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The cost of helping

Robert Heinsohn and Sarah Legge

The study of cooperative breeding in vertebrates aims to understand why some animals forgo independent reproduction and help others to breed instead. Over the past 30 years, the field has developed a rich set of theory^{1–3} and has been wracked by some major debates^{4,5}. However, enough cooperative species have been studied in detail to establish common ground and to test theory. Indeed, in a recent review of the field, Emlen⁶ states that ‘the original paradox of cooperative breeding largely disappeared with the widespread confirmation that (1) helpers frequently do improve their chances of becoming breeders..., and (2) they frequently do obtain large indirect genetic benefits by helping to rear collateral kin’. With identification of these direct and indirect benefits to helpers, the original questions asked by researchers would appear to be ‘largely answered’.

Despite this claim, some important questions remain unanswered. In particular, our understanding of the varying level of helper contributions within and between species

Cooperative breeding in mammals, birds and fish has provided evolutionary biologists with a rich framework for studying the causes and consequences of group-based reproduction. Helping behaviour is especially enigmatic because it often entails an individual sacrificing personal reproduction while assisting others in their breeding attempts. The decision to help others to reproduce is affected by immediate and future costs analogous to those of direct reproduction, but these components of the equation have usually been neglected. Recent research suggests that the type of benefit sought could determine the extent of help given.

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remains poor. The approach to cooperative breeding has often been to compare the outcomes of philopatry and helping with the other options of dispersing to float or dispersing to breed³. Evaluation of the final reproductive rewards for each strategy leads to an ultimate understanding of why a particular decision was made⁷. Implicit in this approach is that the outcome reflects all the costs and benefits of dispersal versus nondispersal, and helping versus nonhelping, but it does not lead to an appreciation of the nature of each cost and benefit. Although we have a large list of benefits to helping⁸, we still lack a cohesive framework that explains when they apply in various taxa or ecological circumstances. Less attention has been paid to the costs of helping.

Consider the cooperatively breeding Seychelles warbler, *Acrocephalus sechellensis*. In an elegant study, Komdeur⁹ showed that helpers much prefer to feed nestlings that are more closely related to themselves; an important result that emphasized the lability and adaptive nature of helping

Box 1. Social prestige and cheating

A challenging and controversial view proposed by Zahavi^{46,47} suggests that helping has been fundamentally misinterpreted in many cases. Instead of facilitating kin selection or any other indirect or delayed benefit, helpers gain from their investment by increasing their 'social prestige'. In analogous fashion to the handicap principle as it applies to sexual selection (e.g. peacock's tails), helping serves as an honest signal of the individual's ability and, therefore, its quality as a potential collaborator or rival. Integral to this hypothesis is the notion that helping must be costly, otherwise the signal would be unreliable and open to cheating.

Zahavi³⁸ has demonstrated the applicability of this principle to understanding many forms of social interactions in Arabian babblers (*Turdoides squamiceps*), some of which are difficult to interpret using any other paradigm (but see Ref. 48). For example, dominant individuals often hinder the helping efforts of slightly lower ranked individuals but not those ranked a long way below them. This is easily interpreted as an attempt by the dominant to reinforce its social position over those that threaten it most.

That it pays to be seen to help has recently received support from another obligately cooperative bird, the white-winged chough (*Corcorax melanorhamphos*)²¹. The difficulty these birds face in foraging means that one- and two-year old helpers cannot feed nestlings as frequently as older choughs, and it is these younger birds that have recently been caught cheating. In up to 30% of cases, helpers in this age-class will carry food to the nest and even place it in the mouth of a gaping nestling before consuming it themselves. Although always seen by the group flying back to the nest with food, they will only consume it themselves if there is no-one else at the nest to witness their behaviour. Birds that fail to deliver the food in this fashion often proceed to preen the young ostentatiously. Interestingly, when food is supplemented experimentally and costs associated with feeding young dwindle, this 'cheating' behaviour almost disappears. It is clear from these observations that although helping in this species has direct and indirect benefits, such as gaining experience and inclusive fitness^{27,28}, helpers also seek the additional direct benefit of being seen to help. The most likely advantage is in the formation of social coalitions from within the group that form and disperse upon the death of a breeder⁴⁹.



(Online: Fig. 1)

behaviour in this species. Intriguingly, however, the figures presented in his article show that helpers raising full sibs do not work as hard as the parents, even though both parents and helpers would gain the same fitness reward (i.e. $r = 0.5$ in both cases). The Seychelles warbler is one of the few species in which an experimental approach has shown a clear helper effect on productivity¹⁰, leading to the question of why helpers do not help more. Indeed, it could also be asked why helpers do not work as hard or harder to raise half-sibs than full-sibs, because any additional increment in reproductive success could compensate for the lower relatedness. Lower investment in less-related young implies a tradeoff in which costs of care outweigh decreasing benefits. This is analogous to the decrease in parental care observed in males with low confidence of paternity¹¹.

In some species, younger individuals are not as good at providing parental care as older individuals^{12,13}. However, such age-specific ability is not a universal explanation for patterns of help, because helpers can work as hard as, or harder than, the breeders¹⁴. Other species have philopatric individuals that fail to help at all^{15,16}, or that only help if they have the incentive of direct paternity¹⁷. Coercion from parents might also be important¹⁸. Some helpers regularly aid nonrelatives¹⁹, whereas others forgo the opportunity to raise close kin^{20,21}. Together, these observations suggest a huge range of costs and benefits to helping that combine in different measure to determine whether, and by how much, helping should occur.

Helping is energetically expensive

Although philopatry carries obvious costs, such as competition for breeding opportunities²², risk of mortality while waiting for reproductive opportunities²³ and higher risk of incest²⁴, the costs of helping *per se* are not well documented. A physiological cost of helping was first demonstrated in a cooperatively breeding cichlid fish, *Lamprologus brichardi*, by Taborsky²⁵, who showed that helpers grow more slowly than nonterritorial fish. The benefits they receive to offset this cost are the protection from predators afforded by a safe territory, and an increase in the size of the clutch raised by the related individuals they help.

The physiological consequences of helping in birds were first demonstrated by Reyer and his colleagues^{7,26} in the pied kingfisher, *Ceryle rudis*. Helpers in this species are always male and come in two forms. 'Primary' helpers are related to the breeders (e.g. offspring) and are with the breeding pair throughout the nesting period⁷. They remain in nonbreeding condition²⁶ and were shown (through measurement of water turn-over) to work as hard as the breeders to provision the young at the nest¹⁴. In contrast, 'secondary' helpers, which are not related to the breeders, are recruited after the eggs have hatched only if food is in short supply. They do not work nearly as hard as the breeders, and remain in reproductive condition²⁶. Although they do not gain direct reproduction when recruited, they do enhance their future access to the breeding female⁷. This elegant contrast between the two types of strategy demonstrates that only those helpers seeking inclusive fitness will bear both 'psychological castration'²⁶ and the physiological costs associated with high levels of alloparental care.

Helping is also costly in white-winged choughs (*Corcorax melanorhamphos*). Cooperative breeding in this Australian passerine is enforced by a difficult foraging niche that requires large amounts of time to dig for invertebrates in soil and leaf litter. Choughs have a long period of skill development (four years) before reaching sexual maturity, but even fully mature breeders must have at least two helpers to breed successfully^{27,28}. Each additional helper, up to group sizes of 14, means additional food brought to the nest and increased productivity through reduced nestling starvation. When supplementary food is provided at the nest, small groups supply as much food to nestlings as large groups and produce as many fledglings, and one- and two-year old helpers, who are normally most limited by inferior foraging ability, supply as much food to the nest as older birds¹³. Thus, it is the inability or unwillingness to provision at higher rates that normally limits small groups from producing as many (or any) young.

The cost of helping in choughs is only detected when helpers contribute excessively. One-year old helpers contribute to incubation only when group size is small (e.g.

four to six birds) and lose weight in proportion to the amount of time they spend on the nest²⁹. Incubation occurs during the cool months of early spring, and time out from foraging appears to have energetic costs. There is no evidence that they are forced to remain on the nest, so the best interpretation is that these young birds help in this fashion only when their contribution is most needed because of a lack of older helpers (but see Box 1 for a fascinating twist).

The most recent example of an energetic cost to helping comes from a mammal, the suricate *Suricata suricatta*³⁰. In these cooperatively breeding mongooses, nonbreeding adults commonly babysit young pups at the burrow and have to forgo foraging for long periods. The energetic costs of this activity are high: over a 24-hour shift, the average babysitter loses 1.3% of its body weight compared with other group members, which gain 1.9% of their weight in their normal foraging rounds. Over the entire reproductive effort, top babysitters lost on average 3.8% of their body weight, whereas one fifth of the sample lost between 6% and 11%. Babysitting young at the burrow is an essential activity that serves to guard them from avian and terrestrial predators but, interestingly, is never performed by the breeding pair themselves. Like choughs, suricates are very sensitive to group size and modify the extent of their help accordingly. Nonbreeders in smaller groups perform a larger share of the babysitting and are prepared to bear greater costs to achieve the required corporate effort (Fig. 1, Box 2).

These studies demonstrating a cost to helping have three important implications. First, becoming a helper can have profound implications for an individual's life-history, forcing, for example, delayed maturation^{25,26}.

Second, helping is not necessarily automatic. Within species, it is a flexible response set by the needs of the breeders and the costs to the helper^{14,29,30}. Such flexibility is important for demonstrating that the behaviour is actually adaptive^{4,9,29,30} (Box 2). Between species, helpers can contribute as much alloparental care as if they were breeding themselves¹⁴ – less than parents but still enough to increase productivity⁹ – or they might remain philopatric without contributing any help at all^{16,20}. At present, we have no real idea what causes this variability.

Third, although attempts to measure the costs of helping have been rare, in many cases, they might fail anyway because of the natural tendency of helpers to set such 'parent-like' behaviour according to their ability^{12,13,31}. Because recruitment of helpers and expression of help might be based on both needs of breeders and helper ability, measurements of costs and how they set the upper limit to helping behaviour might only be possible through experiments or carefully controlled comparisons. Care of young can also occur in more than one form, leading to a division of labour between the sexes and between various age classes³⁰. The costs and benefits of helping in such complex societies might be difficult to compare using a single currency.

Short- versus long-term costs

Logically, the long-term costs of helping can be analysed in the same fashion as ordinary parental care. Costs include reduced body condition, and reduced future survival and fecundity³². Good data are available from stripe-backed wrens (*Campylorhynchus nuchalis*) – a controlled analysis showed that helpers that provision at high rates have lower survival³³. This shows that the decision to help is likely to have cascading effects throughout the individual's

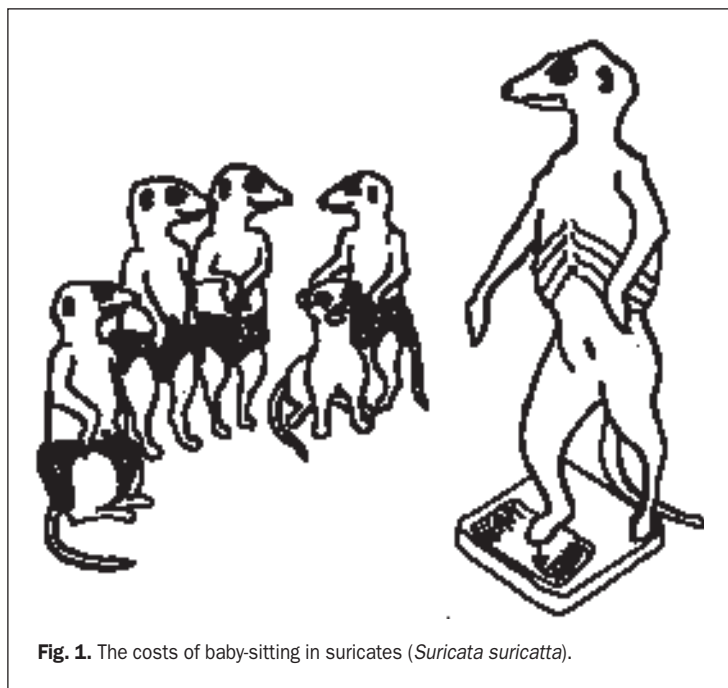


Fig. 1. The costs of baby-sitting in suricates (*Suricata suricatta*).

Box 2. Levels of analysis

Research on helping behaviour has been aimed at finding its adaptive value. However, this adaptationist program was rocked by Jamieson's and Craig's⁴ suggestion that helping behaviour *per se* might not be directly adaptive. Instead, they suggested that helping results from the same stimulus–response link that produces feeding of young by parents. Their explanation was that once a young bird fails to disperse, and accompanies its parents while they breed again, it receives stimuli not normally encountered by nonreproductive individuals. Helping would therefore be an unselected byproduct of the universal feeding response, and hence would not require any further explanation. With this null hypothesis only established belatedly, authors of some studies in which helpers behave similarly to parents might have difficulty in making strong claims about the adaptive value of helping. In other cases, where helping has demonstrable benefits in the present, its origin might still have been nonadaptive.

Jamieson's and Craig's challenge has enforced much needed rigour in interpreting helping behaviour, particularly in the lines of evidence required to refute their argument. These include identifying forms of cooperative behaviour that only helpers perform, showing that helping is a flexible response that varies according to need, and demonstrations that helping is a costly behaviour that cannot be adaptively neutral. The best example of an activity only performed by helpers is babysitting in suricates³⁰, whereas demonstrations of measurable costs and flexibility according to need are given by both suricates (*Suricata suricatta*) and white-winged choughs (*Corcorax melanorhamphos*)²⁹.

lifetime, not just within one breeding season. Thus, all apparent benefits of helping must be discounted by any reduction in future survival or fecundity, with the implication that helping might not always be the best strategy while waiting for a breeding position. Conversely, helpers in stripe-backed wrens and some other species³⁴ stand a high chance of never gaining a breeding position. Consequently, the probability of eventual success could determine the value of working for immediate inclusive fitness.

A confounding explanation for differences in future survival and fecundity is that helpers vary in quality. Those with low chances of independent reproduction might even devote more time or effort to helping. For example, some individuals that help for long periods before breeding themselves have lower success than those that reproduce sooner, and are usually interpreted as being of lower quality^{35,36}. This stands in direct contrast to another demonstration that helping behaviour provides important parenting experience for eventual reproductive efforts¹². Helper

quality and costs incurred through helping are difficult to distinguish as the cause of decreased future fecundity. One way would be to reduce the costs to helpers experimentally¹³, and then monitor their future breeding success compared with individuals who begin breeding without a helping period.

Benefits of helping revisited

The adaptive benefits of helping (as distinct from merely remaining philopatric) have been reviewed thoroughly^{1,3,6,37}, and we do not attempt to re-evaluate them here. For our purposes, we note that the hypothesized benefits fall into two major categories: (1) the enhanced production of non-descendant kin (indirect benefits); and (2) a variety of benefits that increase the chance of survival or direct reproduction, either immediately or in the future (direct benefits). The latter include enhanced social prestige³⁸, the payment of rent in return for enjoying the benefits of philopatry¹⁸, direct access to parentage¹⁷, enhancement of territorial or group quality by increased production of group members³⁹, formation of alliances to aid in competitive situations⁴⁰, and enhancement of skills for later reproduction^{12,27}. Interestingly, only the 'payment of rent' and 'enhanced social prestige' hypotheses explicitly incorporate the idea that helping is costly. The former notes that the actual work involved might not benefit the helper and is only performed to secure a place to stay, whereas the latter explicitly specifies that helping must be costly to achieve the desired effect (Box 1).

Kin selection has played a dominant role in interpreting helping behaviour^{1,6}, even though many studies do not show a positive relationship between the number of helpers and production of young¹⁵. Even when the relationship does exist, it is often difficult to establish whether it is driven by helper contributions rather than territory or breeder quality. Only some experimental studies provide convincing evidence for the former^{10,41}. That help is sometimes withheld from relatives or directed at nonrelatives, combined with the lack of a helper effect, suggests two challenging possibilities for many cooperative breeders: either that helping is selected against even when kin might benefit, or that kin selection is not the driving force for many helpers.

Whereas the costs of helping outlined in this article explain when helping is selected against, a recent review sheds light on the role of kin selection³⁷. Helping behaviour is more common in males, but attempts to explain this sex bias have been lacking. Cockburn³⁷ reviews six hypotheses, but perhaps the most striking aspect of his compilation is a previously unnoticed pattern concerning female help. By using only noncorrelational studies involving comparisons of the same breeders with and without help, or experimental manipulations of helper number or critical resources, he shows that when helping is male-biased, improvements in the productivity of young are usually absent (two out of six studies show a positive effect). Interestingly, the male helpers were not related to the breeders in the two studies that did show a positive effect. However, when helpers are either predominantly female or of both sexes, a positive effect is always found (seven out of seven studies).

These results are based on a relatively small number of studies, but if the trend is confirmed, they have major implications for the study of cooperative breeding. Most important is the possibility that males and females help for different reasons; that is, females are more likely to help for the inclusive fitness benefits of increasing production of young, whereas males help for more direct benefits. In

particular, the higher frequency of male philopatry and inheritance of the natal territory suggests that they stand most to gain from social prestige, paying rent if they have to, enhancing the local territory, or gaining direct parentage. Because male helpers are more common than female ones, this raises the exciting possibility that most cooperative breeding in birds is actually driven by direct benefits to helpers and not inclusive fitness.

If some helpers are motivated by the immediate returns of inclusive fitness, whereas others bank on future reproduction of their own, we might also predict that the former will bear greater costs (e.g. energetic) than the latter. This is particularly true of species in which a large proportion of helpers fail ever to secure a breeding position³³, and immediate inclusive fitness might be their only form of lifetime reproductive success. That helping behaviour, like parental care, must be considered a life-history trait with consequences throughout an individual's life-time has received an important boost in a recent comparative analysis. Arnold and Owens⁴² extended earlier analyses indicating strong taxonomic biases in the distribution of cooperative breeding^{43,44}, to show that the trait is strongly associated with, and might even result from, high longevity. This has the important implication that although habitat saturation might be the proximate cause of philopatry in some species, it is probably low annual mortality that leads to such crowding and lack of space. If a life history trait such as longevity increases the likelihood of cooperative breeding, then patterns of help must be as likely a target for selection over an individual's lifetime as patterns of direct reproduction⁴⁵. Thus, the extent of alloparental care given by the average helper could be as species-specific as parental care itself, and might help explain interspecific differences in this behaviour.

In conclusion, these studies suggest emerging patterns that challenge premature confidence about our understanding of helping behaviour. Although the extent of helping behaviour is known in some species to relate to ability, kinship, coercion or paternity, in most cases the costs and benefits that lead to any particular pattern of helping behaviour remain unclear. The huge variation in the extent of help can be interpreted only by combining knowledge of the type of benefits sought with how the costs of helping limit individuals in the present and future.

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