping behavior can be selected under two divergent conditions, which they termed *passive* and *active* group augmentation. Passive group augmentation occurs when larger group size yields automatic ‘passive’ benefits to group members, whereas active group augmentation involves reciprocation (discussed below). Passive group augmentation can be classified as pseudo-reciprocity because helping provides automatic benefits and individuals cannot cheat by reducing benefits to others (Sachs et al., 2004). Nonetheless, because the benefits of increased group size often have diminishing returns as groups grow, there are limitations to when helping is selected under passive group augmentation (pseudo-reciprocity) (Kokko et al., 2001). Moreover, there are examples of pseudo-reciprocity that work independently of group size. For instance, a parallel case of pseudo-reciprocity is the ‘experience’ model (Skutch, 1961), which predicts that helpers automatically gain from their actions because helping results in practice that increases the likelihood that they will be successful breeders in the future.

2.3. Directed reciprocity and helping behavior

Helping behavior can be maintained when the costs of helping are compensated by benefits received from others (Trivers, 1971; Axelrod and Hamilton, 1981; Ligon, 1983). Either part-

ner choice or fidelity mechanisms are needed to limit cheating in these systems (Sachs et al., 2004). Partner fidelity models of helping are based on the idea that positive fitness feedbacks occur in cohesive groups, or that investment in helping others feeds back to drive increased benefit to the cooperative individual (Sachs et al., 2004; Foster and Wenseleers, 2006). The ‘territory inheritance’ model (Woolfenden and Fitzpatrick, 1978) and the *active* group augmentation model (Kokko et al., 2001) are perhaps the best examples of partner fidelity models. Both models predict that helping is selected because benefits are actively returned by other group members as a rule, and choice mechanisms are not evoked. Although there are other models that have similar characteristics, they are more focused on the evolution of delayed dispersal and breeding as opposed to the evolution of helping *per se* (e.g. Wiley and Rabenold, 1984; Zack, 1990).

In partner choice models, the costly helping behavior is selected by the active choice of other individuals. For instance, the ‘pay-to-stay’ hypothesis (Gaston, 1978) posits that helpers provision the young of others as payment for access to that territory. If the helpers do not provide adequate benefits they can be punished by the dominants, or potentially evicted from the group (e.g. Mulder and Langmore, 1993; Clutton-Brock and Parker, 1995; Goldstein et al., 1998; Balshine-Earn et al., 1998). Pay-to-stay models are examples of partner choice because the cooperative behavior of helpers is selected by the active choice of others (who reward helpers by allowing them to stay on the territory). Zahavi’s (1995) prestige hypothesis suggests that individuals help in order to increase their social standing (and their chances of reproduction), but this is true only insofar as they will receive these benefits from others in the form of future help or matings (Wright, 1999). As in pay-to-stay models, prestige models predict that helpers are actively chosen by others for their cooperative traits (Zahavi, 1995). An important behavior of cooperatively breeding species that is consistent with partner choice occurs when individuals vie with each other to provide help. Some of the classic examples of reciprocity in avian cooperative breeding systems are characterized by competition among individuals to help others (e.g. Ligon and Ligon, 1978; Heinsohn, 1991). Such competition suggests that being observed helping might be important to incite the choice mechanisms of those being helped.

3. The evolution of cheating in cooperative breeding systems

Cheaters are individuals that evolve to exploit the cooperation of others by receiving, but not giving, benefits (Sachs and Simms, 2006). Perhaps the simplest example of cheating behavior in cooperative breeding systems would be individuals that join a social group, but do not help (provide alloparental care). However, there are at least two common exceptions where such a behavior does not represent a cheating strategy: (i) if the non-helper provides some other benefit to the group (such as nest defense), so there is no exploitation; or (ii) if the non-helper is in poor condition and cannot help efficiently, so the behavior does not represent an advantageous strategy. Furthermore, we predict that cheating will likely be subtle and occur by degrees

in cooperatively breeding vertebrates. For instance, we might expect the evolution of strategies that lower the amount of helping some amount, as opposed to ceasing help altogether. In many cases, such behaviors can act as clues to cheating (e.g. Legge, 2000), but to accurately assess cheaters in cooperatively breeding systems, these observations must be coupled with measures of fitness. That is, cheaters are expected to enjoy enhanced fitness compared to cooperative members of a group, and the presence of cheaters should depress the fitness of other group members.

3.1. Cheating on kin systems

In kin systems, cheaters might evolve to obtain benefits from non-relatives who ‘perceive’ them to be kin. However, the predictions for cheaters are different in kin choice versus kin fidelity systems. Hypothetical cheaters of kin choice systems would need to mimic kin phenotypically to gain benefits (Table 1). To the best of our knowledge, there are no known examples of kin mimics in cooperative breeding systems, perhaps because efficient recognition systems are in place (Lessells et al., 1994; Russell and Hatchwell, 2001; Baglione et al., 2003; Sharp et al., 2005; Covas et al., 2006; McDonald et al., 2007). However, we predict mimics could evolve where helping is based on simple kin-recognition mechanisms, such that non-relatives would insinuate themselves into a position to receive help. Kin fidelity systems have no kin recognition systems in place, and cheaters might evolve to place themselves in contexts or locations where kin would normally be found, a strategy termed *kin deceit* (Table 1) (Connor and Curry, 1995). For instance, white-winged choughs, are thought to pose as helpers and form bogus ‘kin’ bonds with young that recognize any helper as kin (Connor and Curry, 1995). An additional route to kin deceit that can occur in cooperatively breeding species is intra-specific brood parasitism, where birds lay eggs into the nests of others. Brood parasites are particularly harmful to ‘host’ in species that provision any young in their nest (kin fidelity). If cooperative breeding is based on kin fidelity, it should be particularly vulnerable to this type of cheating (Zink, 2000).

3.2. Cheating on reciprocity systems

Partner choice can be cheated on if ‘signals’ of cooperation can potentially be faked by some group members, who we term ‘freeloaders’ (Table 1). For instance, in partner choice systems based on prestige, Zahavi (1995) suggested that cheats exist in cases where individuals pose as helpers by stealing food from other potential helpers in order to provision young (Carlisle and Zahavi, 1986). Pay-to-stay systems might also be vulnerable similar kinds of cheaters that exhibit behaviors that mimic helping, but are less costly than actual help. Cheaters can take advantage of partner fidelity systems by being ‘vagrants’, which we define as individuals that constantly move from group to group, taking benefits from each before moving on (Table 1). By moving among groups vagrants escape the effects of fitness feedbacks that result from group cohesiveness (fidelity). Although there is no empirical evidence to suggest the existence of vagrants in cooperative breeding systems, they are

likely to occur in helping species with tight-knit groups that do not require choice systems to maintain helping behavior. However, in Florida scrub-jays, where helping may be maintained by partner fidelity (Woolfenden and Fitzpatrick, 1978), there are mechanisms to protect groups from such vagrants. Groups of Florida scrub-jays often exhibit very strong repulsion towards ‘wanderers’ that visit from other territories (Woolfenden and Fitzpatrick, 1978).

4. Conclusions and new predictions

Our simple framework of cooperation models suggests that there are relatively few conditions under which helping can be both selectively advantageous, as well as robust to cheating. In particular, helping can evolve because of kin benefits, automatic benefits (byproducts), or because of reciprocity. Although choice systems appear to be a critical mechanism to limiting cheating in both kin cooperation as well as in reciprocity systems, research is only beginning to focus on such behaviors in cooperatively breeding vertebrates. We suggest three interesting lines of research. First, and perhaps most importantly, researchers should investigate choice mechanisms in cooperative breeding systems. The presence or absence of choice can greatly affect the evolutionary stability of helping behavior. Second, the specific mechanisms of choice systems need to be better studied. In particular, researchers should analyze whether the signals that stimulate choice are honest. Third, in well studied choice systems, experiments are needed to test for the system’s robustness to cheating. For example, researchers can create experimental cheaters that display a cooperative signal without delivering an actual benefit (e.g. Tibbetts, 2002).

Pseudo-reciprocity models are also of particular interest in studies of helping behavior because they are immune to cheating. However, it is not clear if there are cooperative breeding systems based purely on automatic benefits. In contrast, it is possible that pseudo-reciprocity inevitably acts in concert with kin selection to explain helping behavior in cooperative breeders (Kokko et al., 2001). Detailed studies that measure differences in fitness and relatedness among group members can parse out the importance of these mechanisms.

Research in cooperative breeding vertebrates has only recently begun to focus on selective models to explain the maintenance of helping behavior. However, a critical and still unexplored aspect of any cooperation model is that it must be robust to cheaters. While cheaters have been discussed in theoretical papers on cooperative breeding (Wiley and Rabenold, 1984; Kokko et al., 2001), very little empirical work in these systems has investigated cheaters in nature. We hope to spur biologists to explore the possibility that cheats exist within cooperatively breeding groups.

References

- Axelrod, R., Hamilton, W.D., 1981. The evolution of cooperation. *Science* 211, 1390–1396.
- Baglione, V., Canestrari, D., Marcos, J.M., Ekman, J., 2003. Kin selection in cooperative alliances of carrion crows. *Science* 300, 1947–1949.

- Baglione, V., Canestrari, D., Marcos, J.M., Ekman, J., 2006. Experimentally increased food resources in the natal territory promote offspring philopatry and helping in cooperatively breeding carrion crows. *Proc. R. Soc. B: Biol. Sci.* 273, 1529–1535.
- Balshine-Earn, S., Neat, F.C., Reid, H., Taborsky, M., 1998. Paying to stay or paying to breed? Field evidence for direct benefits of helping behavior in a cooperatively breeding fish. *Behav. Ecol.* 9, 432–438.
- Bergmüller, R., Johnstone, R., Russell, A., Bshary, R., 2007. Integrating cooperative breeding into theoretical concepts of cooperation. *Behav. Process.*
- Brooke, M.D., Hartley, I.R., 1995. Nesting Henderson reed-warblers (*Acrocephalus vaughani taiti*) studied by DNA fingerprinting: unrelated coalitions in a stable habitat? *Auk* 112, 77–86.
- Brown, J.L., 1978. Avian communal breeding systems. *Annu. Rev. Ecol. Syst.* 9, 123–155.
- Brown, J.L., 1983. Cooperation – a biologist's dilemma. *Adv. Study Behav.* 13, 1–37.
- Brown, J.L., 1987. Helping and communal breeding in birds. *Ecology and Evolution*. Princeton University Press, Princeton.
- Bull, J.J., Rice, W.R., 1991. Distinguishing mechanisms for the evolution of cooperation. *J. Theor. Biol.* 149, 63–74.
- Carlisle, T.R., Zahavi, A., 1986. Helping at the nest allofeeding and social-status in immature Arabian babblers. *Behav. Ecol. Sociobiol.* 18, 339–351.
- Clutton-Brock, T.H., Parker, G.A., 1995. Punishment in animal societies. *Nature* 373, 209–216.
- Clutton-Brock, T., 2002. Behavioral ecology – breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296, 69–72.
- Cockburn, A., 1998. Evolution of helping behavior in cooperatively breeding birds. *Annu. Rev. Ecol. Syst.* 29, 141–177.
- Cockburn, A., 2004. Mating systems and sexual conflict. In: Koenig, W.D., Dickinson, J.L. (Eds.), *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge University Press, Cambridge, 81–101P.
- Connor, R.C., 1986. Pseudo-reciprocity – investing in mutualism. *Anim. Behav.* 34, 1562–1566.
- Connor, R.C., Curry, R.L., 1995. Helping non-relatives – a role for deceit. *Anim. Behav.* 49, 389–393.
- Connor, R.C., 1995. The benefits of mutualism – a conceptual-framework. *Biol. Rev. Camb. Philos. Soc.* 70, 427–457.
- Covas, R., Dalecky, A., Caizergues, A., Doutrelant, C., 2006. Kin associations and direct versus indirect fitness benefits in colonial cooperatively breeding sociable weavers *Philetairus socius*. *Behav. Ecol. Sociobiol.* 60, 323–331.
- Dickinson, J.L., Hatchwell, B.J., 2004. Fitness consequences of helping. In: Koenig, W.D., Dickinson, J.L. (Eds.), *Ecology and Evolution of Cooperative Breeding in Birds*. Cambridge University Press, Cambridge, pp. 48–66.
- Dickinson, J.L., McGowan, A., 2005. Winter resource wealth drive's delayed dispersal and family-group living in western bluebirds. *Proc. R. Soc. B: Biol. Sci.* 272, 2423–2428.
- Dunn, P.O., Cockburn, A., Mulder, R.A., 1995. Fairy-wren helpers often care for young to which they are unrelated. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.* 259, 339–343.
- Emlen, S.T., 1982. The evolution of helping 1. An ecological constraints model. *Am. Naturalist* 119, 29–39.
- Emlen, S.T., Reeve, H.K., Sherman, P.W., Wrege, P.H., Ratnieks, F.L.W., Shellman-Reeve, J., 1991. Adaptive versus nonadaptive explanations of behavior – the case of alloparental helping. *Am. Naturalist* 138, 259–270.
- Emlen, S.T., 1995. An evolutionary-theory of the family. *Proc. Natl. Acad. Sci. U.S.A.* 92, 8092–8099.
- Emlen, S.T., 1997. Predicting family dynamics in social vertebrates. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioral Ecology. An Evolutionary Approach*. Blackwell Science, Oxford, pp. 228–253.
- Eshel, I., Cavalli-Sforza, L.L., 1982. Assortment of encounters and evolution of cooperativeness. *Proc. Natl. Acad. Sci. U.S.A.: Biol. Sci.* 79, 1331–1335.
- Foster, K.R., Wenseleers, T., 2006. A general model for the evolution of mutualisms. *J. Evol. Biol.* 19, 1283–1293.
- Foster, K.R., Kokko, H., 2006. Cheating can stabilize cooperation in mutualisms. *Proc. R. Soc. B: Biol. Sci.* 273, 2233–2239.
- Gaston, A.J., 1978. Evolution of group territorial behavior and cooperative breeding. *Am. Naturalist* 112, 1091–1100.
- Goldstein, J.M., Woolfenden, G.E., Hailman, J.P., 1998. A same-sex stepparent shortens a prebreeder's duration on the natal territory: tests of two hypotheses in Florida scrub-jays. *Behav. Ecol. Sociobiol.* 44, 15–22.
- Griffin, A.S., West, S.A., 2003. Kin discrimination and the benefit of helping in cooperatively breeding vertebrates. *Science* 302, 634–636.
- Hamilton, W.D., 1964a. Genetical evolution of social behaviour I. *J. Theor. Biol.* 7, 1–16.
- Hamilton, W.D., 1964b. Genetical evolution of social behaviour 2. *J. Theor. Biol.* 7, 17–52.
- Heinsohn, R.G., 1991. Kidnapping and reciprocity in cooperatively breeding white-winged choughs. *Anim. Behav.* 41, 1097–1100.
- Heinsohn, R., Legge, S., 1999. The cost of helping. *Trends Ecol. Evol.* 14, 53–57.
- Jamieson, I.G., 1989. Behavioral heterochrony and the evolution of birds helping at the nest – an unselected consequence of communal breeding. *Am. Naturalist* 133, 394–406.
- Koenig, W.D., Pitelka, F.A., Carmen, W.J., Mumme, R.L., Stanback, M.T., 1992. The evolution of delayed dispersal in cooperative breeders. *Quart. Rev. Biol.* 67, 111–150.
- Kokko, H., Johnstone, R.A., Clutton-Brock, T.H., 2001. The evolution of cooperative breeding through group augmentation 268. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.*, 187–196.
- Kokko, H., Johnstone, R.A., Wright, J., 2002. The evolution of parental and alloparental effort in cooperatively breeding groups: when should helpers pay to stay? *Behav. Ecol.* 13, 291–300.
- Komdeur, J., 1992. Importance of habitat saturation and territory quality for evolution of cooperative breeding in the seychelles warbler. *Nature* 358, 493–495.
- Legge, S., 2000. The effect of helpers on reproductive success in the laughing kookaburra. *J. Anim. Ecol.* 69, 714–724.
- Lehmann, L., Keller, L., 2006. The evolution of cooperation and altruism – a general framework and a classification of models. *J. Evol. Biol.* 19, 1365–1376.
- Lessells, C.M., Avery, M.I., Krebs, J.R., 1994. Nonrandom dispersal of kin – why do European bee-eater (*Merops apiaster*) brothers nest close together. *Behav. Ecol.* 5, 105–113.
- Ligon, J.D., Ligon, S.H., 1978. Communal breeding in green woodhoopoes as a case for reciprocity. *Nature* 276, 496–498.
- Ligon, J.D., 1983. Cooperation and reciprocity in avian social-systems. *Am. Naturalist* 121, 366–384.
- Magrath, R.D., Whittingham, L.A., 1997. Subordinate males are more likely to help if unrelated to the breeding female in cooperatively breeding white-browed scrubwrens. *Behav. Ecol. Sociobiol.* 41, 185–192.
- McDonald, P.G., Heathcote, C.F., Clarke, M.F., Wright, J., Kazem, A.J.N., 2007. Provisioning calls of the cooperatively breeding bell miner *Manorina melanophrys* encode sufficient information for individual discrimination. *J. Avian. Biol.* 38, 113–121.
- Mulder, R.A., Langmore, N.E., 1993. Dominant males punish helpers for temporary defection in superb fairy-wrens. *Anim. Behav.* 45, 830–833.
- Queller, D.C., 1985. Kinship reciprocity and synergism in the evolution of social-behavior. *Nature* 318, 366–367.
- Reeve, H.K., Shen, S.F., 2006. A missing model in reproductive skew theory: the bordered tug-of-war. *Proc. Natl. Acad. Sci. U.S.A.* 103, 8430–8434.
- Rubenstein, D.R., 2006. The Evolution of the Social and Mating Systems of the Plural Cooperatively Breeding Superb Starling *Lamprolornis superbus*. Cornell University, Ithaca, NY.
- Rubenstein, D.R., 2007. Stress hormones and sociality: integrating social and environmental stressors. *Proc. R. Soc. B: Biol. Sci.* 274, 967–975.
- Russell, A.F., Hatchwell, B.J., 2001. Experimental evidence for kin-biased helping in a cooperatively breeding vertebrate. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.* 268, 2169–2174.
- Sachs, J.L., Mueller, U.G., Wilcox, T.P., Bull, J.J., 2004. The evolution of cooperation. *Quart. Rev. Biol.* 79, 135–160.
- Sachs, J.L., 2006. Cooperation within and among species. *J. Evol. Biol.* 19, 1415–1418.
- Sachs, J.L., Simms, E.L., 2006. Pathways to mutualism breakdown. *Trends Ecol. Evol.* 21, 585–592.
- Sachs, J.L., Wilcox, T.P., 2006. A shift to parasitism in the jellyfish symbiont *Symbiodinium microadriaticum*. *Proc. R. Soc. B: Biol. Sci.* 273, 425–429.

- Sharp, S.P., McGowan, A., Wood, M.J., Hatchwell, B.J., 2005. Learned kin recognition cues in a social bird. *Nature* 434, 1127–1130.
- Skutch, A.F., 1961. Helpers among birds. *Condor* 63, 198–226.
- Stiver, K.A., Dierkes, P., Taborsky, M., Gibbs, H.L., Balshine, S., 2005. Relatedness and helping in fish: examining the theoretical predictions. *Proc. R. Soc. B: Biol. Sci.* 272, 1593–1599.
- Tibbetts, E.A., 2002. Visual signals of individual identity in the wasp *Polistes fuscatus*. *Proc. R. Soc. Lond., Ser. B: Biol. Sci.* 269, 1423–1428.
- Trivers, R.L., 1971. Evolution of reciprocal altruism. *Quart. Rev. Biol.* 46 (35).
- Walters, J.R., 1990. Red-cockaded woodpeckers, a “primitive” cooperative breeder. In: Stacey, P.B., Koenig, W.D. (Eds.), *Cooperative Breeding in Birds*. Cambridge University Press, Cambridge, pp. 67–102.
- West, S.A., Pen, I., Griffin, A.S., 2002. Conflict and cooperation – cooperation and competition between relatives. *Science* 296, 72–75.
- West-Eberhard, M.J., 1975. The evolution of social behavior by kin selection. *Quart. Rev. Biol.* 50, 1–33.
- Wiley, R.H., Rabenold, K.N., 1984. The evolution of cooperative breeding by delayed reciprocity and queuing for favorable social positions. *Evolution* 38, 609–621.
- Wolfenden, G.E., 1975. Florida scrub jay helpers at nest. *Auk* 92, 1–15.
- Wolfenden, G.E., Fitzpatrick, J.W., 1978. Inheritance of territory in group-breeding birds. *Bioscience* 28, 104–108.
- Wolfenden, G.E., Fitzpatrick, J.W., 1990. Florida scrub jays: a synopsis after 18 years of study. In: Stacey, P.B., Koenig, W.D. (Eds.), *Cooperative Breeding in Birds*. Cambridge University Press, Cambridge, pp. 241–266.
- Wright, J., 1999. Altruism as a signal – Zahavi’s alternative to kin selection and reciprocity. *J. Avian Biol.* 30, 108–115.
- Zack, S., 1990. Coupling delayed breeding with short-distance dispersal in cooperatively breeding birds. *Ethology* 86, 186–265.
- Zahavi, A., 1995. Altruism as a handicap – the limitations of kin selection and reciprocity. *J. Avian Biol.* 26, 1–3.
- Zink, A.G., 2000. The evolution of intraspecific brood parasitism in birds and insects. *Am. Naturalist* 155, 395–405.