

On the oxidative cost of begging: antioxidants enhance vocalizations in gull chicks

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Offspring solicit food to their parents by begging displays, which are important in the parent–offspring communication. Most theoretical approximations on this behavior have centered on the view of begging as an honest signal of need or as a form of scramble competition for resources. In both signaling models, costly begging is necessary to stabilize the begging strategy at equilibrium. Nevertheless, evidence supporting begging as costly behavior remains scarce. We investigated whether oxidative stress may represent a general form of proximate cost of begging and also whether begging is related to offspring nutritional condition. To test this, we experimentally modified the chicks' nutritional condition and vitamin E availability and measured the effects on different begging components. The intensity of all begging components increased in chicks that were intake restricted, whereas vitamin E specifically enhance the total number of chatter calls given by chicks, mainly in those with a lower body size. Our results suggest that begging behavior is an antioxidant demanding activity and support the idea that oxidative stress may be a cost of begging. Our findings also suggest that begging behavior may be an honest signal of the nutritional and oxidative status of the chicks. *Key words*: begging, communication, oxidative costs, oxidative stress, parent–offspring, yellow-legged gull. [*Behav Ecol*]

In animals with parental care, offspring commonly perform extravagant behaviors to solicit food and care from their parents. It is thought that conspicuous begging is the outcome of parent–offspring and inter-sibling conflicts of interest (Trivers 1974; Kilner and Johnstone 1997; Royle et al. 2002). The major assumption in most models of the evolution of begging behavior is that the cost of begging prevents a runaway escalation of solicitation (e.g., Macnair and Parker 1979; Harper 1986; Godfray 1991, 1995; Rodríguez-Gironés 1999; Parker et al. 2002). According to these models, the marginal cost of increasing begging balances its marginal benefit, thereby stabilizing the begging strategy at equilibrium (see Maynard-Smith and Harper 2003). Because the assumption that begging is costly is critical to these models, great effort has been devoted to examine the underlying costs, but evidence supporting begging as costly behavior remains scarce (see Roulin 2001; Moreno-Rueda 2007; and references therein).

Research on begging costs has mainly centered on birds, and the energetic cost of exuberant begging has been widely explored (Chappell and Bachman 2002). Energy allocated to begging would no longer be available for other functions (i.e., growth, development, or maintenance) with negative consequences for nestling survival, and as the amount of energy allocated to begging increases, the magnitude of the survival cost also increases. However, in contrast to previous thinking, avian studies that measured energetic expenditures revealed a relatively low metabolic cost of chick begging (Leech and Leonard 1996; McCarty 1996; Bachman and Chappell 1998; Abraham and Evans 1999).

Although other possible costs of begging have been identified (e.g., predation costs; Leech and Leonard 1997; Haskell

2002), the relatively low energetic cost of begging has challenged the generality of costly begging to reach stable solicitation strategies (Bergstrom and Lachmann 1998). Thus, new theoretical models have been developed to demonstrate that begging may not necessarily be costly in order to resolve parent–offspring conflict (Rodríguez-Gironés et al. 1996; Bergstrom and Lachmann 1998). These models (pool equilibrium models) suggest that, despite the conflict of interest, reliable information can be expressed by discrete cost-free signals used by a “pool” of individuals in a particular range of states (e.g., a range of nutritional state), rather than variable intensity predicted by costly models (Godfray 1995; Johnstone 1996a). Empirical evidence showing that offspring beg more intensively when they are in greater need (reviewed in Kilner and Johnstone 1997) fits better with costly models. However, the generality of costly begging remains controversial.

Here we suggest that increased susceptibility to oxidative stress may represent a proximate cost of begging. Oxidative stress is defined as the imbalance between the production of reactive oxygen species (ROS) and antioxidant compounds (Sies 1991). ROS are by-products of normal metabolic activities (Sies 1991; Finkel and Holbrook 2000) and are produced, for example, by complex muscular contractions (Jackson 2008), increased metabolic activity, and oxygen consumption (Leech and Leonard 1996; McCarty 1996; Bachman and Chappell 1998; Abraham and Evans 1999), as occurs during chick begging. ROS are generally unstable and very reactive (Fang et al. 2002) and damage biomolecules such as DNA, proteins, and lipids (Finkel and Holbrook 2000). However, there are a number of endogenous and exogenous antioxidant defenses, which scavenge ROS and limit their toxic effect (Surai 2002). Importantly, during first days of life, chicks are very vulnerable to oxidative stress because their antioxidant machinery is mainly limited to maternal antioxidants (Surai 2002) and they experience profound change in aerobic conditions and a potential oxidative insult at hatching (Surai et al. 1996). Begging intensity may generate oxidative stress, the strength of which depends on the availability and efficiency

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of antioxidant defenses. Oxidative stress may have detrimental effects on chick growth because ROS cause oxidative damage in biomolecules (Finkel and Holbrook 2000) and key organs such as liver and brain (Surai and Sparks 2000; Hilscherova et al. 2003). Moreover, recent studies have shown that the growth of chicks was negatively affected when begging was experimentally increased (Kilner 2001; Rodríguez-Gironés et al. 2001). Surprisingly, however, the link between begging and oxidative stress has only recently been suggested (Moreno-Rueda 2007) and has never been explored.

We report an experimental field study of yellow-legged gulls (*Larus michahellis*) that examines whether begging reflects offspring need and whether oxidative stress is a mechanism underlying costly begging behavior. Because oxidative cost can be alleviated by antioxidants, we carried out an experimental study under natural conditions to analyze the effect of food deprivation and vitamin E supplementation on the intensity of begging behavior of gull chicks. Vitamin E (α -tocopherol) is a major fat-soluble antioxidant (Halliwell and Gutteridge 1999; Surai 2002) that cannot be synthesized de novo and has an important influence on protection against oxidative damages. In birds, vitamin E protects the organism from oxidative stress directly by scavenging free radicals (Surai 2002) or protecting lipid membranes (reviewed in Fellenberg and Speisky 2006) and proteins (Batifoulier et al. 2002). Additionally, vitamin E may indirectly improve antioxidant machinery by enhancing key antioxidant enzymatic activities (i.e., glutathione peroxidase [GPD], Surai 2000; Sodhi et al. 2008).

Yellow-legged gulls nest on the ground and semi-altricial chicks display conspicuous behavior to stimulate parents to feed them. Begging displays consist of complex behavior that involves pecking at the parents' bills accompanied by 2 different calls (Tinbergen and Perdeck 1950; Rubolini et al. 2006). When the parents arrive to feed them, the chicks emit "chatter calls" and "pee calls" (Impekenov 1971; Beer 1979). Chatter calls are used to attract the parents' attention, and the chicks emit them as soon as the parents land at the nest; these calls are characterized by rapidly repetitive sound elements with a wide frequency range (Supplementary Movie S1). The pee calls are low-level uniform sounds emitted by chicks in the hunched posture and while pecking at the parent's bill (Impekenov 1971; Supplementary Movie S2). If begging reflects offspring need, and if oxidative stress is an underlying cost of begging behavior, we expected that 1) the intensity of begging displays should be higher in hungrier chicks and 2) chicks given vitamin E supplements should beg more intensely.

MATERIALS AND METHODS

Experimental design and field procedures

The study was carried out in a large yellow-legged gull colony on Salvora island (42°28' N, 09°00' W, Parque Nacional das Illas Atlánticas de Galicia, Northwest Spain) during May–June 2008. In the last week of May, we examined the colony in order to localize nests in hatching stages. We marked 82 three-egg clutches with a single piped egg (expected to hatch the next day). In order to recognize the chick after hatching, we marked the tip of the bill embryo in the piped egg with a black permanent marker (toluene free). In this species, hatching is asynchronous and the first hatched chick has a strong competitive advantage (Boncoraglio et al. 2006). We installed small enclosures around the marked nests (1.5 m² surrounded with semi-transparent mesh of 30 cm height) to prevent the chicks moving among closed nests. We checked the nests daily and marked the first hatched chicks in each (recognizable by dark markings remaining on the bill) with a colored Velcro strip

and measured the tarsus length (± 0.01 mm) and body mass (± 1 g). The first hatched chick from each nest was randomly assigned to a 2-factorial experiment: vitamin E treatment (supplemented or not supplemented) and restriction intake treatment (restricted or not) (22, 20, 19, and 21 chicks per group). Egg size, body mass, tarsus length, and hatching date of the first hatched chick did not differ among experimental groups ($P > 0.17$ in all cases).

For vitamin E supplementation, chicks received a daily dose of 7.1 mg of vitamin E (dl- α -tocopherol acetate; Chiesi España, Barcelona, Spain) during the first 2 days of life (the day of hatching and the day after), an individual dose of 112 mg/kg of body mass, similar to dosages previously administered to this species (Pérez et al. 2008). The daily amount of vitamin E supplied was within the estimated natural range of intake (Pérez et al. 2008). Vitamin E was mixed with 0.5 ml of vegetable oil and supplemented via oral administration. The control group (not supplemented) was provided with the same amount of vegetable oil but without vitamin E. In the restriction intake treatment, in order to manipulate each chick's needs, we restricted food intake by fastening 5-mm-wide tape ring around the chick's bill, just below the nostril, to prevent ingestion of food. The tape limited bill opening but did not close the bill completely or constrain begging. The tape was put in place in the afternoon of day 1 (1 day after hatching) and was removed the next morning. Nonrestricted chicks were manipulated in the same way, but the tape was loosened to allow food intake. The duration of restriction intake treatment was always within the time that chicks can remain without being fed by their parents in the same colony under natural conditions.

Begging behavior test

In this species, the chicks show conspicuous behaviors to stimulate parents to regurgitate food on the ground. This behavior can be elicited by the presentation of dummies that simulate the head of a parent gull (Tinbergen and Perdeck 1950; Rubolini et al. 2006). Thus, we recorded the intensity of begging behavior directed to the parents by means of the standard protocol described by Tinbergen and Perdeck (1950), with minor modifications. Begging behavioral tests were carried out in the morning on the second day after hatching in a hide placed outside the colony, and they were made blind to the treatments. We transported the chicks individually from their nests to the hide in textile bags. To elicit the begging behavior, we first placed the chick on the ground and covered it with a dull cloth. The chick received a playback stimulation to simulate a natural feeding event (Tinbergen and Perdeck 1950). The playback was composed by 4 mew calls and the presentation of a dummy head. Chicks show an innate reaction to playback as well as to dummy head models, responding with begging calls and vigorously pecking at the red spot painted on the lower mandible, which acts as a releasing stimulus (Tinbergen and Perdeck 1950). Mew calls were previously recorded with a digital recorder (Olympus VN-2100-PC) in the same colony. Mew calls are typically performed by parents to call up young for feeding (Cramp 1998). We selected a volume as similar as possible to that of the parents in the nest. Speakers were placed at similar volume and same distance from the experimental chicks in all behavioral tests. As soon as the playback finished (15.8 s), we removed the cloth and started the visual stimulation by presenting each chick with a dummy, mimicking a natural sized parent head. Chicks were allowed to move freely on the ground. We presented the dummy head nodding 30 times. The head was made of white plaster, and the bill was painted yellow with a red spot on the lower mandible. The size and

color of red spot as well as the yellow were within natural ranges of gulls nesting at Salvora (for details, see Morales et al. 2009). We recorded the number of distinct pecks delivered to the red spot during the dummy presentation and the number of begging calls emitted. We recorded 2 easily discernible begging calls, “chatter” and “pee” call (Tinbergen and Perdeck 1950; Impeken 1971). The duration of tests did not differ among experimental groups (vitamin E: $F_{1,55} = 0.385$, $P = 0.537$; restriction intake: $F_{1,55} = 0.634$, $P = 0.858$; vitamin E \times restriction intake $F_{1,55} = 0.218$, $P = 0.642$).

Statistical analysis

During the experiment, 1 chick was lost and 3 chicks died from natural causes. Moreover, in the restricted intake treatment, 5 chicks were excluded from the analyses because the tapes fell off during feeding. The difference in begging behavior (number of pecks, pee, and chatter calls) among the groups was analyzed by generalized linear models with Poisson errors and log link. We included vitamin E and restriction intake treatments as fixed factors and laying date (in Julian days) and initial size (tarsus length) as covariates. All 2-way interactions and main effects of all factors were included in the initial models, and final models were developed with a backward deletion procedure. Two-way interactions were first removed, then the main effects. Differences in sample sizes reflect missing values due to, for instance, the death or loss of chicks. Data are presented as mean \pm standard error, and α significance level was set at 0.05.

RESULTS

Two days after hatching, body mass was affected by the restriction intake treatment ($F_{1,65} = 57.46$, $P < 0.001$; Figure 1) and hatchling body mass ($F_{1,65} = 46.62$, $P < 0.001$; Figure 1) but not by vitamin E treatment or laying date ($P > 0.49$ in both cases). Restricted intake chicks increased the frequency of all components of begging behavior, which suggests that begging is a reliable signal of nutritional state (Table 1). Thus, restricted chicks pecked the dummy head more frequently (51%, Figure 2a) and produced more pee (47%; Figure 2b) and chatter calls (43%; Figure 3a) than nonrestricted chicks.

The administration of vitamin E did not affect the number of the pecks, and the frequency of pee call, but, did affect the number of chatter calls produced during the experiment

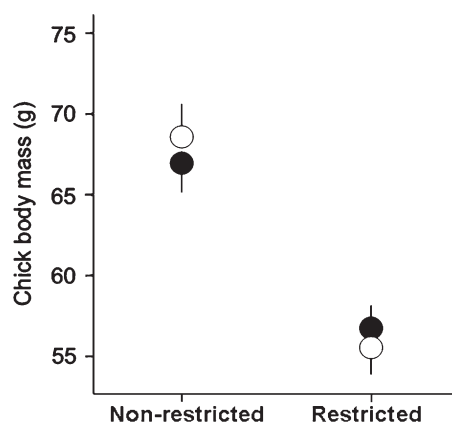


Figure 1
Effects of restricted intake and vitamin E treatments on chick body mass (mean \pm standard error). Filled circles and open circles represent, respectively, vitamin E supplemented and non-supplemented chicks.

Table 1

Generalized lineal models of begging behavior during behavior tests (total number of pecks and total number of pee and chatter calls) in relation to treatments and covariates

Dependent variables	Source of variation	<i>F</i>	df	<i>P</i>
Total number of pecks	Restricted intake	15.897	1,71	<0.001
Total number of pee calls	Restricted intake	16.371	1,71	<0.001
Total number of chatter calls	Vitamin E	6.655	1,67	0.012
	Restricted intake	8.132	1,67	0.006
	Tarsus length at hatching	0.397	1,67	0.531
	Vitamin E \times tarsus length	6.406	1,67	0.014

For each dependent variable, the minimal adequate model is shown.

(Table 1; Figure 3a). There was also a significant interaction between vitamin E treatment and hatchling size (Table 1). In the vitamin E–treated group, chicks with smaller tarsus length at hatching produced more chatter calls than larger chicks; this effect was not found in chicks not administered vitamin E (Figure 3b).

DISCUSSION

In this experimental study, we found that begging is an honest signal of a chick’s nutritional state, that is, reflects individual’s true need. Moreover, we found that antioxidants enhance some types of begging behavior. Thus, vitamin E had a positive effect on the number of chatter calls emitted by chicks, especially in smaller chicks, whereas it did not affect pee calls or pecks. Overall, the results suggest that begging behavior is an antioxidant demanding activity (at least some components) and may honestly reflect the nutritional and oxidative status of the chicks.

Food deprivation had significant effects on all 3 components of chick begging behavior. This is consistent with previous studies in which similar effects of short-term deprivation in gull chicks were found (Iacovides and Evans 1998) and suggests that begging is an honest signal of need. A common problem in the interpretation of data in begging studies is the potentially confounding effect of sibling competition (Kilner and Johnstone 1997). In this context, when they are food

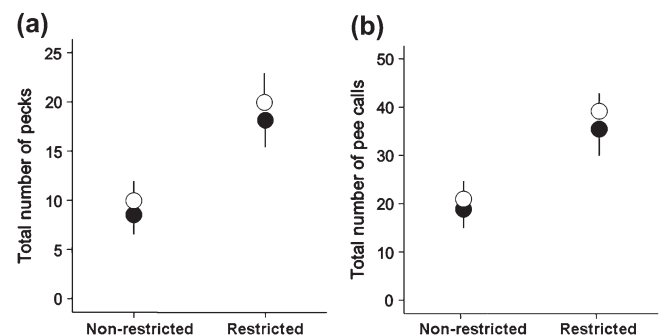


Figure 2
Different types of begging behavior in chicks—(a) total number of pecks and (b) total number of pee calls (mean values \pm standard error) in relation to restricted intake treatment and to vitamin E supplementation treatment (filled circles) or no treatment (open circles).

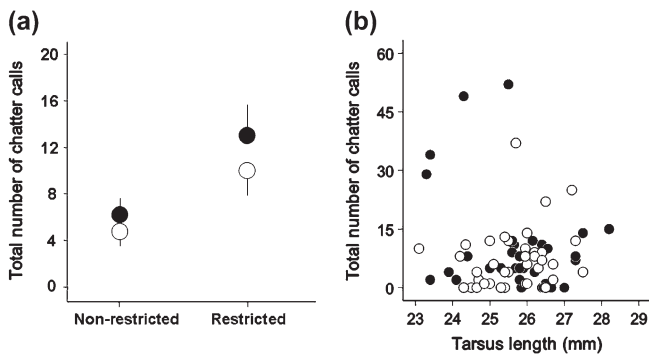


Figure 3

Chatter call responses performed by chicks during behavioral tests in relation to (a) restricted intake treatment (Least square means \pm standard error from statistical model is shown), (b) tarsus length, and whether vitamin E supplementation treatment was given (filled circles) or not (open circles).

deprived, chicks may also beg more intensively because competition is intense (Smith and Montgomerie 1991), thus confounding the effect of the real need on begging. In our study, by selecting clutches of first chicks from clutches with high asynchrony, we avoided the confounding effects of sibling competition. The begging test was performed in the morning of the second day after hatching, whereas the second chick in each brood was only a few hours old, and the third chick was still hatching. Moreover, the behavioral test was carried out without the presence of rival chicks. Overall, our begging study in the absence of sibling competition suggests that begging signals the true needs of chicks.

The effect of vitamin E on begging supports the idea that oxidative stress is a mechanism underlying begging behavior. Only those chicks alleviated by the antioxidant treatment were able to afford the oxidative cost of begging and were able to emit a great number of chatter calls. In fact, begging has been suggested to increase oxidative stress due to increases in the metabolic rate and oxygen consumption (Moreno-Rueda 2007). Moreover, during begging, respiratory patterns may be altered, thus, causing partial apnea, as occurs during song (Franz and Goller 2003), and the lack of oxygen has been related to a higher demand for ROS scavengers under laboratory conditions (Ratych et al. 1987). Begging can also be limited by ROS that affects muscle performance generating fatigue (Barclay and Hansel 1991). In bird chicks, vitamin E supplementation provides beneficial effects against lipid peroxidation and improves antioxidant machinery such as superoxide dismutase (SOD) and GPD activities (Sodhi et al. 2008; Tsai et al. 2008). Thus, in our study, vitamin E supplementation probably alleviated organs and tissues from any possible ROS produced during begging. Similarly, yolk antioxidants may improve begging behavior (Helfenstein et al. 2008; but see Rubolini et al. 2006). Alternatively, vitamin E treatment could have produced an indirect effect on begging, for instance, via improved growth. Vitamin E supplementation may have produced an increase in nestling growth (De Ayala et al. 2006) and chick demanding resources that, in turn, may result in increased begging behavior (Royle et al. 2002). Nevertheless, we did not find any effect of vitamin supplementation on the growth of chicks. Thus, our results best fit with the idea that vitamin E alleviates the cost of begging. Interestingly, an improvement of chick growth after Vitamin E supplementation, as previously found (e.g., De Ayala et al. 2006), may be also explained by an increase of parental feeding effort induced by enhanced food solicitation (see Morales et al. 2009) in vitamin E chicks.

Our finding that vitamin E affects begging behavior by increasing chatter calls indicates that chatter call is a costly activity as suggested by handicap and scramble models of begging. As far as we know, this is the first experimental evidence that increased susceptibility to oxidative stress may represent a proximate cost of begging. The fact that only supplemented chicks were able to increase begging intensity suggests that chatter calls may act as a handicap signal. Nevertheless, whether oxidative costs, as found in this study, are enough to maintain honesty (Johnstone and Godfray 2002) remains to be explored in future studies.

Under the handicap model of begging individuals of different quality differ in the cost of signaling (Godfray 1995; Johnstone 1996a). Accordingly, high quality chicks, for instance with improved antioxidant status, may beg at higher intensities for a given level of need because for them begging is less costly to produce. However, individuals of different quality may also differ in the benefits they gain by signaling. For instance, smaller and larger chicks may differ in terms of benefits and costs derived from begging, which may result in differences in marginal benefits that they obtain by begging (Lotem 1998). In such cases, for the same level of need, smaller chicks would obtain more benefits than larger chicks if they beg more and they are fed because their survival would be compromised to a greater extent. Thus, if begging is costly in terms of oxidative stress and vitamin E reduces such costs, we would expect that vitamin E would have a greater effect on smaller chicks. This could explain why vitamin E mainly affected smaller chicks in which the marginal benefits would be higher than for larger chicks.

In our study, vitamin E supplementation had an effect on chatter calls, but no effect was found on pee calls and pecks. This suggests that not all components of begging behavior of gull chicks incur the same costs. The chatter call is characterized by high and wide frequency range (Impeken 1971) and is accompanied by heavy movements in order to facilitate location of the chick. Because chicks are semiprecocial, gull chicks are commonly dispersed throughout the territory. As soon as parents land, chicks start to emit chatter calls and crane their necks and run, while looking for their parents. In contrast, pee calls and pecks are displayed in a hunched posture when parents are close. The latter components are therefore probably less energetic and antioxidant demanding activities. Different begging components may be used in different contexts (i.e., fast localization by parents or parental feeding) or, alternatively, begging chicks could be revealing diverse components of their general state ("multiple message" hypothesis; Johnstone 1996b; Killner 2002) due to the cost associated with an individual signal's component.

Overall, our results suggest that oxidative stress is a cost underlying some begging components. Begging for food may be a costly signal, and our results further suggest that at least chatter calls incur an oxidative cost for nestlings. Begging components reflect chick's need, but pecks and pee calls were apparently not antioxidant dependent. Future studies should explore if oxidative cost is enough to prevent cheating, whether parents decode complex begging signals and also whether they are able to employ oxidative costly components of begging to determine food allocation.

SUPPLEMENTARY MATERIAL

Supplementary Movies S1 and S2 can be found at <http://www.behco.oxfordjournals.org/>.

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REFERENCES

- Abraham CL, Evans RM. 1999. Metabolic costs of heat solicitation calls in relation to thermal need in embryos of American white pelicans. *Anim Behav*. 57:967–975.
- Bachman GC, Chappell MA. 1998. The energetic cost of begging behaviour in nestling house wren. *Anim Behav*. 55:1607–1618.
- Barclay JK, Hansel M. 1991. Free radicals may contribute to oxidative skeletal muscle fatigue. *Can J Physiol Pharmacol*. 69:279–284.
- Batifoulier F, Mercier Y, Gatellier P, Renner M. 2002. Influence of vitamin E on lipid and protein oxidation induced by H₂O₂-activated MetMb in microsomal membranes from turkey muscle. *Meat Sci*. 61:389–395.
- Beer CG. 1979. Vocal communication between laughing gull parents and chicks. *Behaviour*. 70:118–146.
- Bergstrom CT, Lachmann M. 1998. Signaling among relatives. III. Talk is cheap. *Proc Natl Acad Sci USA*. 95:5100–5105.
- Boncoraglio G, Rubolini D, Romano M, Martinelli R, Saino N. 2006. Effects of elevated yolk androgens on perinatal begging behavior in yellow-legged gull (*Larus michahellis*) chicks. *Horm Behav*. 50:442–447.
- Chappell MA, Bachman GC. 2002. Energetic cost of begging behaviour. In: Wright J, Leonard ML, editors. *The evolution of begging: competition, cooperation and communication*. Dordrecht (The Netherlands): Kluwer Academic Press. p. 143–162.
- Cramp S. 1998. *The complete birds of the Western Palearctic on CD-ROM*. Oxford: Oxford University Press.
- De Ayala RM, Martinelli R, Saino N. 2006. Vitamin E supplementation enhances growth and condition of nestling barn swallows (*Hirundo rustica*). *Behav Ecol Sociobiol*. 60:619–630.
- Fang YZ, Yang S, Wu G. 2002. Free radicals, antioxidants, and nutrition. *Nutrition*. 18:872–879.
- Fellenberg MA, Speisky YH. 2006. Antioxidants: their effects on broiler oxidative stress and its meat oxidative stability. *Worlds Poultry Sci J*. 62:53–70.
- Finkel T, Holbrook NJ. 2000. Oxidants, oxidative stress and the biology of ageing. *Nature*. 408:239–247.
- Franz M, Goller F. 2003. Respiratory patterns and oxygen consumption in singing zebra finches. *J Exp Biol*. 206:967–978.
- Godfray HCJ. 1991. Signalling of need by offspring to their parents. *Nature*. 352:328–330.
- Godfray HCJ. 1995. Signalling of need between parents and young: parent–offspring conflict and sibling rivalry. *Am Nat*. 146:1–24.
- Halliwell B, Gutteridge JMC. 1999. *Free radicals in medicine and biology*. Oxford: Oxford University Press.
- Harper AB. 1986. The evolution of begging: sibling competition and parent–offspring conflict. *Am Nat*. 128:99–114.
- Haskell D. 2002. Begging behaviour and nest predation. In: Wright J, Leonard ML, editors. *The evolution of begging: competition, cooperation and communication*. Dordrecht (The Netherlands): Kluwer Academic Press. p. 163–172.
- Helfenstein F, Berthouly A, Tanner M, Karadas F, Richner H. 2008. Nestling begging intensity and parental effort in relation to prelaying carotenoid availability. *Behav Ecol*. 19:108–115.
- Hilscherova K, Blankenship AL, Nie M, Coady KK, Upham BL, Trosko JE, Gicsy JP. 2003. Oxidative stress in liver and brain of the hatchling chicken (*Gallus domesticus*) following in ovo injection with TCDD. *Comp Biochem Physiol C*. 136:29–45.
- Iacovides S, Evans RM. 1998. Begging as graded signals of need for food in young ring-billed gulls. *Anim Behav*. 56:79–85.
- Impekoven M. 1971. Calls of very young black-headed gull chicks under different motivational states. *Ibis*. 113:91–96.
- Jackson MJ. 2008. Free radicals generated by contracting muscle: by-products of metabolism or key regulators of muscle function? *Free Radic Biol Med*. 44:132–141.
- Johnstone RA. 1996a. Begging signals and parent-offspring conflict: do parents always win? *Proc R Soc Lond B Biol Sci*. 263:1677–1681.
- Johnstone RA. 1996b. Multiple displays in animal communication: “backup signals” and “multiple messages”. *Philos Trans R Soc Lond B Biol Sci*. 351:329–338.
- Johnstone RA, Godfray HCJ. 2002. Models of begging as a signal of need. In: Wright J, Leonard ML, editors. *The evolution of begging: competition, cooperation and communication*. Dordrecht (The Netherlands): Kluwer Academic Press. p. 1–20.
- Kilner R. 2001. A growth cost of begging in captive canary chicks. *Proc Natl Acad Sci USA*. 98:11394–11398.
- Kilner R. 2002. The evolution of complex begging displays. In: Wright J, Leonard ML, editors. *The evolution of begging: competition, cooperation and communication*. Dordrecht (The Netherlands): Kluwer Academic Press. p. 87–106.
- Kilner R, Johnstone RA. 1997. Begging the question: are offspring solicitation behaviours signals of need? *Trends Ecol Evol*. 12:11–15.
- Leech SM, Leonard ML. 1996. Is there an energetic cost to begging in nestling tree swallows (*Tachineta bicolor*)? *Proc R Soc Lond B Biol Sci*. 263:983–987.
- Leech SM, Leonard ML. 1997. Begging and the risk of predation in nestling birds. *Behav Ecol*. 8:644–646.
- Lotem A. 1998. Higher levels of begging behavior by small nestlings: a case of a negatively correlated handicap. *Israel J Zool*. 44:29–45.
- Macnair M, Parker GA. 1979. Models of parent–offspring conflict. III. Intra-brood conflict. *Anim Behav*. 27:1202–1209.
- McCarty JP. 1996. The energetic cost of begging in nestling passerines. *Auk*. 113:178–188.
- Maynard-Smith J, Harper D. 2003. *Animal signals*. Oxford: Oxford University Press.
- Morales J, Alonso-Álvarez C, Pérez C, Torres R, Serafino E, Velando A. 2009. Families on the spot: sexual signals influence parent-offspring interaction. *Proc R Soc Lond B Biol Sci*. 276:2477–2483.
- Moreno-Rueda G. 2007. Is there empirical evidence for the cost of begging? *J Ethol*. 25:215–222.
- Parker GA, Royle NJ, Hartley IR. 2002. Begging scrambles with unequal chicks: interactions between need and competitive ability. *Ecol Lett*. 5:206–215.
- Pérez C, Lores M, Velando A. 2008. Availability of nonpigmentary antioxidant affects red coloration in gulls. *Behav Ecol*. 19:967–973.
- Ratych RE, Chuknyiska RS, Bulkeley GB. 1987. The primary localization of free radical generation after anoxia/reoxygenation in isolated endothelial cells. *Surgery*. 102:122–131.
- Rodríguez-Gironés MA. 1999. Sibling competition stabilizes signalling resolution models of parent–offspring conflict. *Proc R Soc Lond B Biol Sci*. 266:2399–2402.
- Rodríguez-Gironés MA, Cotton PA, Kacelnik A. 1996. The evolution of begging: signalling and sibling competition. *Proc Natl Acad Sci USA*. 93:14637–14641.
- Rodríguez-Gironés MA, Zúñiga JM, Redondo T. 2001. Effects of begging on growth rates of nestling chicks. *Behav Ecol*. 12:269–274.
- Roulin A. 2001. On the cost of begging vocalization: implication of vigilance. *Behav Ecol*. 12:506–510.
- Royle NJ, Hartley IR, Parker GA. 2002. Begging for control: when are offspring solicitation behaviours honest? *Trends Ecol Evol*. 17:434–440.
- Rubolini D, Romano M, Bonisoli Alquati A, Saino N. 2006. Early maternal, genetic and environmental components of antioxidant protection, morphology and immunity of yellow-legged gull (*Larus michahellis*) chicks. *J Evol Biol*. 19:1571–1584.
- Sies H. 1991. *Oxidative stress: oxidants and antioxidants*. New York: Academic Press.
- Smith HG, Montgomerie R. 1991. Nestling American robins compete with siblings by begging. *Behav Ecol Sociobiol*. 29:307–312.
- Sodhi S, Sharma A, Brar APS, Brar RS. 2008. Effect of α -tocopherol and selenium on antioxidant status, lipid peroxidation and hepatopathy induced by malathion in chicks. *Pestic Biochem Physiol*. 90:82–86.

- Surai PF. 2000. Effect of selenium and vitamin E content of the maternal diet on the antioxidant system of the yolk and the developing chick. *Br Poult Sci.* 41:235–243.
- Surai PF. 2002. Natural antioxidants in avian nutrition and reproduction. Nottingham (UK): Nottingham University Press.
- Surai PF, Noble RC, Speake BK. 1996. Tissue-specific differences in antioxidant distribution and susceptibility to lipid peroxidation during development of the chick embryo. *Biochim Biophys Acta.* 1304:1–10.
- Surai PF, Sparks NH. 2000. Tissue-specific fatty acid and alpha-tocopherol profiles in male chickens depending on dietary tuna oil and vitamin E provision. *Poult Sci.* 79:1132–1142.
- Tinbergen N, Perdeck AC. 1950. On the stimulus situation releasing the begging response in the newly hatched herring gull chick (*Larus argentatus argentatus* Pont.). *Behaviour.* 3:1–39.
- Trivers RL. 1974. Parent–offspring conflict. *Am Zool.* 14:249–264.
- Tsai HL, Sam KC, Chang YF, Lin SJ Chang. 2008. Beneficial effects of maternal vitamin E supplementation on the antioxidant system of the neonate chick brain. *Asian Australas J Anim Sci.* 21:225–231.