

Commentary

Cooperative behaviour in cooperative breeders: Costs, benefits, and communal breeding

Jason S. Gilchrist^{a,b,*}

^a School of Life Sciences, Napier University, 10 Colinton Road, Edinburgh EH10 5DT, UK

^b Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

Received 11 December 2006; accepted 12 December 2006

In this issue, [Bergmüller et al. \(2007\)](#) have provided a valuable review paper, re-establishing cooperative breeding within a theoretical framework in field studies of cooperative breeding vertebrates. I am in agreement with the authors in their outlook and suggestions. In this critical review, I wish to (1) review the costs and benefits approach previously taken in the field, (2) evaluate communal breeding species with regard to the game-theoretical approach promoted by [Bergmüller et al. \(2007\)](#), and (3) consider the reasons why empiricists researching cooperative breeding have generally side-stepped a game-theoretical approach.

There is no doubting the great interest in cooperative breeding systems, in particular which individuals care for young, and the distribution of costs and benefits to care to determine whether and how individuals accumulate evolutionary fitness ([Heinsohn and Legge, 1999](#)). However, as [Bergmüller et al. \(2007\)](#) point out—this has proceeded relatively independently of game-theoretical approaches to cooperative behaviour.

1. Alloparental care: costs and benefits

Whilst [Bergmüller et al. \(2007\)](#) are clear in their definition of cooperative breeding systems, characterised by individuals contributing care to offspring that are not their own ([Cockburn, 1998](#); [Solomon and French, 1997a](#); [Stacey and Koenig, 1990](#)), they are less clear in their use of the terms “helper” and “helping”. The use of the terms “helping” and “helper” in cooperative breeding literature is often unfortunate. These terms are loaded and implicitly suggest an active altruistic behaviour: a cost to helper and benefit to recipient. According to the Collins Concise Dictionary, the primary definition of “help” is “to assist (some-

one to do something), esp. by sharing the work, cost, or burden of something”. The term “alloparental care”, defined simply as providing care for offspring of other individuals carries less baggage ([Jennions and Macdonald, 1994](#)).

[Bergmüller et al. \(2007\)](#) comment that in studies of cooperative breeding, researchers have mainly focussed on the outcomes of helping. Historically, studies of cooperative breeding have been concerned with whether alloparental care in cooperative breeding species is adaptive, with two principal questions: (1) is care costly to the donor, and (2) is care beneficial to the recipient. The adaptive nature of alloparental care is then determined by whether the end inclusive fitness benefits to the carer exceed the costs of care, with benefits to carers potentially accrued along two axes: direct–indirect and present–future ([Brown, 1983](#)).

Numerous studies have found evidence that “helpers” directly improve the survival and present or future reproductive success of breeders ([Emlen, 1991](#)). However, some studies have failed to detect benefits of the presence of “helpers” to breeders or their reproductive success ([Leonard et al., 1989](#); [Magrath and Yezerinac, 1997](#); [Packer et al., 1992](#); [Zahavi, 1990](#)) or have even shown a negative effect of “helpers” on the fitness of breeders (e.g. [Legge, 2000](#); [Woodroffe and Macdonald, 2000](#)). This casts doubt on whether “help” is necessarily adaptive and whether “helpers” actually “help”. In such cases alloparental care may represent unselected or even maladaptive misplaced parental care ([Jamieson, 1989, 1991](#)). It is important to keep this in mind when we consider cooperation and cooperative breeding—we should not simply assume that cooperative behaviour is adaptive.

In order for a behaviour to qualify as true “help” it must be (1) conducted by individuals directly to individuals that are not their offspring (otherwise such behaviour is simply accounted for as parental behaviour), (2) costly to the individual conducting the behaviour, and (3) beneficial to the receiver ([Clutton-Brock et al., 1998](#)). Alloparental care has been shown to be costly in a variety of studies, both in terms of conditional costs ([Arnold, 1990](#); [Clutton-Brock et al., 1998](#); [Heinsohn and Cockburn, 1994](#);

* Correspondence address: School of Life Sciences, Napier University, 10 Colinton Road, Edinburgh EH10 5DT, UK.

E-mail address: j.gilchrist@napier.ac.uk.

Taborsky, 1984) and survival (Rabenold, 1990; Reyer, 1984). Additionally alloparental care has been shown to benefit breeders in a variety of studies. Helpers can increase the condition (Hatchwell, 1999) or survival of the young they rear (Emlen and Wrege, 1991). Alternatively helpers can reduce the workload of the parents they help through “load lightening” (Crick, 1992). This can increase the probability that the parents survive to breed again (Koenig and Mumme, 1987; Reyer, 1984; Russell and Rowley, 1988), or increase their future productivity, by decreasing inter-birth interval or increasing productivity per litter, e.g. the grey crowned babbler *Pomatostomus temporalis* (Brown et al., 1978), pine vole *Microtus pinotorum* (Powell and Fried, 1992), dwarf mongoose *Helogale parvula* (Creel et al., 1991), stripe-backed wren *Camphylorhynchus nuchalis* (Rabenold, 1990) and splendid fairy wren *Malurus splendens* (Rowley and Russell, 1990).

Bergmüller et al. (2007) acknowledge that alloparents commonly accrue indirect fitness benefits, and briefly summarise the principal hypothesised direct fitness benefits to contributors of alloparental behaviour. Individuals may contribute alloparental care as a payment of rent (pay-to-stay), to increase group size (group augmentation), or as an advertisement of status (prestige or competitive altruism) (see reviews by Clutton-Brock, 2002; Cockburn, 1998; Emlen, 1991). An additional possibility is that individuals contribute alloparental care to gain experience of parental care. Such experience can improve their own future success as parents (Brown, 1987; Heinsohn, 1991; Skutch, 1961). Evidence that helpers improve their reproductive success from experience gained by helping is available for some species (Komdeur, 1996; Rowley and Russell, 1990). Notably, within a species alloparents may gain fitness along different axes, e.g. in the pied kingfisher primary helpers gain indirect fitness and secondary helpers “queue” for a mate (Reyer, 1986).

It is also notable that in some “cooperative” species, apparent “helpers” may gain personal reproductive success, as for male stripe-backed and white-browed scrubwrens *Sericornis frontalis* (Magrath and Whittingham, 1997; Whittingham et al., 1997), and male callitrichids (Tardif, 1997). Indeed some authors regard direct access to parentage as an adaptive reason for “help” (e.g. Cockburn, 1998), when such examples are perhaps better regarded as parental care, with care of the young of other breeders a by-product of an inability to distinguish their own from others young.

This is an important point when considering communal breeders, where most group members breed and the main benefit to carers may be direct fitness through their own offspring. Interestingly, in at least one study, subordinates are regarded as “helpers” even when they have parentage, whereas dominants in the same group, who are also caring for others’ offspring are not regarded as “helping” (Magrath and Whittingham, 1997; Whittingham et al., 1997).

2. A communal breeding perspective

Whilst it is not crucial to the main points of their review, Bergmüller et al. (2007) are guilty of falling into the familiar trap of overlooking communal breeding species (those with low

reproductive skew) in their consideration of cooperative breeding species. Throughout the review, Bergmüller et al. (2007) refer to breeders and helpers with the implicit assumption of reproductive role division. However, reproductive skew is indeed a continuum (Sherman et al., 1995; Vehrencamp, 2000), and there are a number of cooperative breeding species in which it is the norm for breeders to contribute care to offspring that are not their own, e.g. banded mongooses (*Mungos mungo*) and grey mouse lemurs (*Microcebus murinus*) (Eberle and Kappeler, 2006; Gilchrist, 2004).

The majority of cooperative breeding species exhibit high reproductive skew, where reproduction is monopolised by one or a few of the adult group members, and most adults do not reproduce but help to rear the breeder’s offspring (Solomon and French, 1997a; Stacey and Koenig, 1990). However, at the opposite end of the continuum from high skew species are plural breeding species, with low reproductive skew, where subordinates commonly breed. Cooperative breeding systems of this kind include communal breeders (or “joint-nesting plural breeders”, Brown, 1987), in which more than one female lays eggs or gives birth to young in the same nest or den. For a full discussion of the problems and inconsistencies of terminology in the literature surrounding cooperatively breeding birds and mammals see Solomon and French (1997b). Communal breeding is particularly rare. Within mammals it occurs at a high frequency only in the banded mongoose (Cant, 2000; Rood, 1975) and some rodent species, for example, the house mouse (*Mus musculus domesticus*), Norway rat (*Rattus norvegicus*) and various caviés (Hayes, 2000; Solomon and Getz, 1997). Within birds, communal breeding is typical in only a few species, including the groove-billed ani *Crotophaga sulcirostris* (Koford et al., 1990), pukeko *Porphyrio porphyrio* (Craig and Jamieson, 1990) and Guira cuckoo *Guira guira* (Macedo, 1992).

Whilst it is simpler to consider cooperative breeding systems with distinct differentiation between the role of breeder and (non-breeding) helper (as in systems with high reproductive skew), this overlooks the interesting dynamics within systems with low reproductive skew where the roles of breeder and helper (or carer) are not clearly differentiated (Lewis and Pusey, 1997). In communal breeding systems the majority of individuals may accrue direct fitness through their own offspring, with the causes and consequences of cooperative behaviour possibly fundamentally different to those in high skew systems (e.g. the banded mongoose) (Gilchrist, 2006; Gilchrist and Russell, 2007). If care of offspring in communal breeding systems is unbiased with regard to relatedness (between donor and recipient), this presents a case for group selection (as for colonies of social arthropods) (Aviles, 1997; Bourke and Franks, 1995).

In my opinion we also require a reevaluation of the theory behind cooperative breeding and reproductive skew. The implications of reproductive skew for cooperation are implicit in reproductive skew models that incorporate reproductive concessions by the dominant to subordinates for alloparental contributions to rearing the dominant’s offspring (pay-to-reproduce) (Keller and Reeve, 1994). Concession models of reproductive skew implicitly incorporate breeders trading reproductive allowances for help (an expansion of pay-to-stay).

However, concession theory (dominants trading reproductive allowance for “help”) and pay-to-stay models (dominants trading tenure for “help”) are riddled with interpretational problems (Clutton-Brock, 1998; Clutton-Brock et al., 2001b). Nevertheless, such models have obvious implications for the evolution and maintenance of communal breeding systems and have the potential to explain variation in both reproductive skew and cooperative behaviour in general.

3. Evaluating costs and benefits

There are probably good reasons for the relative independence of game-theory models and considerations of vertebrate cooperative breeding systems. The principal problems are getting meaningful data on costs and benefits of multiple interactions between individuals within groups of individuals with relative longevity and overlapping generations.

Bergmüller et al. (2007) recommend that game-theory options are “carefully investigated to allow a thorough understanding of the game structure”. However, pinning down the specific strategy requires a thorough evaluation of costs and benefits of all direct and indirect interactions between individuals within a group or cooperating network. This is rarely feasible in vertebrates, unless such interactions have major fitness consequences, and even then a full understanding requires life-history data over the entire lifespan of individuals (and across generations). Short-term indirect evaluation of fitness pay-offs of interactions could be achieved by energetic analysis (e.g. by use of weight or the Doubly Labelled Water technique) (Clutton-Brock et al., 1998; Speakman, 1997). In addition, as suggested by Bergmüller et al. (2007), short-term manipulations may also overcome some of the restrictions for understanding interactions amongst individuals within cooperative breeding vertebrate species. However, short-term analyses can never provide answers to long-term questions, e.g. active group augmentation where the young that helpers rear later help to rear the helpers young. Indeed, the lack of long-term data could explain the lack of evidence for active group augmentation. As Bergmüller et al. (2007) state, selection acts on individual strategies not individual interactions. Invertebrates with relatively short lifespans and generation times may be the answer for lifetime evaluation of costs and benefits of interactions and strategies, although invertebrates do not lend themselves to the aforementioned short-term energetic analyses.

A fundamental difficulty in testing game-theory is determining who is the “receiver” of alloparental care or other cooperative behaviour. The receiver could be considered to be either the parents of the “helped” offspring or the offspring themselves. This could prove complicated in differentiating between alternative game-theory explanations for care.

3.1. Who receives care?

The issue within cooperative breeding species of who receives alloparental care is a crucial one to evaluating game-theory alternatives. It could be argued that both the offspring and the parent gain direct fitness benefits from alloparental care

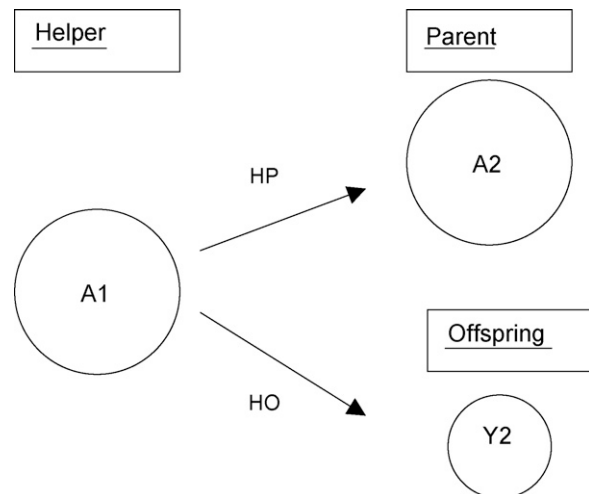


Fig. 1. Step 1: A1 (helper) provides alloparental care to A2 (parent)/Y2 (offspring). Circles denote individuals. Large circles denote adults. Small circles denote young. Squares denote labels for individual status (helper, parent, offspring). Arrows indicate direction of alloparental care. Alloparental care can be interpreted as passing from helper to parent (route HP) or helper to offspring (route HO).

and that both are recipients. If an alloparent provisions young with food, both the young and the parent(s) of the young benefit (in terms of direct fitness). However, double-counting must be avoided. There are several possible interpretations of an apparently simple alloparental interaction (see Fig. 1) and I deal with this issue on two levels: (1) who receives care, and (2) interpretations of third party interactions. Deciding whether the parent of the offspring or the offspring themselves are the recipients of alloparental care is crucial in determining whether responses are direct or indirect, and in differentiating between alternative game-theory explanations for alloparental care.

At the first interaction (step 1, see Fig. 1), the alloparent (A1) can be interpreted as providing care to the parent of the offspring (A2, route = help parent (HP)) or to the offspring itself (Y2, route = help offspring (HO)). There are then two alternative outcomes at the second interaction (step 2: a or b, see Fig. 2). In step 2a (Fig. 2), the parent in the first interaction (A2) can be interpreted as providing care to the original alloparent (A1, route = help parent (HP)) or to the offspring of the original alloparent (Y1, route = help offspring (HO)). If we interpret the alloparental care donated at step 1 (by A1) to be received by the original parent (A2), then at step 2a we must interpret the return investment (by A2) as being directed toward to the original alloparent (A1) and we classify the two-step interaction as direct reciprocity. If we interpret the alloparental care donated at step 1 (by A1) to be received by the offspring (Y2) of the original parent (A2), then at step 2a we must interpret the return investment (by A2) as being directed toward to the offspring (Y1) of the original alloparent (A1) and there is no direct or indirect transfer of care between the two adults in the interaction—whilst cooperative, the interaction does not constitute reciprocity.

In step 2b (Fig. 2), the offspring in the first interaction (Y2) can be interpreted as providing care to the original alloparent (A1, route = help parent (HP)) or to the offspring of the original

alloparent (Y1, route = help offspring (HO)). If we interpret the alloparental care donated at step 1 (by A1) to be received by the original parent (A2), then at step 2b we must interpret the return investment (by Y2) as being directed toward to the original alloparent (A1), and whilst there are two cooperative donations, the interaction does not constitute reciprocation. If we interpret the alloparental care donated at step 1 (by A1) to be received by the offspring (Y2) of the original parent (A2), then at step 2b we must interpret the return investment (by Y2) as being directed toward to the offspring (Y1) of the original alloparent (A1) and whilst there are two cooperative donations, the interaction does not constitute reciprocation.

Under the constraints of this simple two-step dyadic model—deciding who receives alloparental care (parent or offspring) determines whether we recognise reciprocal cooperative behaviour or not.

3.2. Third party interactions and group augmentation

The above consideration simplifies matters by ignoring third party interactions and by only considering alloparental care. However, if we consider the recipients of alloparental care to be the offspring (rather than the parents), even if we expand our consideration to allow third party interactions, indirect reciprocity is not possible. If the recipient of alloparental care is defined as the offspring (not the parent) it is not possible for the original alloparent to receive alloparental care, e.g. at step 2 Y2 could provide alloparental care to the offspring of A1 (not A1) and therefore this would not classify as indirect reciprocity.

Bergmüller et al. (2007) provide an example of indirect reciprocity “the recipient [of alloparental care] will later indirectly invest in return (costly response) by helping to raise the former helper’s offspring”. Bergmüller et al. (2007) do not specify in their manuscript who they interpret as the recipient (parent or offspring), but consider the donor to provide alloparental care to the young (not the parents of the young) and the return alloparental care from the recipient young as being directed to the young of the original donor (not the donor parent) (Bergmüller et al., personal communication), therefore classifying this as indirect reciprocity. I do not agree with this interpretation. In this example if alloparental care is taken as investment in recipient offspring and the recipient offspring subsequently provide alloparental care to the offspring of the donor, there is no reciprocation. However, if the recipient of alloparental care is the parent of the offspring, and the parent subsequently provides alloparental care for the original donor, this is direct reciprocation (see above). For this interaction to be classified as indirect reciprocity it requires a third party interaction, with the recipient of alloparental care (the parent) subsequently providing alloparental care to a third party, who subsequently provides alloparental care to the original donor. This is not made clear in the example by Bergmüller et al. (2007), and highlights the importance of definitions in determining game-theory pathways.

The only way to enable direct or indirect reciprocation via alloparental care to offspring (not parent) is to expand cooperative behaviour considered beyond alloparental care to other behaviours. Note however that with our interest in coopera-

tive breeding, the first step must always be alloparental care in order to conserve the cooperative breeding perspective. We are interested in why individuals invest in the offspring of other individuals. If we remove alloparental care from our model we have abandoned cooperative breeding and are simply examining game-theory models. If at step 1, A1 contributed alloparental care to the offspring (Y2), and the offspring subsequently contributed directly beneficial behaviour toward the original donor (A1) (by definition not alloparental behaviour), e.g. provisioning A1, direct reciprocation has occurred. If at step 1, A1 contributed alloparental care to parent (A2) or offspring (Y2), and parent or offspring subsequently contributed directly beneficial behaviour toward a third party that subsequently contributed directly beneficial behaviour toward the original donor (A1) (by definition not alloparental behaviour), indirect reciprocation has occurred. Direct reciprocation involves a dyadic exchange. Indirect reciprocity, requiring third parties, is a form of group augmentation.

The response need not be costly, in which case we have pseudo-reciprocity, another group augmentation route to cooperative breeding (Bergmüller et al., 2007). Where the recipients of alloparental care then behave selfishly to the benefit of the original donor, e.g. individuals receiving benefits from alloparental care (parent or offspring) then contribute to nest maintenance or anti-predator behaviour, we have direct pseudo-reciprocity. For example, where the recipient of alloparental care at step 1 is the parent (A2) and it then selfishly invests in a common good that benefits the original donor (A1), we have direct pseudo-reciprocity. Similarly, where the recipient of alloparental care at step 1 is the offspring (Y2) and it then selfishly invests in a common good that benefits the original donor (A1), we have direct pseudo-reciprocity. However, whilst the game-theory literature recognises direct pseudo-reciprocity, it does not acknowledge indirect pseudo-reciprocity (Bergmüller et al., personal communication). Indirect pseudo-reciprocity will occur where the recipient of alloparental care (A2 or Y2) then benefits a third party, that in turn selfishly invests in a common good to the benefit of the original donor (A1). This is acknowledged by Bergmüller et al. (2007) in Fig. 2.

It is probably simplest to classify alloparental care in terms of the direct recipient of care, e.g. a provisioned offspring receives food, a babysat offspring receives protection and thermoregulatory benefits. Where an individual provides direct care to the parent (e.g. provisioning the parent) then the recipient is the parent. However, alloparental care may benefit parent fitness via load lightening, directly benefiting the parent in addition to the increased fitness of the current offspring (Crick, 1992). Determining the currencies and relationships of interactions is not a simple business.

An additional problem considered by Bergmüller et al. (2007) is that of cooperative behaviour not directed to individuals but in which all group members benefit (communal/colonial behaviour) via investment in common goods. Examples of such behaviour include social digging in mammals (e.g. meerkats, mole rats), nest building/maintenance in social birds (e.g. social/colonial weavers) and social spiders, co-ordinated vigilance (e.g. dwarf mongooses), and babysitting (e.g. meerkats, banded mongooses). Babysitting in communal breeding species

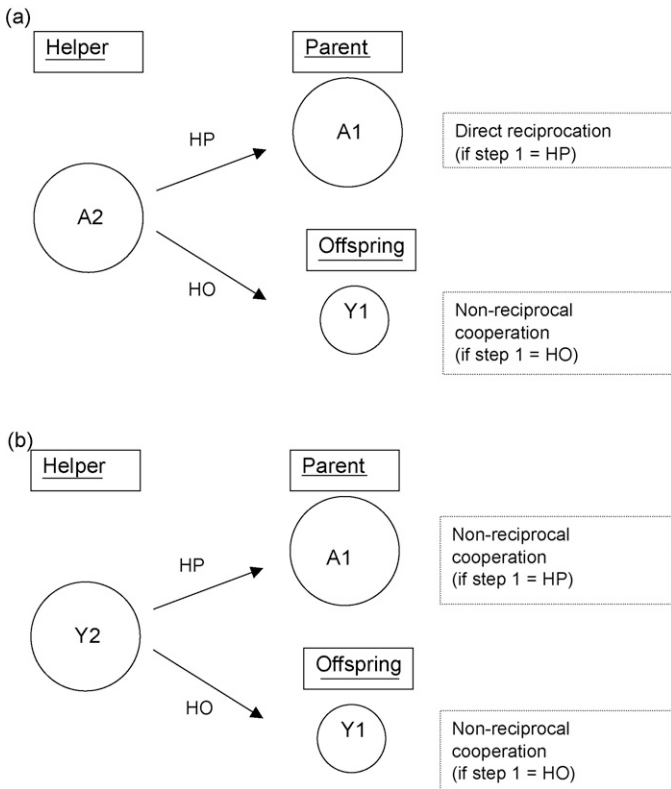


Fig. 2. Step 2a: A2 (original parent) provides alloparental care to A1 (original helper)/Y1 (offspring of original helper). Step 2b: Y2 (offspring of original parent) provides alloparental care to A1 (original helper)/Y1 (offspring of original helper). Circles denote individuals. Large circles denote adults. Small circles denote young. Squares denote labels for individual status (helper, parent, offspring). Arrows indicate direction of alloparental care. Alloparental care can be interpreted as passing from helper to parent (route HP) or helper to offspring (route HO). Dashed boxes to right of steps 2a and b indicate classification of cooperative behaviour.

is most notable in this respect, with individuals potentially providing protective and thermoregulatory benefits to a communal litter of mixed parentage (e.g. in banded mongooses, up to 10 females may have contributed young to the communal litter, Cant, 2003; Gilchrist et al., 2004). Breaking such behaviour down into dyadic cost/benefit data is certainly not straightforward.

Whilst data of a precise dyadic nature is lacking, numerous studies of cooperative breeders provide evidence of energetic or fitness costs incurred by individuals via contributions to rearing offspring that are not their own. For example, helpers have been found to have higher mortality in the pied kingfisher, *Ceryle rudis* (Reyer, 1984) and stripe-backed wren, *Campylorhynchus nuchalis* (Rabenold, 1990), and in both cases the inferred cause was increased energy expenditure. Manipulations by feeding have proved useful in demonstrating costs of care and condition dependence of contributions to care by helpers in meerkats (*Suricata suricatta*), where experimentally fed helpers provision pups more than control helpers, and helpers lose more weight when litter size is artificially increased (Clutton-Brock et al., 2001a,c). It may be possible for future field studies to break such data down into short-term dyadic interactions to enable evaluation from a game-theory perspective.

4. Conclusion

I agree with Bergmüller et al. (2007) that studies of cooperative breeding systems should place greater effort on integrating behavioural data within a game-theory framework. However, for long-lived vertebrates with overlapping generations this is not straightforward. Such an approach would be better employed on those cooperative breeders with small group sizes where the complexity of dyadic interactions is simplified, building up to N -player models. In addition, communal breeding systems should not be overlooked in such considerations—despite their difficulties (indistinct role division) they may differ fundamentally in the evolutionary motives for cooperation.

References

- Arnold, W., 1990. The evolution of marmot sociality: II. Costs and benefits of joint hibernation. *Behav. Ecol. Sociobiol.* 27, 239–246.
- Aviles, L., 1997. Causes and consequences of cooperation and permanent sociality in spiders. In: Choe, J.C., Crespi, B.J. (Eds.), *The Evolution of Social Behaviour in Insects and Arachnids*. Cambridge University Press, Cambridge, pp. 476–499.
- Bergmüller, R., Johnstone, R., Russell, A., Bshary, R., 2007. Integrating cooperative breeding into theoretical concepts of cooperation. *Behav. Process.*
- Bourke, A.F.G., Franks, N.R., 1995. *Social Evolution in Ants*. Princeton University Press, Princeton, New Jersey.
- Brown, J.L., 1983. Cooperation—a biologist's dilemma. *Adv. Study Anim. Behav.* 13, 1–37.
- Brown, J.L., 1987. *Helping and Communal Breeding in Birds*. Princeton University Press, Princeton, New Jersey.
- Brown, J.L., Dow, D.D., Brown, E.R., Brown, S.D., 1978. Effects of helpers on feeding and nestlings in the grey-crowned babbler (*Pomatostomus temporalis*). *Behav. Ecol. Sociobiol.* 4, 43–59.
- Cant, M.A., 2000. Social control of reproduction in banded mongooses. *Anim. Behav.* 59, 147–158.
- Cant, M.A., 2003. Patterns of helping effort in co-operatively breeding banded mongooses (*Mungos mungo*). *J. Zool.* 259, 115–121.
- Clutton-Brock, T., 2002. Behavioral ecology—breeding together: kin selection and mutualism in cooperative vertebrates. *Science* 296, 69–72.
- Clutton-Brock, T.H., 1998. Reproductive skew, concessions and limited control. *Trends Ecol. Evol.* 13, 288–292.
- Clutton-Brock, T.H., Brotherton, P.N.M., O'Riain, M.J., Griffin, A.S., Gaynor, D., Kinsky, R., Sharpe, L., McIlrath, G.M., 2001a. Contributions to cooperative rearing in meerkats. *Anim. Behav.* 61, 705–710.
- Clutton-Brock, T.H., Brotherton, P.N.M., Russell, A.F., O'Riain, M.J., Gaynor, D., Kinsky, R., Griffin, A., Manser, M., Sharpe, L., McIlrath, G.M., Small, T., Moss, A., Monfort, S., 2001b. Cooperation, control, and concession in meerkat groups. *Science* 291, 478–481.
- Clutton-Brock, T.H., Gaynor, D., Kinsky, R., MacColl, A.D.C., McIlrath, G., Chadwick, P., Brotherton, P.N.M., O'Riain, J.M., Manser, M., Skinner, J.D., 1998. Costs of cooperative behaviour in suricates (*Suricata suricatta*). *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 265, 185–190.
- Clutton-Brock, T.H., Russell, A.F., Sharpe, L.L., Brotherton, P.N.M., McIlrath, G.M., White, S., Cameron, E.Z., 2001c. Effects of helpers on juvenile development and survival in meerkats. *Science* 293, 2446–2449.
- Cockburn, A., 1998. Evolution of helping behavior in cooperatively breeding birds. *Annu. Rev. Ecol. Syst.* 29, 141–177.
- Craig, J.L., Jamieson, I.G., 1990. Pukeko: different approaches and some different answers. In: Stacey, P.B., Koenig, W.D. (Eds.), *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behaviour*. Cambridge University Press, Cambridge, pp. 385–412.
- Creel, S.R., Monfort, S.L., Wildt, D.E., Waser, P.M., 1991. Spontaneous lactation is an adaptive result of pseudopregnancy. *Nature* 351, 660–662.
- Crick, H.Q.P., 1992. Load-lightening in cooperatively breeding birds and the cost of reproduction. *Ibis* 134, 56–61.

- Eberle, M., Kappeler, P.M., 2006. Family insurance: kin selection and cooperative breeding in a solitary primate (*Microcebus murinus*). *Behav. Ecol. Sociobiol.* 60, 582–588.
- Emlen, S.T., 1991. Evolution of cooperative breeding in birds and mammals. In: Krebs, J.R., Davies, N.B. (Eds.), *Behavioural Ecology: An Evolutionary Approach*, third ed. Blackwell Scientific Publications, Oxford, pp. 301–337.
- Emlen, S.T., Wrege, P.H., 1991. Breeding biology of white-fronted bee-eaters at nakuru—the influence of helpers on breeder fitness. *J. Anim. Ecol.* 60, 309–326.
- Gilchrist, J.S., 2004. Pup escorting in the communal breeding banded mongoose: behavior, benefits, and maintenance. *Behav. Ecol.* 15, 952–960.
- Gilchrist, J.S., 2006. Reproductive success in a low skew, communal breeding mammal: the banded mongoose, *Mungos mungo*. *Behav. Ecol. Sociobiol.* 60, 854–863.
- Gilchrist, J.S., Otali, E., Mwanguhya, F., 2004. Why breed communally? Factors affecting fecundity in a communal breeding mammal: the banded mongoose (*Mungos mungo*). *Behav. Ecol. Sociobiol.* 57, 119–131.
- Gilchrist, J.S., Russell, A.F., 2007. Who cares? Individual contributions to pup care by breeders versus non-breeders in the cooperatively breeding banded mongoose (*Mungos mungo*). *Behav. Ecol. Sociobiol.* 61, 1053–1060.
- Hatchwell, B.J., 1999. Investment strategies of breeders in avian cooperative breeding systems. *Am. Nat.* 154, 205–219.
- Hayes, L.D., 2000. To nest communally or not to nest communally: a review of rodent communal nesting and nursing. *Anim. Behav.* 59, 677–688.
- Heinsohn, R., Cockburn, A., 1994. Helping is costly to young birds in cooperatively breeding white-winged choughs. *Proc. R. Soc. Lond. Ser. B-Biol. Sci.* 256, 293–298.
- Heinsohn, R., Legge, S., 1999. The cost of helping. *Trends Ecol. Evol.* 14, 53–57.
- Heinsohn, R.G., 1991. Slow learning of foraging skills and extended parental care in cooperatively breeding white-winged choughs. *Am. Nat.* 137, 864–881.
- Jamieson, I.G., 1989. Behavioral heterochrony and the evolution of birds helping at the nest—an unselected consequence of communal breeding. *Am. Nat.* 133, 394–406.
- Jamieson, I.G., 1991. The unselected hypothesis for the evolution of helping behavior: too much or too little emphasis on natural selection? *Am. Nat.* 138, 271–282.
- Jennions, M.D., Macdonald, D.W., 1994. Cooperative breeding in mammals. *Trends Ecol. Evol.* 9, 89–93.
- Keller, L., Reeve, H.K., 1994. Partitioning of reproduction in animal societies. *Trends Ecol. Evol.* 9, 98–103.
- Koenig, W.D., Mumme, R.L., 1987. *Population Ecology of the Cooperatively Breeding Acorn Woodpecker*. Princeton University Press, Princeton.
- Koford, R.R., Bowen, B.S., Vehrencamp, S.L., 1990. Groove-billed anis: joint-nesting in a tropical cuckoo. In: Stacey, P.B., Koenig, W.D. (Eds.), *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behaviour*. Cambridge University Press, Cambridge, pp. 333–356.
- Komdeur, J., 1996. Influence of helping and breeding experience on reproductive performance in the Seychelles warbler: a translocation experiment. *Behav. Ecol.* 7, 326–333.
- Legge, S., 2000. The effect of helpers on reproductive success in the laughing kookaburra. *J. Anim. Ecol.* 69, 714–724.
- Leonard, M.L., Horn, A.G., Eden, S.F., 1989. Does juvenile helping enhance breeder reproductive success—a removal experiment on moorhens. *Behav. Ecol. Sociobiol.* 25, 357–361.
- Lewis, S.E., Pusey, A.E., 1997. Factors influencing the occurrence of communal care in plural breeding mammals. In: Solomon, N.G., French, J.A. (Eds.), *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge, pp. 335–363.
- Macedo, R.H., 1992. Reproductive patterns and social-organization of the communal Guira cuckoo (*Guira guira*) in central Brazil. *Auk* 109, 786–799.
- Magrath, D., Yezerinac, S.M., 1997. Facultative helping does not influence reproductive success or survival in cooperatively breeding white-browed scrubwrens. *J. Anim. Ecol.* 66, 658–670.
- 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.
- Packer, C., Lewis, S., Pusey, A., 1992. A comparative-analysis of nonoffspring nursing. *Anim. Behav.* 43, 265–281.
- Powell, R.A., Fried, J.J., 1992. Helping by juvenile pine voles (*Microtus pine-torum*) growth and survival of younger siblings, and the evolution of pine vole sociality. *Behav. Ecol.* 3, 325–333.
- Rabenold, K.N., 1990. *Camplorhynchus* wrens: the ecology of delayed dispersal and cooperation in the Venezuelan savannah. In: Stacey, P.B., Koenig, W.D. (Eds.), *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behaviour*. Cambridge University Press, Cambridge.
- Reyer, H.U., 1984. Investment and relatedness: a cost/benefit analysis of breeding and helping in the pied kingfisher, *Ceryle rudis*. *Anim. Behav.* 32, 1163–1178.
- Reyer, H.U., 1986. Breeder–helper-interactions in the pied kingfisher reflect the costs and benefits of cooperative breeding. *Behaviour* 96, 277–303.
- Rood, J.P., 1975. Population dynamics and food habitats of the banded mongoose. *East Afr. Wildlife J.* 13, 89–111.
- Rowley, I., Russell, E., 1990. Splendid fairy-wrens: demonstrating the importance of longevity. In: Stacey, P.B., Koenig, W.D. (Eds.), *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behaviour*. Cambridge University Press, Cambridge.
- Russell, E., Rowley, I., 1988. Helper contributions to reproductive success in the splendid fairy-wren (*Malurus splendens*). *Behav. Ecol. Sociobiol.* 22, 131–140.
- Sherman, P.W., Lacey, E.A., Reeve, H.K., Keller, L., 1995. The eusociality continuum. *Behav. Ecol.* 6, 102–108.
- Skutch, A., 1961. Helpers among birds. *Condor* 63, 198–226.
- Solomon, N.G., French, J.A., 1997a. *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge.
- Solomon, N.G., French, J.A., 1997b. The study of mammalian cooperative breeding. In: Solomon, N.G., French, J.A. (Eds.), *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge, pp. 1–10.
- Solomon, N.G., Getz, L.L., 1997. Examination of alternative hypotheses for cooperative breeding in rodents. In: Solomon, N.G., French, N.G. (Eds.), *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge.
- Speakman, J.R., 1997. *Doubly Labelled Water; Theory and Practice*. Chapman & Hall, London.
- Stacey, P.B., Koenig, W.D., 1990. *Cooperative Breeding in Birds: Long-term Studies of Ecology and Behavior*. Cambridge University Press, Cambridge, p. 615.
- Taborsky, M., 1984. Broodcare helpers in the cichlid fish *Lamprologus richardi*: their costs and benefits. *Anim. Behav.* 32, 1236–1252.
- Tardif, S.D., 1997. The bioenergetics of parental behaviour and the evolution of alloparental care in marmosets and tamarins. In: Solomon, N.G., French, J.A. (Eds.), *Cooperative Breeding in Mammals*. Cambridge University Press, Cambridge, pp. 11–33.
- Vehrencamp, S.L., 2000. Evolutionary routes to joint-female nesting in birds. *Behav. Ecol.* 11, 334–344.
- Whittingham, L.A., Dunn, P.O., Magrath, R.D., 1997. Relatedness, polyandry and extra-group paternity in the cooperatively-breeding white-browed scrubwren (*Sericornis frontalis*). *Behav. Ecol. Sociobiol.* 40, 261–270.
- Woodroffe, R., Macdonald, D.W., 2000. Helpers provide no detectable benefits in the European badger (*Meles meles*). *J. Zool.* 250, 113–119.
- Zahavi, A., 1990. Arabian babblers: the quest for social status in a cooperative breeder. In: Stacey, P.B., Koenig, W.D. (Eds.), *Cooperative Breeding in Birds*. Cambridge University Press, Cambridge, pp. 103–130.