Animal Behaviour 84 (2012) 1229–1236

Contents lists available at SciVerse ScienceDirect

Animal Behaviour

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

Dominant nestlings displaying female-like melanin coloration behave altruistically in the barn owl

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A R T I C L E I N F O

Article history:
Received 8 May 2012
Initial acceptance 18 June 2012
Final acceptance 21 August 2012
Available online 23 September 2012
MS. number: 12-00348R

Keywords:
altruism
barn owl
cooperation
egoism
food sharing
food stealing
melanin
selfish
sibling competition
Tyto alba

When competing over parental resources, young animals may be typically selfish to the point of siblicide. This suggests that limited parental resources promote the evolution of sibling competition rather than altruistic or cooperative behaviours. In striking contrast, we show here that in 71% of experimental three-chick broods, nestling barn owls, *Tyto alba*, gave food to their siblings on average twice per night. This behaviour prevailed in the first-born dominant nestlings rather than the last-born subordinate nestlings. It was also more prevalent in individuals displaying a heritable dark phaeomelanin-based coloration, a typical female-specific plumage trait (owls vary from dark reddish to white, females being on average darker reddish than males). Stealing food items from siblings, which occurred in 81% of the nests, was more frequent in light than dark phaeomelanic dominant nestlings. We suggest that food sharing has evolved in the barn owl because parents store prey items in their nest that can be used by the offspring to feed their nestmates to derive indirect (kin selection) or direct benefits (pseudoreciprocity or by-product mutualism). The cost of feeding siblings may be relatively low for dominant individuals while the indirect genetic benefits could be high given that extrapair paternity is infrequent in this species. Thus, in situations in which young animals have access to more food resources than they currently need, they can altruistically share them with their siblings.

The evolution of helping where an individual increases the direct fitness of another individual is a fascinating topic. Two categories of evolutionary pathways can account for the emergence of helping behaviour. When individuals gain direct material benefits from helping they are said to behave cooperatively and when they derive indirect genetic benefits the helping behaviour is referred to as altruistic (Lehmann & Keller 2006; Bshary & Bergmüller 2007). The typical situation in which individuals derive indirect fitness benefits is when the genetic benefits of helping related individuals outweigh the cost of helping (Hamilton 1964; Hatchwell 2010). An individual may also help a conspecific (related or not) in the hope that it will reciprocate on another occasion (Trivers 1971); even if reciprocation does not occur the helper may still derive material benefits if increasing the survival of surrounding individuals is beneficial (pseudoreciprocity or by-product mutualism hypotheses, Leimar & Hammerstein 2010). For instance, helping may increase group size, which can decrease the risk of predation (Kokko et al. 2001) or induce parents to provide more food resources at the nest (Kilner et al. 2004). Helping behaviour among family members has been studied in depth in the context of so-called cooperative breeding where mature offspring help raise their parents' new offspring (Clutton-Brock 2002; Bergmüller et al. 2007). In contrast, interactions between siblings still dependent on their parents are considered as conflictual rather than harmonious (Trivers 1974).

Conflicts between siblings take their root in the mismatch between parental food supply and offspring food demand leading to intense sibling competition to monopolize the limited resources. Parents do not provide all the food requested by their offspring because reproductive activities are costly, they face a trade-off between offspring number and quality, and they often produce more offspring than they can rear to independence (Mock & Parker 1997). The evolutionary outcome of limited parental resources is therefore predicted to be sibling rivalry rather than sibling cooperation or altruism. This led biologists interested in the evolutionary implications of parental care to consider Hamilton's rule useful not only to specify the conditions promoting altruism but also the conditions that promote selfish behaviour. This so-called 'inverse Hamilton's rule' states that an allele coding for

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http://dx.doi.org/10.1016/j.anbehav.2012.08.033

selfishness will spread if the benefits of being selfish exceed the costs to the victim multiplied by the coefficient of relatedness between the selfish individual and the victim (Mock & Parker 1997).

In line with the view that interactions between siblings are conflictual rather than harmonious, altricial offspring have only been anecdotally reported to help their siblings obtain parental resources (Marti 1989). Frequent observations of aggressive competition between siblings over parental attention to the point of siblicide suggest that conflicts of interests between young siblings indeed promote the evolution of selfish rather than altruistic or cooperative behaviours (Mock & Parker 1997). Sibling rivalry over parental resources may hamper the evolution of helping relatives if the indirect genetic benefits gained from helping kin are inferior to their costs (West et al. 2002). For instance, dominant offspring may behave more selfishly with their siblings to impose their physical superiority (Drummond et al. 2003). Since altruistic or cooperative interactions between young siblings that are still dependent on their parents appear to be infrequent (with the exception of humans; Kramer 2011), little is known about the factors that could induce helping behaviours among them. As sharing the same family unit is an individual's first social experience, family interactions may have facilitated the evolutionary transition from selfishness to helping, while helping behaviours may reinforce family bonds (von Bayern et al. 2007).

Sharing parental food resources with siblings may occur in species in which parents store food in their nest. If some individuals have privileged access to stored resources and are unable to utilize all of them, they may be selected to share them with hungry siblings that have less access to these resources. Such helping behaviour can evolve if individuals that help their siblings obtain parental resources derive direct or indirect fitness benefits (Lehmann & Keller 2006; Bshary & Bergmüller 2007; West et al. 2007). Reciprocity would be the most likely type of direct benefits. An individual may share food with a sibling in expectation of a future return from it that will compensate for the costs of the initial cooperative investment (e.g. Wilkinson 1992). In other words, a helper individual shares surplus parental resources with their hungry siblings in the hope that they will reciprocate once the helper is hungry. Another category of direct benefits, so-called pseudoreciprocity or by-product mutualism, is if, by feeding siblings, helper offspring release their parents from spending time distributing food among the progeny, which would allow them to invest more time in foraging and increase the total amount of food brought to the progeny. Alternatively, helping siblings may enhance their survival and thereby reduce the helper's risk of being killed by a predator or increase the total begging solicitation levels produced by progeny to stimulate parents to come back rapidly with food. Indirect genetic benefits may occur through kin selection, if the costs entailed by food sharing are compensated for by the increased survival of related individuals.

Species such as raptors, in which food is often stored in the nest (e.g. Korpimäki 1987; Bakaloudis et al. 2012), are prime candidates to examine the evolution of helping behaviour between young siblings that are still dependent on their parents. We performed a study in the barn owl, *Tyto alba*, in which sharing food between siblings has been observed in both Europe (Epple 1979; Bühler 1981; Kniprath & Stier-Kniprath 2010) and North America (Marti 1989). Parents usually bring prey items more rapidly than their offspring can consume them (Baudvin 1980; Roulin 2001, 2004a). If food-satiated nestlings do not relinquish the accumulated prey remains, they can defend access to the prey for later consumption, for instance, by sitting on them to reduce the risk of being robbed, which is relatively frequent in barn owls (Roulin et al. 2008a). Alternatively, nestlings may feed their siblings if the latter did not notice the presence of surplus prey remains in their dark nest. The barn owl is particularly interesting also because pronounced hatching asynchrony gives an edge to the first-born individuals, which have easier access to parental food resources than later-born siblings. The 2–10 eggs hatch on average every 2–3 days, which generates a pronounced age and size hierarchy between siblings. The first-born dominant individuals may face a choice between monopolizing stored food for later consumption or feeding their subordinate siblings. Furthermore, barn owl plumage varies strongly from dark reddish (phaeomelanic) to white (nonphaeomelanic) and from immaculate (noneumelanic) to heavily marked with large black spots (eumelanic), traits for which the expression is under strong genetic control and not, or weakly, sensitive to environmental factors (Roulin & Dijkstra 2003). Appetite is higher in lightly eumelanic and darker phaeomelanic individuals (Dreiss et al. 2010a), and darker phaeomelanic individuals increase their body mass more rapidly than lighter coloured ones when food is available in large quantities (Roulin et al. 2008b). Plumage traits might thus advertise the propensity to share food with siblings.

We examined whether barn owl nestlings are more likely to derive direct or indirect fitness benefits by sharing food with siblings. Under the reciprocity hypothesis, helpers share food with their siblings in the hope that they will reciprocate at a later time. If this is the case, we predicted that an individual that received a food item from a sibling would feed it on another occasion. Alternatively, dominant nestlings may feed their younger siblings to release their parents from taking care of offspring that still need assistance in the nest, thereby inducing their parents to spend more time foraging. In this case, we expected parental feeding rate to be higher in broods in which food sharing occurred. Because higher parental feeding rates will be more beneficial to hungry than satiated individuals, we also predicted food sharing would prevail mainly in nests in which nestlings were in poorer condition. Under the kin selection hypothesis (but also the pseudoreciprocity and by-product mutualism hypotheses), we expected that food sharing would be expressed by individuals for which the costs of being generous were low while the potential benefits were high. Thus, in contrast to the reciprocity hypothesis, only nestlings with privileged access to food resources would share them with the siblings that were so needy that they were unlikely to reciprocate at a later time. In the barn owl, since the first-born nestlings (so-called seniors) are better able to obtain food than their younger siblings (i.e. juniors; Roulin 2004b), sharing food with siblings should be less costly for seniors while the benefit of being fed by nestmates should be greater for juniors. Therefore, if nestling barn owls share food with siblings because they derive indirect genetic benefits (or direct benefits as predicted by the pseudoreciprocity and by-product mutualism hypotheses), we predicted that seniors would feed their junior siblings more frequently than the opposite.

To test these predictions, we recorded interactions between nestlings in the field in experimentally reduced broods of three individuals: a senior, a junior and a middle-born sibling. Observations were carried out for one night from 1900 to 0700 hours the following morning. Since short-term experimental brood reduction does not alter parental feeding rate (Roulin et al. 2000), our design ensured that food was available in large enough quantities to induce food sharing. Therefore, intrinsically altruistic individuals were expected to have the opportunity to feed siblings with prey items that accumulated in the nest. Since barn owl nestlings frequently steal food from each other (Roulin et al. 2008a), we also investigated whether the degree of generosity (i.e. food sharing) was inversely related to the degree of selfishness (i.e. food stealing).