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REVIEW

Is there empirical evidence for the cost of begging?

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Abstract Offspring should demand more food than the optimal amount for the parents to bring (parent–offspring conflict), and models on the evolution of parent–offspring communication suggest that an equilibrium is reached when the costs associated with begging make it unprofitable for the offspring to increase its level of begging. Empirical evidence for this cost, however, is mixed, and the conclusions of most of authors are that begging is inexpensive. In this study, the existing empirical evidence for this cost is reviewed. One cost proposed is the attraction of predators due to begging calls, but empirical support for this cost is low. However, studies performed cannot dismiss such a cost. Another possible cost is the metabolic expenditure, but empirical evidence for this cost is mixed, with some works contending that it is low, while others deem it important. Other possible metabolic costs have not been studied. A loss of inclusive fitness may be an important cost for the evolution of begging, and robust empirical evidence does exist for this cost. Costs associated with brood reduction also are reviewed. In conclusion, there is not enough empirical evidence to test the models on the evolution of begging. Most costs proposed have not yet been studied or the approach used has been insufficient to reject the null hypothesis (i.e., absence of cost).

Keywords Parent–offspring conflict · Begging behavior · Begging costs · Kin selection · Brood reduction · Experimental design

Introduction

Parent–offspring communication has evolved in species with parental care in which the offspring demands food and other care from their parents (Jensen et al. 1998; Rauter and Moore 1999; Budden and Wright 2001). The parents allocate food within the brood and determine the quantity of food they should bring to the brood, in part according to the begging behavior of offspring, which is composed of calls as well as non-signaling components such as wing flapping or neck stretching (Redondo and Castro 1992a; Kilner and Johnstone 1997). However, because each individual offspring has a relationship with itself of 1, while it has a relationship with the parents and siblings of 0.5 or less, natural selection encourages offspring to demand a greater share of resources than is optimal for the parents to provide (the parent–offspring conflict; Trivers 1974; Lazarus and Inglis 1986). In fact, offspring might use begging to blackmail parents for extra food (Eshel and Feldman 1991; Zahavi and Zahavi, 1997). According to this scenario, many different models have been performed in order to explain the evolution of begging (Stamps et al. 1978; Macnair and Parker 1979; Harper 1986; Eshel and Feldman 1991; Godfray 1991, 1995a, b; Kilner and Johnstone 1997; Mock and Parker 1997; Rodríguez-Gironés et al. 2001b; Parker et al. 2002a; Price et al. 2002). Although models vary on some key questions (Royle et al. 2002), almost all the models assume that begging is costly, and

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the system is stable where benefits of begging for the offspring equalize begging costs. In other words, the higher the level of begging of one offspring, the higher the food quantity that offspring receives, increasing its fitness. Nevertheless, as the level of begging increases, the higher are the costs of begging, reducing the fitness of the offspring. The models predict an equilibrium in the begging level, where the offspring do not beg more loudly because the costs associated with begging would be greater than the benefits (reviews in Godfray 1995a; Mock and Parker 1997; Wright and Leonard 2002).

Therefore, knowing the costs associated with the begging behavior is fundamental for understanding its evolution. Birds are the primary empirical model used to study this issue. Begging chicks emit loud calls while making conspicuous body movements (Redondo and Castro 1992a; Price et al. 1996; Kilner et al. 1999). Movements and calls are assumed to be energetically costly, implying that one cost of begging would be energetic. Moreover, begging calls may attract predators to the nest, by which another cost of begging may be the attraction of a predator. Since the formulation of the model by Godfray (1991), many empirical studies have been performed to detect such costs. Conclusions from these studies are generally that the begging cost is low (Roulin 2001a; Chappell and Bachman 2002; Haskell 2002; Wells 2003), and, as an alternative, new models have examined the evolution of a cheap or cost-free begging (Bergstrom and Lachmann 1997, 1998; Lachmann and Bergstrom 1998; Brilot and Johnstone 2003). Therefore, what models are correct depend on the existence of begging costs. In the present paper, I discuss the evidence contributed by these empirical works to the cost of begging.

The cost of predation

When nestlings are hungry, they emit loud calls, which may attract predators. As begging calls become louder, the feeding rate by parents becomes higher (Clark and Lee 1998; Price 1998; Kilner et al. 1999). If the predation risk increases with the level of begging calls, at a certain point the probability of predation outweighs the benefits of louder begging.

Experimental studies on this issue compare the predation rate on empty nests playing begging calls from a playback with control nests without begging calls. With this method, Haskell (1994) and Leech and Leonard (1997) correlated a predation cost with begging for the Western bluebirds (*Sialia mexicana*) and the tree swallows (*Tachycineta bicolor*), respectively. However, both species are hole-nesting, and the cost of their begging was tested in open nests. An adaptation of nestlings against predation may be to modify the begging-call structure to minimize the attraction of predators, and the begging calls of hole-nesting birds (which have a lower predation risk) are easier to locate than those of species that nest in open nests, which are more cryptic (Redondo and Arias de Reyna 1988). Similarly, the species of Parulidae that nest on the ground have begging calls that are harder to detect than those of the species that nest in trees (Haskell 1999), and when the predation rate is higher, the begging calls of the chicks are more difficult to locate (Briskie et al. 1999). Therefore, these experiments did not demonstrate a predation cost, but showed that a cost would exist if those species nested in open nests. In accordance with this idea, Haskell (1999) experimentally showed that when a species nesting on the ground emits begging calls resembling those of species nesting in the trees, the predation risk becomes higher. With the same method, there is not evidence of a predation cost for the indigo bunting (*Passerina cyanea*) (Dearborn 1999), the black-throated blue warbler (*Dendroica caerulescens*) and the ovenbird (*Seiurus aurocapillus*) (Haskell 1999), all open-nesting species.

Moreover, it should be taken into account that these experimental studies removed the possible effect on predation exerted by the defensive behavior of parents and chicks, whatever increases the predation rate (Markman et al. 1995). When a predator is present, parent birds emit alarm calls, and nestlings respond with defensive behavior, such as to cease begging (Nuechterlein 1988; Kleindorfer et al. 1996; Platzen and Magrath 2004). For example, detectability, height and size of blackbird (*Turdus merula*) nests did not affect the probability of being depredated when the parents were present, but did when they were absent (Møller 1990; Cresswell 1997b). Therefore, parents may compensate with their behavior for the higher risk of predation, and, in louder nests, parents may use strategies to diminish the predation risk, but this has not been directly addressed. Chicks, on the other hand, may frighten predators by screaming when they are caught, reducing the risk of predation (Roulin 2001b).

Furthermore, the level of begging positively affects the feeding rate by the parents, and hence the activity at the nest (Ottoson et al. 1997; Clark and Lee 1998; Price 1998). An augment in the parental activity at the nest may attract predators, increasing the predation risk (Martin et al. 2000). Experimental studies have assumed that only begging calls may attract predators, but other begging behavior may attract predators by increasing the parental activity. For example, visual components of begging also increase the feeding rate by parents (Götmark and Ahlström 1997; Kilner 1997; Kilner et al. 1999), and, consequently, they may increase the probability of predation. Both parental and chick activity, therefore, should be considered in studies on the predation cost associated with begging, because it may increase as well as diminish the risk of predation.

Descriptive studies also fail to give support for the predation cost of begging. Many works have found no differences in the probability of predation between the stages of eggs (silent nests) and nestlings (audible nests) (Cresswell 1997a; Roper and Goldstein 1997; Dearborn 1999). Nevertheless, because they were correlational studies, alternative interpretations are possible; for example, differences in the density of potential predators correlated with the nesting cycle may offset the attraction of predators by nestlings. Nests of the black-billed magpie (*Pica pica*) with more chicks begging (louder nests) have more probabilities of being depredated (Redondo and Castro 1992b). Nonetheless, in broods where more nestlings begged, the brood had more need of food, implying poorer parental quality. Parents of bad quality might have placed their nests in suboptimal sites, where nests were easily localized by predators (Martin et al. 2000), or they might have been less competent to defend the nests against predators (Reyer et al. 1998; Álvarez 2000). In a similar study with meadow pipits (*Anthus pratensis*), louder nests (where nestlings were hungrier) were not more depredated than quiet nests (Halupka 1998). This result may be due to defensive behavior by the parents.

In short, according to results in these works, there is no solid evidence that begging increases the risk of predation (Haskell 2002), but there is no hard evidence, either, that begging does not increase such risk. New approaches considering the defensive behavior by parents and chicks are necessary to resolve this issue.

The metabolic cost of begging

Another important cost that could limit the evolutionary scaling of the begging level is the energy expenditure. Begging behavior implies a scramble for the best position in the nest, with many movements (neck extension, wing flapping, etc.) and powerful calls, all of which are apparently energetically costly. Moreover, movements as well as calls by nestlings increase with the level of begging (Redondo and Castro 1992a). Therefore, it is predictable that the energy cost increases with the level of begging. The evolutionary equilibrium would be reached when the energy spent in begging balances the energy received in food.

Many workers have measured the aerobic cost (oxygen consumption) of begging, comparing it with resting consumption. McCarty (1996) reported an energy-expenditure ratio (ratio between begging and resting consumption) of about one for seven bird species, with the highest ratio for the tree swallow (1.27). This energy expenditure increased with the begging-call intensity and with the time employed in begging (McCarty 1996). However, this expenditure appears to be minor compared with the energy spent in other activities (Table 2 in McCarty 1996). Leech and Leonard (1996) reported practically the same results as McCarty for the tree swallow. These authors concluded that the begging cost was low in comparison with the energy obtained by nestlings through the day, but, in conditions of bad climatology, this expenditure might be an important share of the daily energy budget.

Bachman and Chappell (1998) found that the begging expenditure of house wren (*Troglodytes aedon*) nestlings in the field was 27% higher than when they rested. However, begging involved only a 0.02–0.25% of the energy budget, and only a 0.05–2.30% of energy employed in growth. In fact, house wren chicks can invest more energy in begging, but usually they do not (Chappell and Bachman 1998). The limit in the begging level, therefore, appears to be behavioral instead of physiological. Chicks of the black-billed magpie and of the great spotted cuckoo (*Clamator glandarius*) that were stimulated to beg fiercely did not register a higher metabolic expenditure than nestlings that did not beg (Soler et al. 1999). Schleich and Busch (2004) did not find a significant increase in the oxygen consumption when pups of the rodent *Ctenomys talarum* called compared with the resting metabolic consumption. Abraham and Evans (1999) studied the cost of begging for heat in embryos of the American white pelican (*Pelecanus erythrorhynchus*). These authors found high costs (between 1.2 and 2.0 times the energy spent by silent embryos), and commented that, because food quantity is fixed in the egg, these costs might be very important for the fitness of embryos.

Therefore, findings of different studies are similar, independently of the technique used, with a metabolic expenditure usually less than a 30% of the base expenditure, but some authors consider these costs too low to explain the models on the resolution of the parent–offspring conflict, while the interpretation is different for others. Other costs related to metabolism have been proposed, but not studied. The main energy cost of begging could be anaerobic instead of aerobic (Weathers et al. 1997), but the subsequent metabolism of the lactic acid would provoke oxygen consumption, which was not detected by Bachman and Chappell (1998), suggesting that there is not a significant anaerobic expenditure. However, more formal analyses of this hypothesis are necessary. Nestlings might incur an immunological cost as a consequence of their state of alertness to be the first to beg at the parental arrival (Roulin 2001a). Begging may be costly because it reduces the time available to sleep (Roulin 2001a; Wells 2003). A possible cost associated with condition-dependent sexual signals may be an increase in oxidative free radicals (Von Schantz et al. 1999). Similarly, begging signals by the offspring might increase the oxidative stress, reducing nestling fitness, but this possibility has not been tested, either.

Although the energy expenditure is low, its interpretation in evolutionary terms is complex. Low energy expenditure may have important effects on fitness. For this reason, more direct measurements of the metabolic cost of begging, in terms of residual fitness, are needed to evaluate the importance of this cost (Verhulst and Wiersma 1997; Kilner 2001). Energy spent in begging cannot be invested in growth, and nestling fitness is closely related to their size at fledging (Martin 1987). For these reasons, measuring the effect of begging on growth is more informative than quantifying the energy expenditure of begging. Canary (*Serinus canaria*) and black-billed magpie nestlings grew more slowly when they were forced to beg at high rates than when they begged at normal rates (Kilner 2001; Rodríguez-Gironés et al. 2001a). However, the same experiment did not find any effect of begging on the growth rate in the house sparrow (*Passer domesticus*; Kedar et al. 2000), the ring dove (*Streptopelia risoria*; Rodríguez-Gironés et al. 2001a) or the tree swallow (Leonard et al. 2003). In fact, within the four passeriformes studied, the two where a begging cost in growth has not been detected (house sparrow and tree swallow) are species that nest in holes, while those where a cost of growth has been detected (magpie and canary) do not. Nestlings of hole-nesting species compete strongly for the access to the nest entrance, because the nestling in that position has the highest probabilities of being fed (Kacelnik et al. 1995). For this reason, when the nestlings with the highest size acquire access to the nest entrance, they reduce their level of begging (Cotton et al. 1999). In the aforementioned studies on the growth cost of begging, experimental design in the laboratory might have encouraged chicks in these hole-nesting species to invest less energy in begging compared with open-nesting species.

On the other hand, to ascertain whether or not the energy cost of begging is sufficient to explain the models, the benefits of increased begging (food received) need to be compared to the costs. The studies performed to date have measured only the cost of increased begging, but not its benefit. Only when the benefit of extra begging is compared with the growth cost can it be confirmed whether or not an energy cost is limiting an evolutionary increase in the level of begging. Martín-Gálvez (2006) provided cyproheptadine (a chemical that stimulates hunger in chicks, without side effects) to magpie nestlings, with control nestlings provided with water. This treatment increased the level of begging of the manipulated nestlings, increasing the food received, at the same time that it also increased the cost of begging. The result was that, although experimental chicks loss more mass, at the end of development they were in better condition than control nestlings. As far as I know, this is the only study showing that the benefits of increased begging are higher than the begging costs, and therefore, that begging seems cheap. The authors proposed that magpie chicks do not beg more intensely because they incur a loss of inclusive fitness.

The cost of inclusive fitness

The family is usually viewed as an entity where conflicts are frequent (Parker et al. 2002b). Nestlings must compete for food and must attempt to induce their parents to deliver more food (Mock and Parker 1997). However, siblings have a genetic relationship among themselves and with their parents. Therefore, some cooperation among chicks is also predictable (Hamilton 1964; Wilson and Clark 2002). The siblings may negotiate together, indicating their need to their nestmates, and reaching an ‘‘agreement’’ on which nestling should take the food, thereby minimizing the cost of begging (Johnstone and Roulin 2003), and this has been found in the barn owl (*Tyto alba*; Roulin et al. 2000). In some species (e.g., budgerigards, *Melopsittacus undulatus*, Stamps et al. 1985) nestlings feed their needier siblings. Therefore, because family members have a genetic relationship, a cost in inclusive fitness may be associated with begging (McCarty 1997), and theory predicts that as the relationship among family members is higher, the optimal level of begging should be lower, and therefore its costs (e.g., Godfray 1995b; Johnstone 1999; Nöldeke and Samuelson 1999; Price et al. 2002; Johnstone and Roulin 2003). When a chick begs for food at a certain level, it directly increases its own fitness, but, at the same time, it reduces its inclusive fitness, because the food received by this chick is not consumed by the siblings, and the parental foraging behavior reduces the future reproduction of the parents (Stearns 1992). This might explain why Chappell and Bachman (1998) found that house wren nestlings usually beg for food at a level below their physiological limit.

Empirical data do support the contention that the inclusive fitness cost of begging may be an important factor in its evolution. As the percentage of extra pair young (EPY) in a nest is higher, the genetic relationship within the family is lower, and, therefore, higher levels of begging are predictable in species with higher levels of EPY (Godfray 1995b; Reeve 1997; Price et al. 2002). Indeed, the higher the EPY rate is, the louder the begging calls (Briskie et al. 1994), and the redder the mouthes of the chicks (Kilner 1999) (the red color in the mouth increases the probability of being fed, e.g., Kilner 1997).

Another prediction is that brood parasites, which have no relationship with the adults that feed them, should beg for food with higher levels than host chicks. In fact, this has been found in various brood parasites [the brown-headed cowbird (*Molothrus ater*): (Dearborn 1998; Lichtenstein and Sealy 1998; Lichtenstein 2001); the common cuckoo (*Cuculus canorus*): Kilner et al. 1999; the great spotted cuckoo: Soler et al. 1999; Redondo and Zúñiga 2002]. However, brood parasites may beg louder than hosts due to their bigger size (Kilner and Davies 1999) or to manipulate hosts (Redondo 1993).

Costs associated with brood reduction

Brood reduction, frequent in birds and other taxa, may be provoked when a chick monopolizes a large share of the food delivered by the parents to the brood (Mock and Parker 1997). Eliminating directly or indirectly one competitor, the winning chick should gain a higher share of food from its parent, and, therefore, it would be benefited (Parker et al. 1989). However, the surviving chick may incur costs associated with the loss of a nestmate (reviewed in Wilson and Clark 2002).

First, thermoregulation is easier when there are many nestlings in the nest (Dunn 1976, 1979), and when brood reduction occurs, nestlings have to invest more energy in thermoregulation at the expense of growth. In some species, siblings continue together after fledging, increasing their social and foraging skills (Edwards 1989), and the loss of siblings might be costly in the future. The loss of a nestmate might increase the probability of becoming the prey in a partial predation event (Wilson and Clark 2002). According to the tasty-chick hypothesis (Christe et al. 1996), runt nestlings have a poorer immune system, and are therefore preferentially attacked by nest parasites with respect to their siblings, thus reducing the parasitic load of their siblings. If this is correct, brood reduction, by increasing the parasitic load of the surviving chicks would present a disadvantage for these chicks.

Furthermore, the assumption that brood reduction allows the surviving chicks to attain more food may be challenged (Drummond 2001). The food delivered by parents to the brood depends on the begging level of the whole brood (Kilner et al. 1999), but bigger chicks may take a higher share of food (Smiseth et al. 1998; Cotton et al. 1999; Ostreiher 2001). Hence, bigger nestlings may be benefited by the begging behavior of their siblings (Forbes 1993), and they might reduce their begging in order to allow the survival of their small siblings. Experimentally simulated brood reduction in nests with three chicks in the brown pelican (*Pelecanus occidentalis*) provoked a reduction in the quantity of food delivered to the brood, and, as a consequence, the second chicks in the size rank received a lower quantity of food than in control nests where brood reduction did not occur (Ploger 1997). Brood reduction did not pay off for these chicks. These costs of brood reduction would select against brood reduction, and a form to avoid brood reduction would be to reduce the level of begging. Mathematical models predict that nestlings should collaborate in begging signals that affect food delivery (Johnstone 2004), and, effectively, black-headed gull (*Larus ridibundus*) chicks coordinate their begging to increase the parental investment (Mathevon and Charrier 2004).

Moreover, if begging attracts predators, the predation cost may affect the complete brood, being a shared cost (Mock and Parker 1997). Therefore, it would be profitable for all nestlings that none of the nest-mates are hungry.

Other costs of begging

Other cost of begging may be punishment by parents toward chicks begging louder, which has been described in some species (e.g., the black-capped chickadee, *Parus atricapillus*, Leonard et al. 1991). Because begging nestlings strongly jostle for better positions in the nest (McRae et al. 1993), they also incur a risk of falling out of the nest (Bize and Roulin 2006).

Final considerations

The models on the evolution of begging conclude that escalated begging becomes evolutionarily stable as a consequence of the costs of begging. Two main costs have been proposed: the risk of predation and energy expenditure. Previous reviews (Chappell and Bachman 2002; Haskell 2002; Roulin 2001a; Wells 2003) have concluded that these costs are too low to explain the resolution of this parent–offspring conflict proposed by models. However, in the light of this review, there is not sufficient evidence either in favor of or against the costs usually proposed. A predation cost appears to have existed in the past and to have affected the structure of begging calls (Redondo and Arias de Reyna 1988; Briskie et al. 1999; Haskell 1999). Did predation risk also affect the level of begging? Probably the answer is yes, but no study has provided adequate evidence on this issue. The energy cost exists, although it is low. The question is whether it is sufficiently high to explain the resolution of the parent–offspring conflict. Some studies have concluded that it is (Leech and Leonard 1996; Furlow 1997; Abrahams and Evans 1999; Kilner 2001; Rodríguez-Gironés et al. 2001a; Wells 2003), while others have concluded that the energy expenditure is probably too low to limit the begging level (McCarty 1996; Bachman and Chappell 1998; Chappell and Bachman 1998; Soler et al. 1999; Leonard et al. 2003). But only one study (Martín-Gálvez 2006) has analyzed simultaneously the costs and the benefits of begging, concluding that the cost is lower than the benefits. A number of other possible costs reviewed here have not been studied. A primary question is the relative importance of these costs with respect to the cost of inclusive fitness. Although competition among relatives may cause them not to cooperate (West et al. 2002), this cost seems to exist, as suggested by comparative studies (Briskie et al. 1994; Kilner 1999). In reality, there is robust empirical evidence only for this cost. The main conclusion in this work is that the data available are insufficient to reach a conclusion on the correctness of the models developed on this issue, and new, more ambitious empirical approaches are necessary to understand the evolution of begging and the resolution of this parent–offspring conflict.

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