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An immunological cost of begging in house sparrow nestlings

Gregorio Moreno-Rueda^{*,†}

Konrad Lorenz Institut für Vergleichende Verhaltensforschung, Österreichische Akademie der Wissenschaften,
Savoyenstrasse 1a, 1160 Wien, Austria

Parent–offspring conflict predicts that offspring should demand a greater parental investment than is optimal for their parents to deliver. This would escalate the level of offspring demand *ad infinitum*, but most of the models on the evolution of parent–offspring communication predict that begging must be costly, such costs limiting the escalation and defining an optimal level of begging. However, empirical evidence on this issue is mixed. A potential begging cost that remains to be accurately explored is a decrease in immunocompetence for offspring begging fiercely. This study experimentally analyses this cost in house sparrow (*Passer domesticus*) nestlings. A group of nestlings was forced to beg fiercely for a prolonged time while a control group begged at low levels, both groups receiving the same quantity of food. At the same time, the nestling response to an antigen (phytohaemagglutinin) was measured. Nestlings forced to beg fiercely showed a reduction in immunocompetence with respect to control chicks, but the two groups showed no difference in growth rate. The largest and the smallest nestlings in each brood showed a similar response to the treatment. These results strongly suggest a trade-off between begging and immunocompetence in this species. This trade-off may be a consequence either of resources from the immune system being reallocated to begging behaviour, or of adaptive immunosuppression in order to avoid oxidative stress. Steroid hormones are proposed as mediators of such a trade-off.

Keywords: growth costs; honest signalling; parent–offspring conflict; sibling competition; trade-offs

1. INTRODUCTION

The parent–offspring conflict determines that, given the genetic differences between siblings, and between parents and their offspring, each offspring will demand a greater parental investment than is optimal for their parents to deliver, elevating the level of offspring begging signals in species with parent–offspring communication (Trivers 1974; Lazarus & Inglis 1986; Clutton-Brock 1991; Mock & Parker 1997). This conflict may be resolved if offspring begging is costly, and thus there would be an optimal begging level for each offspring (according to its state) in which costs balance benefits (reviewed in Kilner & Johnstone 1997; Mock & Parker 1997; Godfray & Johnstone 2000; Johnstone & Godfray 2002; Harper & Maynard Smith 2003; Wells 2003). Such costs are therefore necessary for the stability of begging, according to these models, independent of whether begging is used in the honest communication of need or in sibling competition (Royle *et al.* 2002).

However, empirical evidence for the existence of begging costs is mixed (Roulin 2001; Wright & Leonard 2002; Moreno-Rueda 2007). It has been proposed that begging signals, by attracting predators, may increase the risk of predation, which would limit begging escalation; but evidence for such a cost is unclear (Haskell 2002; Moreno-Rueda 2007). Given that begging usually

implies conspicuous movements and loud calls (e.g. Redondo & Castro 1992), it is assumed to be energetically costly. However, estimations of the energetic expenditure have proved difficult to interpret (Moreno-Rueda 2007). A trade-off between begging and growth has been shown in two bird species (canary, *Serinus canaria*, Kilner 2001; magpie, *Pica pica*, Rodríguez-Gironés *et al.* 2001). These studies suggest that energy allotted to begging is diverted from energy allocated for growth, implying fitness consequences, given that size at fledging frequently influences survival in birds (Ringsby *et al.* 1998; Schwagmeyer & Mock 2008). However, no growth cost associated with begging has been found in three other bird species (house sparrow, *Passer domesticus*, Kedar *et al.* 2000; ring dove, *Streptopelia risoria*, Rodríguez-Gironés *et al.* 2001; tree swallow, *Tachycineta bicolor*, Leonard *et al.* 2003), nor in a burying beetle (*Nicrophorus vespilloides*, Smiseth & Parker 2008).

Such inconsistencies in results have led some researchers to suggest that the physiological costs of begging are relatively low (Chappell & Bachman 2002; Wells 2003; Searcy & Nowicki 2005), and the aforementioned models therefore lack support. Later models predicted relatively cheap begging (Bergstrom & Lachmann 1997, 1998), but cheap begging is probably uninformative with respect to offspring need (Brilot & Johnstone 2002). To ascertain the cost of begging is a central pillar in order to identify which models most accurately describe the resolution of the parent–offspring conflict. At this point, to claim that begging cost is relatively low is premature, as many types of costs have not yet been tested (Moreno-Rueda 2007). In fact, a possible

*gmr@ugr.es

†Present address: Estación Experimental de Zonas Áridas (CSIC), La Cañada de San Urbano, Ctra. Sacramento s/n, 04120 Almería, Spain.

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explanation for the contrasting results for the trade-off between begging and growth is that, in some species (such as the house sparrow), resources used in begging may be diverted from resource-demanding functions other than growth.

A good candidate might be the immune system (Roulin 2001; Goodship & Buchanan 2007; Moreno-Rueda 2007; Loiseau *et al.* 2008; Ros 2008). The immune system is costly (Lochmiller & Deerenberg 2000; Schmid-Hempel 2003; Ardia & Schat 2008), and it has been shown that it may take resources from other costly functions (Sheldon & Verhulst 1996; Norris & Evans 2000; Zuk & Stoehr 2002). In fact, several studies have shown a trade-off between offspring growth and the function of the immune system (Fair *et al.* 1999; Soler *et al.* 2003; Brommer 2004; Mauck *et al.* 2005). Therefore, there could be a three-way trade-off among begging, growth and the immune system, some species re-allocating resources for begging signals from growth while others re-allocate resources from the immune system.

Here, I test whether begging signals entail a cost in the form of lower immunocompetence. Given that less immunocompetent animals have a higher mortality risk (Møller & Saino 2004), there would be an optimal begging level, the marginal benefit of increased begging (more food delivered by parents) being balanced by an increase in mortality risk related to decreased immunocompetence. I empirically test this hypothesis with a species in which a growth cost has been looked for and not demonstrated: the house sparrow (Kedar *et al.* 2000), using similar methodologies to previous studies (Kilner 2001; Rodríguez-Gironés *et al.* 2001; Leonard *et al.* 2003).

2. MATERIAL AND METHODS

The study was carried out in 2009 with house sparrow nestlings from 22 pairs breeding in captivity in an outdoor aviary in Moraleda de Zafayona (SE Spain). The birds were supplied with dipteran larvae for feeding the nestlings (Moreno-Rueda & Soler 2002). From each nest, I removed the largest and the smallest nestlings (brood sizes: 2–4, mean = 3 ± 0.87 (s.d.)), when they were 5 days old (0 = hatching), and I placed them in an adjacent laboratory. At least one nestling (alien when brood size was 2) was consistently left in the nest to avoid desertion. In an alternate routine, each brood was assigned to a high-begging (HB) or a low-begging (LB) treatment, the biggest and the smallest chicks in each brood receiving the same treatment. The experimental trials lasted 6 h, beginning at 08.15 (local time, ± 15 min) and ending at about 14.15. Nestlings were then returned to their nests. The experiment had no negative effects on nestlings, and none died during the experiment or the days after. During the experiment, nestlings were maintained at 28–32°C (peripheral temperature) in a cup simulating a nest. Nestlings were weighed with an electronic balance (accuracy of 0.01 g) at the start and the end of the trial, and I estimated the mass gained (M_G) during the trial as final mass minus initial mass, as well as relative mass gain as a percentage of initial mass. I fed the nestlings each 30 min with a dipteran larva, the same food as they received in the aviary. The average mass of a larva was 0.087 g, and each nestling received 12 larvae during the trial (i.e. all nestlings were fed with 1.044 g during the

complete trial). In this way, all nestlings received the same quantity of food (M_I). I also weighed the faeces excreted by the chicks (M_F). Mass ingested by the nestlings during the trials (M_I , which was constant) could be excreted (M_F), used in growth (M_G), or expended in other metabolic activities implied in self-maintenance, begging or immune response (M_M). Therefore, I estimated the metabolic expenditure as $M_M = M_I - M_G - M_F$ (Kilner 2001; Leonard *et al.* 2003).

In the HB treatment, every 10 min I stimulated begging for 60 s by using three different stimuli: acoustic (a characteristic and standardized whistle), tactile (gently touching their gapes with a forceps) and visual (blocking the light of a lamp). All these stimuli successfully elicited begging in nestlings. Thus, nestlings in the HB treatment begged for a total of 2160 s. Each 30 min, the stimulation coincided with feeding, and then the nestling was fed at the end of the 60 s of begging. In the LB group, nestlings begged only when they were fed, and always for less than 5 s. Nestlings showed no begging in the absence of stimulus. Thus, the LB nestlings begged for a total of less than 90 s during the complete trial. In the aviary, parents visited the nests each 2–6 min (average: 3 min; $n = 8$ broods 4–6 days old), and therefore nestlings were probably stimulated to beg more frequently than in my HB treatment (10 min). In the aviary, each nestling was fed approximately every 10–40 min (average: 20 min). Therefore, the rhythm at which I fed the nestlings (30 min) was similar to that used by their parents in the aviary. This regularity of stimulation and feeding matches that used in other studies with this species (Grodzinski *et al.* 2009).

To test the effect of begging on the immune response, immediately before the start of the trials I injected, in the left patagium of the chicks, 0.1 mg of phytohaemagglutinin (PHA-P; Sigma Aldrich, L-8754) diluted in 0.02 ml of isotonic phosphate buffer (following Smits *et al.* 1999). PHA-P is an innocuous protein that provokes an immune response in birds mediated by T-cells (Kennedy & Nager 2006), although other components of the immune system are also involved in the response (Martin *et al.* 2006; Tella *et al.* 2008). Previously, I measured (three times) the patagium thickness with a pressure-sensitive micrometer (Mitutoyo Inc.; accuracy: 0.01 mm). At the end of the experiment (6 h), I again measured the patagium thickness, calculating the T-cell-mediated immune response as the difference between the second and first measurements. Previous studies have shown that 6 h is sufficient time to detect an immune response in the house sparrow (Navarro *et al.* 2003; Martin *et al.* 2006). The repeatability of measuring the patagium thickness was 0.98 ($n = 8$; Bailey & Byrnes 1990).

Therefore, during the trials, all nestlings received the same input of resources, but HB nestlings begged 24 times more than LB nestlings. If there is a three-way trade-off between growth, immune response and begging, the house sparrow nestlings begging more fiercely should decrease their investment in growth, or immune response, or both. However, given that previous studies found no evidence that house sparrow nestling, reduce growth rate in response to increased begging (Kedar *et al.* 2000), I predict that the trade-off is translated to the immune response, which should be lower in HB nestlings.

In the statistical analyses, the variable ‘immune response’ was log-transformed to follow the requisites of parametric

Table 1. Means \pm standard deviations of the dependent variables used in the study, for largest and smallest nestlings in the high-begging (HB) and low-begging (LB) treatments. Immune response was measured as patagium swelling in response to PHA inoculation. Raw data are shown, although analyses were performed with transformed data when necessary.

	largest nestlings		smallest nestlings	
	high-begging ($n = 11$)	low-begging ($n = 11$)	high-begging ($n = 11$)	low-begging ($n = 11$)
immune response (mm)	20.64 \pm 12.61	49.30 \pm 31.82	21.79 \pm 15.45	28.61 \pm 10.11
initial body mass (g)	8.80 \pm 1.25	8.97 \pm 1.11	6.50 \pm 0.97	6.61 \pm 1.32
mass gain (g)	0.45 \pm 0.21	0.36 \pm 0.18	0.48 \pm 0.22	0.50 \pm 0.19
relative mass gain (%)	5.28 \pm 3.18	4.21 \pm 2.19	7.93 \pm 5.22	8.17 \pm 3.67
faecal mass (g)	0.32 \pm 0.10	0.34 \pm 0.08	0.28 \pm 0.13	0.22 \pm 0.13
estimated metabolic expenditure (g)	0.26 \pm 0.15	0.34 \pm 0.13	0.26 \pm 0.14	0.29 \pm 0.13

statistics (normality, homoscedasticity; Quinn & Keough 2002). The analyses were performed with a repeated measures analysis for variance (RM-ANOVA). This test was used to analyse the difference in the dependent variables between the smallest and the largest nestlings in a paired way (within-subjects component), as well as the interaction with the treatment, in order to examine whether the effect of the treatment varied with nestling rank. Moreover, in the between-subjects component, the test analysed the effect of the treatment on the dependent variables, considering the brood as a statistical unit, thereby avoiding pseudoreplication (von Ende 2001). In a final analysis I used general linear models (GLM), in which I introduced date, brood size and initial nestling body mass as covariates, given that these factors affect (directly or indirectly) the immune response in the house sparrow (Westneat *et al.* 2004). In this last analysis, RM-ANOVA was not possible, and the largest and the smallest nestlings were analysed separately.

3. RESULTS

No significant differences appeared in initial body mass between LB (low-begging) and HB (high-begging) nestlings (RM-ANOVA, between-subjects component, $F_{1,20} = 0.10$; $p = 0.75$; table 1). In an initial analysis, as predicted, the higher begging effort expended by HB nestlings depressed their immune response (between-subjects component, $F_{1,20} = 5.87$; $p = 0.02$; table 1). No significant difference was found in the immune response between largest and smallest nestlings (within-subjects component, $F_{1,20} = 3.15$; $p = 0.09$), and the interaction with the treatment was not significant ($F_{1,20} = 1.80$; $p = 0.20$). When the effect of the treatment was analysed separately for the largest and smallest nestlings, the begging level was found to have a significant influence on the immune response in the largest nestlings (ANOVA, $F_{1,21} = 8.04$; $p = 0.01$), but a non-significant influence in the smallest nestlings ($F_{1,21} = 2.77$; $p = 0.11$; table 1). Therefore, there was evidence of a trade-off between begging and immune response in the house sparrow, at least for the largest nestlings.

Consistent with the findings of Kedar *et al.* (2000), the treatment had no impact on mass gained in house sparrow nestlings (RM-ANOVA, between-subjects component, $F_{1,20} = 0.18$; $p = 0.68$; table 1). The smallest nestlings tended to gain more mass than largest ones (within-subjects component, $F_{1,20} = 4.03$; $p = 0.06$; table 1), but there was no significant interaction with

Table 2. Effect of date, brood size, initial body mass and treatment on the strength of immune response in the (a) largest and (b) smallest nestlings.

		d.f.	F	p	β	s.e.
(a)	intercept	1	4.84	0.04		
	date	1	4.82	0.04	-0.40	0.18
	body mass	1	2.02	0.17	0.24	0.17
	brood size	1	0.31	0.59	0.11	0.20
	treatment	1	12.01	0.003		
	error	17				
(b)	intercept	1	7.76	0.01		
	date	1	7.74	0.01	-0.51	0.18
	body mass	1	1.53	0.23	0.23	0.18
	brood size	1	1.81	0.20	0.28	0.21
	treatment	1	7.98	0.01		
	error	17				

treatment ($F_{1,20} = 1.63$; $p = 0.22$). Measured as a percentage of initial mass, relative mass gain was also unaffected by the treatment (between-subjects component, $F_{1,20} = 0.10$; $p = 0.76$; table 1) and the interaction with rank was not significant ($F_{1,20} = 1.43$; $p = 0.25$). No effect of the treatment on faeces mass was found (between-subjects component, $F_{1,20} = 0.33$; $p = 0.57$; table 1). The largest nestlings excreted significantly heavier faeces than did the smallest nestlings (within-subjects component, $F_{1,20} = 8.35$; $p < 0.01$; table 1), but there was no interaction with treatment ($F_{1,20} = 1.98$; $p = 0.18$). The estimated metabolic expenditure was not affected by the treatment (between-subjects component, $F_{1,20} = 1.45$; $p = 0.24$), did not vary with nestling rank (within-subjects component, $F_{1,20} = 0.78$; $p = 0.39$; table 1) nor showed a significant interaction ($F_{1,20} = 0.56$; $p = 0.46$).

Finally, given that the immune response is (directly or indirectly) affected by date, brood size and body mass (Westneat *et al.* 2004), I repeated the models controlling for these variables. For the largest nestlings, the immune response significantly diminished with date, and it remained significantly affected by treatment, so that nestlings begging more fiercely showed a depressed immune response (table 2a). Similar results were found for the smallest nestlings (table 2b). In this case, when controlling for date, the difference in immune response between HB and LB treatments proved significant. When the same model was applied to mass gain, relative

mass gain and estimated metabolic expenditure, the effect of the treatment on these variables remained non-significant (see the electronic supplementary material).

4. DISCUSSION

This is the first study showing that offspring begging at high levels undergo depressed immunocompetence when challenged by an antigen (PHA), implying a trade-off between begging signalling and the immune system. At the same time, this study confirms an absence of trade-off, between growth and begging in the house sparrow, as previously reported by Kedar *et al.* (2000). Therefore, a cost of nestling begging is a reduction of their immune capacity, which may jeopardize their resistance to infections and their survival (Møller & Saino 2004).

Immune response is energetically costly (Demas 2004), and begging is presumably also energetically costly. Canary and magpie chicks forced to beg for a prolonged time divert growth energy to begging, thereby reducing growth rates (Kilner 2001; Rodríguez-Gironés *et al.* 2001). This effect, nevertheless, has not been detected in house sparrow nestlings (Kedar *et al.* 2000; this study), in which the energy needed for begging may have been diverted from the immune system, thereby weakening it. This could explain also why in other species (ring dove, tree swallow and a burying beetle) intense begging does not decrease the growth rate, either. Growth rate and immune response are also compromised (Fair *et al.* 1999; Soler *et al.* 2003; Brommer 2004), suggesting a three-way trade-off between growth, immune response and begging in nestlings, with the optimal strategy of energy allocation varying between species. Intraspecific variation in the optimal energy allocation according to the risk of parasitism is also possible. For example, great tit (*Parus major*) parents exposed to nest ectoparasites reduce yolk-androgen deposition, presumably to increase nestling immunocompetence (Tscharren *et al.* 2004), and by varying yolk-androgen deposition birds also modify nestling begging (e.g. Hinde *et al.* 2009).

On the other hand, physical effort provoked by the begging behaviour, with loud calls and many movements, probably increases the level of reactive oxygen species, disturbing the balance between pro-oxidative and anti-oxidative molecules (Costantini 2008). The immune response also increases the release of reactive oxygen species (Costantini & Møller 2009; Sorci & Faivre 2009). Both processes functioning simultaneously could increase oxidative stress over the levels that the nestling physiology may endure, and immune response could be adaptively reduced in order to diminish the risk of oxidative stress (Råberg *et al.* 1998; Monaghan *et al.* 2009). This could explain why great tit nestlings supplemented with carotenoids (an antioxidant; McGraw & Ardia 2003, 2004), beg more fiercely than do control chicks (Helfenstein *et al.* 2008), because these nestlings would have more resources to reduce the oxidative stress generated by begging.

The trade-off between begging and immunocompetence is probably mediated by steroids (Ricklefs & Wikelski 2002; Adkins-Regans 2005; French *et al.* 2009). In house sparrow nestlings, food deprivation raises the plasma level of corticosterone, and the

exogenous administration of this hormone heightens the level of begging at the same time as it lowers the immune response (Loiseau *et al.* 2008). Testosterone increases begging intensity in chicks of a number of species (reviewed in Schwabl & Lipar 2002; Gil 2008; Ros 2008) at the same time as inducing immunosuppression (Navara & Mendonça 2008). Also, intense nestmate competition elevates the levels of both steroids (Naguib *et al.* 2004). Testosterone, in fact, mediates the trade-off between growth and begging in canary nestlings (Buchanan *et al.* 2007). Therefore, begging effort by nestlings probably stimulates the secretion of these hormones, which in turn would reduce immunocompetence.

In conclusion, this study reveals physiological costs related to begging behaviour in house sparrow nestlings, depressing the immune response. These costs may limit the evolutionary escalation of begging, allowing an offspring to signal its feeding needs or its disposition to compete honestly by means of begging, as predicted by the models based on costly begging (e.g. Godfray 1991; Johnstone 1998; Rodríguez-Gironés 1999; Parker *et al.* 2002). Moreover, this cost implies that an infected offspring cannot afford the costs of begging while combating disease. In the barn swallow (*Hirundo rustica*), nestlings injected with sheep red-blood cells (SRBC), which elicit an immune response, begged at the same rate as control nestlings (Saino *et al.* 2000a), but showed reduced mouth redness (Saino *et al.* 2000b), and parents preferentially feed chicks with redder mouths (Saino *et al.* 2003). Furthermore, the findings suggest that, in some species, the cost of begging may be reflected in a reduction of the growth rate (e.g. the canary; Kilner 2001), while in others (such as the house sparrow) it may be expressed in lower immunocompetence.

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