Forum

On the cost of begging vocalization: implications of vigilance

Alexandre Roulin
Department of Zoology, University of Cambridge, Downing Street, Cambridge CB2 3EJ, UK

Begging vocalization is thought to have evolved as a consequence of the parent-offspring conflict over parental investment (Mock and Parker, 1997). Under this conflict, parents are reluctant to provide all the resources requested by current offspring because they are saving resources for future broods (Trivers, 1974). In this scenario, begging has evolved as an honest signal of need with the most hungry offspring begging most conspicuously. This information allows parents to optimally adjust reproductive investment, since they can accurately assess offspring food requirement (Godfray, 1991). Given the conflict of interest over resources between parents and offspring, the evolutionary stability of begging would be ensured by its cost for two reasons. First, the benefit of obtaining additional resources from the parents increases with need, and hence the benefit to be fed outweighs the cost of begging only when hungry. Second, if all offspring, independent of need, were to beg at the same level, parents would be rapidly selected to ignore begging solicitation (Godfray, 1991; MacNair and Parker, 1979).

The hypothesis that begging is a costly signal of need has prompted numerous experiments to test its predictions. Empiricists have found that parents increase feeding rate when begging level is amplified via play-back experiments (Burford et al., 1998; Davies et al., 1998; Ottosson et al., 1997; Price, 1998; but see Clark and Lee, 1998) and that parents preferentially allocate food to the offspring begging most vigorously (e.g., Hofstetter and Ritchison, 1998; Kilner, 1995; Roulin et al., 2000). Another avenue of experimentation has focused on the cost of begging, and three different costs have been detected so far. These are reviewed below.

Predation cost

Loud begging vocalization attracts predators (Briskie et al., 1999; Dearborn, 1999; Haskell, 1994, 1999; Leech and Leonard, 1997; Redondo and Castro, 1992; but see Halupka, 1998). As a consequence, predation imposes an intense selective pressure on begging calls to be less easy to locate (Haskell, 1999; Redondo and Arias de Reyna, 1988); on larger broods to be less noisy (Harper, 1986); on nestlings to reduce escalation of begging calls when competing with siblings (Briskie et al., 1999), and on parents to alert offspring to be silent when a predator is close to the nest (Halupka, 1998; Nuechterlein, 1988). Although the predation cost of begging is often substantial, in some predatory species (e.g., eagles) there is no such cost, since nestlings do not suffer predation despite begging intensely (Cramp and Simmons, 1980).

Punishment cost

In some species, begging elicits aggressive behavior from parents (Leonard et al., 1988, 1991) and siblings (Braun and Hunt, 1983; Drummond and Chavelas, 1989; Nuechterlein, 1981). For instance, in the black-capped chickadee (*Parus atricapillus*), parents are aggressive towards fledglings that persistently beg for food. This parental behavior may force offspring to forage independently (Leonard et al., 1991). In the western grebe (*Aechmophorus occidentalis*), dominant nestlings peck younger siblings that beg for food perhaps because such intimidative behavior facilitates the monopolization of a larger than equal share of the resources provided by the parents (Nuechterlein, 1981). Although punishment costs may play a role in the maintenance of begging as an honest signal of need in some species, few actual cases of punishment have been reported in the literature. This suggests that such costs may not be particularly widespread.

Physical cost

Begging involves conspicuous vocalization and stretching of the neck and legs. The observation that the intensity of these activities predicts which nestling is fed first (e.g., Dearborn, 1998; Hofstetter and Ritchison, 1998; Lichtenstein and Sealy, 1998; Teather, 1992) motivated researchers to investigate the cost of begging imposed by physical effort. To date, only five studies have examined the energetic cost of begging, by comparing the quantity of oxygen consumed by begging and nonbegging nestlings under laboratory conditions. Using closed-chamber respirometry, nestlings of seven bird species were tested one at a time (Bachman and Chappell, 1998; Chappell and Bachman, 1998; Leech and Leonard, 1996; McCarty, 1996). Nestlings were removed from their nest 30–120 min beforehand and tested over a 15 min period. Begging was found to elevate the metabolic rate of chicks by only 1.05–1.28 times (Leech and Leonard, 1996; MacCarty, 1996), in stark contrast to song and sexual displays that raise metabolic rate by up to 15.6 times (Leech and Leonard, 1996). Soler et al. (1999) used the doubly labeled water technique in the great spotted cuckoo (*Clamator glandarius*) and magpie (*Pica pica*), a method that allowed them to measure begging effort over a complete day. Two cuckoo and two magpie nestlings were removed from different nests a day before being tested together in a same artificial nest. Under laboratory conditions, they were stimulated four times during 20 min every 2 h (i.e., one feeding session). A total of 7–8 such feeding sessions were performed during the day of the experiment. Begging nestlings consumed a nonsignificantly higher quantity of oxygen than nonbegging nestlings, suggesting that begging is not extremely costly.

The apparently low energetic expenditure found in all five studies may be due to the fact that: (a) measurement of oxygen consumption disregards anaerobic metabolism, a possible source of energy during short-term begging activities that require intense muscular activities (Chappell and Bachman, 1998; Weathers et al., 1997); (b) nestlings were not begging constantly during the tests (Kilner and Johnstone, 1997); and (c) low energetic expenditure does not necessarily imply that begging does not impose fitness penalties (Verhulst and Wiersma, 1997).

In the following section, I point out an overlooked aspect of begging, namely vigilance, that may entail energetic costs and other more intricate costs. I refer to this cost as "the vigilance cost of begging."

The vigilance component of begging

Definition and assessment of the vigilance component of begging
In the context of begging studies, I define vigilance as the process by which offspring look out for parents' arrival in order to start to beg as quickly as possible. Vigilance requires selective attention, that is the ability to distinguish relevant (e.g., the noise made by an arriving parent) from nonrelevant stimuli (e.g., the noise made by wind), but also the ability to react quickly once the relevant stimuli occurred. The assessment of interindividual variation in the level of vigilance and of within individual alteration in vigilance performance can be done at two levels. From a behavioral perspective, one can measure the time required to beg once a parent is detected, that is the rapidity to resume vocalization behavior (particularly important in the context of parent-offspring interactions) or to move body (particularly important in the context of sibling competition). From a physiological perspective, vigilance can be assessed via electrophysiology using electroencephalogram (EEG) and via cardiovascular activity using electrocardiogram (ECG). In human, it has been shown that more vigilant individuals differ from others in the form taken by the alpha-, beta- and delta-waves on a EEG (Schulz et al., 1996; Schwarz-Ottersbach and Goldberg, 1986) but also in interbeat interval and heart rate (Beh, 1990). Thus, it may be worth developing these physiological methods to assess the level of vigilance in nonhuman organisms.

Evidence that more vigilant nestlings are fed first
Chicks should be vigilant by watching out for their parents' return, if a rapid begging reaction increases the likelihood to be fed before nest-mates. This may be so either because parents feed them in priority or because rapid chicks have advantages in sibling competition. Correlational evidence that a nestling increases the likelihood of receiving a food item from its parents when it starts to beg before its nest-mates has been given in indigo buntings (*Passerina cyanea*) (Dearborn, 1998), red-winged blackbirds (*Agelaius phoeniceus*) (Teather, 1992), and Eastern screech-owls (*Otus asio*) (Hofstetter and Ritchison, 1998). Apparently, in the latter study the difference in the rapidity with which fed and unfed chicks started to beg once a parent arrived was relatively larger than the differences in calling rate and volume.

To further examine whether in the face of sibling competition nestlings benefit from being vigilant, I recorded begging activity of barn owls (*Tyto alba*) located in western Switzerland. This species is especially interesting as nestlings vocalize both in the absence and presence of the parents. Calls produced in their absence have been shown to facilitate sibling negotiation over resources next delivered by the parents (Roulin et al., 2000). I created 65 two-chick broods (five of them were tested twice using different chicks) by temporarily removing other siblings out of their nest, randomly chosen. These broods were created in the evening, and from 2130 to 2330 h. I filmed them using an infra-red sensitive camera and a microphone. On the videos, I counted the number of calls produced by the two siblings during 15 min before a parent arrived with the first prey item of the night. I also counted calls in the presence of the parent, that is just before it delivered its prey item to one of the two offspring identified with a ring placed on a different leg. The more vigilant nestling was defined as the one that reacted first (i.e., that made a body movement) after a parent landed on the perch. In some cases, I could not determine which nestling moved first, and both siblings were considered as similarly vigilant.

In the absence of the parent, the more vigilant nestling vocalized more intensely than its less vigilant sibling (Wilcox-
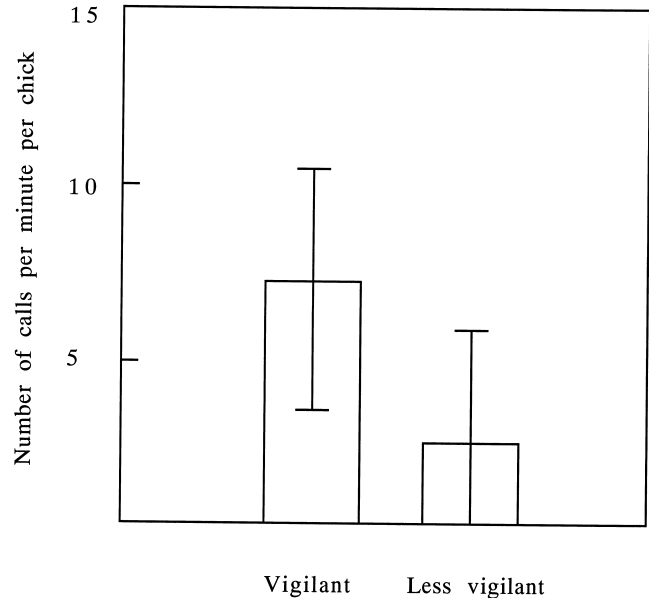

Figure 1
Calling rate of two siblings in the absence of the parents. The most vigilant individual was defined as the one that moved body most rapidly when a parent landed on the perch of the nest-box. Sample size is 47 experimental two-chick broods (10 in 1997, two in 1998, and 35 in 2000). Histograms represent median and bars interquartiles.

on matched-pair signed-rank test, $z = 2.86$, $p = .004$, $n = 47$; Figure 1), and tended to do so in the presence of parents ($z = 1.61$, $p = .11$, $n = 37$; note that sample size is lower since nestlings were sometimes not visible in the presence of the parents precluding any assignment of begging calls to one of the two siblings). When the nestling that monopolized the item vocalized more intensely than its sibling, it was more vigilant in 27 cases (85%), as vigilant in two cases (6%), and less vigilant in three cases (9%). To determine whether vigilance may provide competitive advantages independently of begging intensity, I considered 21 broods for which the nestling that received the first prey item delivered of the night vocalized less intensely than its sibling. In this sample of broods, the less vocal chick was more vigilant than its sibling in 11 cases (52%), as vigilant in four cases (19%), and less vigilant in the last six cases (29%). Thus, a high level of vigilance appears to be correlated to the probability of being fed first despite low begging level (in 71% of the 21 broods, binomial test, $p = .039$, one-tailed). Note that vigilance level was not related to hatching asynchrony given that in 25 out of 47 cases (53%, binomial test, $p > .50$) the younger chick was more vigilant than its older sibling. Taken together, the three above mentioned studies (Dearborn, 1998; Hofstetter and Ritchison, 1998; Teather, 1992) and my observations suggest that a chick is more likely to be fed first when it reacts more quickly than siblings at the arrival of a parent.

Is the vigilance component of begging costly?
Although a nestling increases the likelihood of receiving a food item from its parents when it starts to beg before its nest-mates (Dearborn, 1998; Hofstetter and Ritchison, 1998; Lichtenstein and Sealy, 1998; Teather, 1992; present study), the rapidity with which nestlings commence begging has not yet been considered as potentially costly. Vigilance may be expensive as nestlings that start to beg rapidly at the arrival of a parent often resume begging for irrelevant stimuli such as the noise of wind or rain (Dearborn, 1998). Thus a high level of

vigilance may lead nestlings to beg on inappropriate occasions. However, this may not be the only cost of vigilance.

The competitive advantage provided by a rapid begging reaction surely requires a high level of vigilance that involves extra activity in the brain, one of the most metabolically active organs in the body (Roland, 1993). In human, vigilance for attention and decision making is energetically demanding and is sustained over a long time period only with difficulty (Åhsberg et al., 2000; Davies and Parasuraman, 1982). Vigilance tasks involve mental processes such as information processing, requiring glucose (Benton et al., 1994) and oxygen (Moss et al., 1998). The energy released by the oxidation of glucose enhances the synthesis of acetylcholine (among other neurotransmitters; Buchanan, 2000), a crucial molecule for maintaining a high level of vigilance (Wesnes and Warburton, 1984) and locomotion (Sholomenko et al., 1991). Depletion in energy due to vigilance thus leads to depletion in acetylcholine levels. This, in turn, leads to a further reduction in vigilance and a lowered motivation to invest in expensive activities (Åhsberg et al., 2000). Since vigilance appears to provide advantages in sibling competition, nestlings would be expected to invest a substantial amount of energy in vigilant behavior, perhaps at the expense of the intensity of begging (since both activities rely on energy). However, the trade-off here may not be simple. In humans, a slight physical effort enhances vigilance, where intense physical effort sustained over a longer time period impairs vigilance (Davey, 1973).

A physiological cost of vigilance may not solely lie in energetic terms, but also in the capacity to mount an efficient immune response against invading parasites and pathogens. The nervous and immune systems are tightly linked (Maier et al., 1994). Acetylcholine, the previously described neurotransmitter that is important for sustaining vigilance tasks, has been shown to have immunosuppressive effects and, conversely, the activation of the immune system partly suppresses the synthesis of acetylcholine (Qiu et al., 1996). Although these interactions may be adaptive, the requirement for a high level of vigilance may trade off against the efficiency of the immune system.

Finally, a high level of vigilance prevents nestlings from sleeping, and thus recovering from energetically expensive activities including begging. Sleep deprivation is generally stressful and leads to reduced vigilance (Cameron, 1973). Nestlings may be so tired that even when they are hungry, they may stop being vigilant and rest. This may explain why only a fraction of the nestlings in a brood beg when the parents arrive at the nest, unless, individuals that rested were all food-satiated (Bengtsson and Rydén, 1981; Lessells and Avery, 1989). This cost of vigilance may be particularly relevant in species in which brood size is large and feeding rate is high. Although a target nestling has ample occasion to be vigilant when parents regularly bring food items, the probability of being fed on a given parental visit is low when the number of competitors is high. Moreover, when food is not divisible, a nestling that is fed last in a sequence may not sustain a high level of vigilance throughout the time its nest-mates are being fed.

Methodological consequences of vigilance for the study of the cost of begging

The hypothesis of a vigilance cost of begging has several consequences for how the cost of begging should be measured. First, although two chicks may expend the same effort in physical begging, the chick begging first may pay a greater cost of vigilance. Several experiments (Bachman and Chappell, 1998; Chappell and Bachman, 1998; Leech and Leonard, 1996; McCarty, 1996) have measured the amount of energy consumed by a nestling by isolating it from its nest-mates and inducing it to beg. However, since high levels of vigilance are needed most when sibling competition is intense, such measurements may underestimate the cost of begging under natural conditions.

Second, since vigilance can be sustained only over a short time period (Åhsberg et al., 2000; Davies and Parasuraman, 1982), the energy nestlings invest in begging should be measured over a long time period. This may be crucial if the cost of vigilance increases exponentially with time, that is, where nestlings do not have sufficient time available to rest and restore depleted energy, due to the accumulation of fatigue. Therefore, one way to assess the cost of begging may be to quantify the extent to which nestlings are able to sustain begging and vigilance, but also the time required for recovering from those activities. Another way may be to provide extra energy (e.g., addition of glucose) to the chicks and to monitor their subsequent begging behavior. If begging entails costs, provided chicks should beg more intensely than nonprovided ones and be more vigilant, although chicks may be less hungry due to the consumption of glucose. Furthermore, one could assess whether the ability to outcompete siblings in successive contests increases when vigilance is sustained during a short time period but falls down when nestlings are forced to be vigilant during a longer period. As a consequence, the removal of nestlings from their nest followed by testing for oxygen consumption 30–120 min later (Bachman and Chappell, 1998; Chappell and Bachman, 1998; Leech and Leonard, 1996; McCarty, 1996) may fail to stimulate the conditions under which a vigilance cost could be detected. Nestlings were no longer under the stress of sibling competition and have had ample time to restore from the costs incurred by begging (perhaps, nestlings that were stimulated to beg in the laboratory were in prime conditions). In this context, one could manipulate the predictability of parental feeding visits. If visits are predictable nestlings know exactly when they can start to beg and thus, they may not require a high level of vigilance. By contrast, if parental visits are unpredictable chicks may need to be more vigilant to commence begging as rapidly as possible when a food item is delivered. In other words, the cost of begging may be large when feeding visits are not predictable due to the requirement of a high level of vigilance. However, note that the opposite prediction may apply as well. Indeed, when feeding intervals are fixed, nestlings may start to invest substantially in vigilance a short time before the expected arrival of a parent, thereby paying a larger vigilance cost than in broods for which feeding intervals are not fixed (e.g., Zeichner et al., 1990).

Finally, because vigilance relies on the nervous system, measurements of a vigilance cost may be confounded by the stress researchers provoked when eliciting begging. Therefore, it would be worth considering field experiments instead of laboratory experiments to assess the cost of begging, since unnatural designs may stress birds. Furthermore, given the immunosuppressive effect of acetylcholine (and of other neurohormones; Buchanan, 2000), it would be interesting to measure immune response toward an artificially administered antigen in situations where a high degree of vigilance has to be sustained. One should also be able to distinguish between the effect of begging intensity and vigilance on immunosuppression. A potential experimental design is to increase the level of environmental noise (e.g., the noise made by leaves) between parental visits to render more difficult the ability to determine the exact moment when a parent arrives at the nest, and thereby to force nestlings to be more vigilant (e.g., Carter and Beh, 1989). Noise during parental visits should not be manipulated to avoid altering parent-offspring interactions.

Evolutionary consequences of vigilance

The parent-offspring conflict over parental investment may be resolved through begging behavior (Godfray, 1995a). Begging involves several components and the function of each is likely to differ. Escalation in vocalization may be the outcome of sibling competition to attract the attention of parents (Harper, 1986; MacNair and Parker, 1979; Rodríguez-Gironés et al., 1996), but also to honestly signal hunger level (Godfray, 1995b). By contrast, mouth coloration may reflect an aspect of quality such as health (Saino et al., 2000), although this does not exclude the possibility that this signal may also reveal hunger levels (Kilner, 1997). Furthermore, stretching of the neck and legs may indicate size and thereby influence parents if they preferentially feed larger chicks (Slagsvold, 1997). Clearly, begging has several components on which selection can act.

Suggestive evidence that the vigilance component of begging is or has been subject to selection is provided by the studies of Dearborn (1998) and Lichtenstein and Sealy (1998). These researchers studied brown-headed cowbirds (*Molothrus ater*), a species that lays eggs in the nests of other species, in their case indigo buntings. Unlike many other brood parasites, cowbirds do not eject the host's eggs and nestlings. This provides an exceptional opportunity to study parent-offspring conflict at the genetic level, because (a) parents are related to the young they are caring for, except for the cowbird nestlings, and (b) cowbird nestlings are not related to their nest-mates. The latter condition implies that a cowbird nestling does not gain any inclusive fitness benefits from allowing its nest-mates to be fed first, and hence it should be under strong selection to outcompete its nest-mates by responding very rapidly to the arrival of the parent. The monopolization of a disproportionate share of the resources by cowbird chicks (Dearborn, 1998; Lichtenstein and Sealy, 1998) may compensate for the cost involved by their more rapid begging response when the foster parent arrives at the nest. This implies that the evolution of a higher degree of vigilance in cowbirds may have occurred. In other words, selection may have favored the evolution of a better ability to detect sooner an approaching parent (hearing), to process this information, and to develop body structures allowing rapid movements. In contrast, the host's offspring gain inclusive fitness benefits by sharing resources with their siblings, and therefore they may be under a weaker selection pressure to develop a high degree of vigilance. If parasitism by cowbirds is sufficiently rare, selection is unlikely to be strong enough to enable host nestlings to outcompete cowbird chicks. This example suggests that begging escalation resulting from sibling competition may not always be apparent in terms of the frequency and volume of begging calls, but also in the latency period before offspring start to vocalize once parents are at the nest.

Escalation in vigilance may not only result from sibling competition, but may signal food requirement to parents. Here, I provide two examples where the hypothesis of a vigilance component of begging may help us to understand how the environment may interact with the evolution of honest signals of need. First, species that are under intense predation pressure have evolved begging calls of different acoustic structure (Haskell, 1999), and may therefore be constrained in the way they can honestly signal food requirement. If loudness is a signal of food requirement, but also attracts predators, begging calls may evolve to be less conspicuous so that parents have to rely on other cues to accurately assess hunger level (Marín, 1997). One such cue may be the speed with which nestlings react to their arrival or to parental calls that stimulate begging behavior (e.g., Dee Boersma and Davis, 1997; Leonard et al., 1997). Since the arrival of a parent may not be predictable, parents can be confident that the nestling that resumes begging most rapidly is the most vigilant. Parents may also benefit themselves from a rapid offspring reaction, since they may return to forage again more quickly. If this is the case, the vigilance component of begging may also be selected in species producing a single chick.

As a second example, recent theoretical developments have incorporated the realistic possibility that parents may not always accurately assess signals of need. For instance, background noise may be so high that the difficulty in assessing begging signals correctly may select for more conspicuous signals and hence more costly signals (Johnstone, 1998). For instance, colonies of the king penguin (*Aptenodytes patagonicus*) can number up to 300,000 pairs, and the noise created by so many individuals may have selected for begging signals that are very efficiently transmitted from chicks to parents (Aubin and Jouventin, 1998). However, as pointed out by Johnstone (1998), if the level of noise or perceptual error by the parents is so great that the costs of an efficiently transmitted begging signal cannot be met by the offspring, then the signaling system is no longer evolutionarily stable. In such cases, the species may develop other cues that are not degraded by environmental noise. One such cue may be a high level of vigilance.

Conclusion

Many theoretical developments on begging in the context of parent-offspring conflict have emerged recently (Godfray, 1995a). These models are based on the assumption that begging entails fitness costs. To date, empirical evidence for such costs are limited, and even raise the question of whether costs exist at all (e.g., Leech and Leonard, 1996). Some workers have also envisaged cost-free begging in new theories of signaling (Bergstrom and Lachmann, 1998). After reviewing the evidence for costs of begging, I have outlined some of the implications arising from the suggestion that begging may entail a vigilance cost. Although vigilance appears to entail costs, these may be different from those so far considered (predation, punishment, and physical costs), and therefore selection for honest signals of need may independently be exerted on several components of begging, depending on the constraints facing each species. This review points out that apparently cost-free signals may entail complex costs that are not immediately apparent. Consideration of a vigilance cost of begging opens up new areas of research in the context of parent-offspring conflict.

Address correspondence to A. Roulin. E-mail: ra241@cam.ac.uk.

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Flight, fitness, and sexual selection

Anders Pape Møller and Andres Barbosa
Laboratoire d'Ecologie Evolutive Parasitaire, CNRS FRE 2365, Université Pierre et Marie Curie, 7 quai St. Bernard, Case 237, F-75252 Paris Cedex 05, France, and Museo Nacional de Ciencias Naturales (CSIC), Dept. Ecología Evolutiva, J. Gutierrez Abascal 2, E-28006 Madrid, Spain

Buchanan and Evans (2000) have recently suggested that the length of the tail streamer of the barn swallow *Hirundo rustica* is influenced to a large extent by natural selection, although sexual selection also plays a role. This conclusion was reached from analyses of video films of the flight of males and females after reducing the length of their tails by a variable amount ranging from 0 to 20 mm. Evans (1998) has previously made a similar experiment with a 20 mm manipulation. The optimum phenotype was subsequently derived from analyses of the flight parameters, while taking a number of other factors such as sex, farm, morphology, and date into account. Here we suggest that although it is likely that in fact streamer evolution was due to both natural and sexual selection, there is little direct evidence to support the reported conclusions. Although natural selection obviously plays a role in determining the selective landscape affecting tail length (e.g., Møller, 1989; Møller et al., 1995; Saino and Møller, 1996; Saino et al., 1997), it is far from clear that the cost is mainly measured in terms of foraging ability. Other factors like parasitism and disease have already been shown to be important (Saino and Møller, 1996; Saino et al., 1997). The reasons why the paper by Buchanan and Evans (2000) does not resolve whether tail length is mainly influenced by natural or sexual selection are as follows. (1) Buchanan and Evans did not standardize the conditions under which the measurements were made. (2) They provide no direct evidence for any of their aerodynamic parameters having a fitness consequence. (3) The birds were filmed at variable intervals since the experimental manipulation. (4) The context in which the flight behavior was recorded does not represent the relevant selective pressure.

The first problem concerns lack of standardization of experimental conditions. Buchanan and Evans (2000) filmed 68 barn swallows during brood provisioning of first and second broods. This was done when the birds were entering and leaving the building housing the nest site. This procedure (and that adopted by Evans, 1998) is problematic for at least three reasons. First, the flight trajectory will obviously depend on the way in which a bird will enter its nest site. Sites differ in location from those positioned in a way so the bird must turn sharply to enter, to those that allow a direct, straight approach. Entrances to buildings also differ from open doors to tiny holes in window, requiring different behavior during approach. These differences in the nest sites will obviously affect the flight parameters recorded during the approach. The second reason why the video recordings are problematic is that

the age of the nestlings and brood size was not standardized (or even entered as covariates in the analyses). Both the number and the size of the nestlings will affect the work level of the parent and hence its behavior. We know from extensive studies of barn swallows in seven European countries that reproductive success increases strongly with male tail length, but not or only very little with female tail length (Møller, 1994). Thus, individuals with different tail lengths will differ in their provisioning rate and hence working rate. This is likely to have consequences for their flight performance. Third, there are no fitness consequences of the flight behavior of parent barn swallows when they approach and leave their nest. A superficially simple interpretation of the data would be that all these factors would increase the error term in the analyses, and that the analyses hence would be conservative. However, interpretations should be made cautiously when relatively small sample sizes are used. How can we in such situations discern effects due to experimental noise and true biological effects? This interpretation is supported by a lack of consistency in measures between studies. Evans (1998) reported an increase of flight velocity of 10 m/s, when comparing controls and birds with 20 mm shortening. Buchanan and Evans (2000) reported a reduction. Agility increased from 300 to 600 degrees/s in Evans (1998), when comparing controls and birds with 20 mm shortening, while Buchanan and Evans (2000) report an increase from 2500 to 3000 degrees/s for the same treatments. This lack of consistency across studies needs explanation, since it is not only caused by differences in base vs. tip manipulations (see Evans, 1998 where both types of manipulations were done), and it renders the reported results unlikely to be robust. Alternatively, there are errors in the calculations and the reported findings. Hence, any interpretation will depend on whether Evans (1998) or Buchanan and Evans (2000) is used as the basis.

The second major problem with the study by Buchanan and Evans (2000) is that they never quantify the fitness consequences of the aerodynamic parameters. If there is a natural selection advantage of long tails in the barn swallow (Norberg, 1994), it should be possible to predict reproductive performance, for example measured in terms of number of fledglings, number of broods and quality of offspring, from the aerodynamic parameters, as obtained in this experiment. If there is a natural selection cost of long tails, it should result in a reduction in fitness components. We have in a large number of studies shown intermediate to strong effects (explaining 10 to 25% of the variance [Cohen, 1988] or even more) of male tail length on reproductive success due to sexual selection (reviews in Møller, 1994 and Møller et al., 1998; more recent studies showing similar effects include Møller et al., 1998; Kose and Møller, 1999; Kose et al., 1999; and several as yet unpublished studies). This has been done using sample sizes of the same order of magnitude as those used by Buchanan and Evans (2000). However, we have been unable to demonstrate similar effects on fitness components of the females (Cuervo et al., 1996a,b), which contrasts with the large degree of similarity between the sexes reported by Buchanan and Evans (2000). Furthermore, we have been unable to demonstrate natural selection advantages of a long tail in male barn swallows. Suggestions that males benefit from a long tail streamer (Norberg, 1994) should be supported by rejection of the null hypothesis. Until that has happened we must as good scientists assume no effects. Most recently, Cadée (2000) has used natural variation in tail asymmetry of barn swallows to investigate the consequences for reproductive success and offspring quality. The latter was measured as tarsus length, body mass, body condition, the size of the buffy coat (a measure of health status) and a T cell mediated response to an immune challenge. None of these variables were related to differences in parental tail length. This was even

the case when examining the quality of offspring produced by adults with broken, and hence highly asymmetric, tail feathers. Thus, we can conclude that while sexual selection as measured in different experiments accounts for intermediate to large amounts of variance in success, there is not even a small (explaining 1% of the variance [sensu Cohen, 1988]) effect of natural selection in this case. Thus, current estimates of natural and sexual selection pressures on the length of the tail in male barn swallows indicate that there is at least a difference of an order of magnitude between these two components. Some might state that it is obvious that aerodynamic parameters as determined by morphology affects fitness, even when no explicit effects on reproductive success were found. However, the nest approach flight investigated by Buchanan and Evans to study the importance of natural selection on streamer morphology is unlikely to affect fitness components, as discussed below. Moreover, given that even tiny costs are sufficient to cause large degrees of evolutionary change, small costs may be sufficient to have molded the shape of tail feathers during evolutionary time.

Third, Buchanan and Evans (2000) filmed manipulated barn swallows from 1 to 7 days after manipulation of the tail feathers. Barn swallows with manipulated tail feathers have altered flight behavior after release (own observations), but we would expect that birds eventually adjust their flight behavior to their morphology. Such adjustment would be adaptive in the case of feather breakage, which is a common phenomenon in barn swallows during and after the breeding season (Kose and Møller, 1999; Møller, 1994). Adjustment would also be able to account for the apparent absence of effects of tail manipulation of females on their fitness components (Cuervo et al., 1996a,b). Without entering the interval since manipulation as a covariate in the statistical analyses, the findings can have been seriously biased by differences in the duration of habituation to the novel morphology.

The interpretation of the results in terms of costs and benefits and their evolutionary implications are not straightforward. An example of this problem can be seen in Figure 3 in Buchanan and Evans (2000). According to this figure the experimental change in tail length by 10 mm (the consistent turning point of Buchanan and Evans, 2000) has to be explained by different mechanisms in long-tailed and short-tailed birds, while a further reduction reverses the pattern. In addition, tails that are approximately 100 mm long cannot be explained by any of the proposed mechanisms, as there is almost no effect of manipulation. A likely explanation is that it might be difficult to determine costs and benefits of a certain morphology, if estimates derive from approach flights to the nest rather than more important foraging flight.

Finally, but not least important, is the time when the birds were filmed. Filming the bird when entering or leaving the breeding site introduces a bias since the flight requirements are different in these two circumstances. Most importantly, the selective pressure associated with flight used when provisioning nestlings is biologically and aerodynamically irrelevant in comparison with foraging flight. This makes it unlikely that the reported results have the evolutionary implications intended. Thus, the authors cannot conclude anything about the evolutionary mechanisms for their experiment, since the relevant selection pressures will operate during foraging (which takes place throughout the year) rather than the actual approach to the nest (which occupies a small amount of the annual cycle).

In conclusion, Buchanan and Evans (2000) have used potentially biased data on aerodynamics to test their hypothesis. They have not corrected their findings for habituation by the experimental birds, and, most seriously, they have shown no evidence of a natural selection advantage of the flight parameters caused by experimental or natural differences in tail length. This sug-

gests that there is no measurable natural selection in their experiment and hence no measurable fitness consequences of the so-called Norberg effect (Norberg, 1994).

Address correspondence to A.P. Møller. E-mail: amoller@hall.snv.jussieu.fr.

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Flight, fitness, and sexual selection: a response

K. L. Buchanan and M. R. Evans
Department of Biological and Molecular Sciences, University of Stirling, Stirling FK9 4LA, UK

We are disappointed to find that Møller and Barbosa (2001) view our recent reporting of a naturally selected portion of the tail streamer of the barn swallow as unconvincing. They raise four points, which we will deal with in turn.

The lack of standardization of environmental conditions is an unfortunate consequence of conducting this kind of work in the field. The general approach to this problem in the ecological literature is to use random allocation of birds to experimental groups. This makes it unlikely that different groups vary systematically in environmental conditions and would mean that significant results were harder to obtain with differing environmental conditions inflating the error term in any analysis. Møller and Barbosa raise two particular issues—nest site geography and breeding effort.

We agree that the geography of the nest site may have some influence on the flight trajectory and this is why the farm was entered (as a categorical variable) into the analyses, to control for variation in the building structure at the nest site. The farm factor explained significant variance in three variables (Buchanan and Evans, 2000: Table 4). We therefore feel that we have controlled for any variance due to this factor. We would also point out that all the flights we recorded were outside buildings and were therefore not constrained by internal structures within the buildings.

Møller and Barbosa also argue that the manipulations should have been standardized both to the breeding attempt and to chick age. Unfortunately we did not record breeding variables during our study as we focussed entirely on the flight of the birds. We reiterate that birds were randomly allocated into experimental groups, therefore any differences in breeding activity between birds would increase the variance between them making significant results harder, rather than easier to obtain. Furthermore, it should be noted (as stated in the Methods) that date of the assessment of flight performance was added into all models during the analysis and was eliminated each time, as it was not found to explain significant variation in individual flight performance. We would also point out that we calculated repeatability estimates for all our flight variables, and these suggested that the between individual variation in flight performance was significantly greater than the within individual variation. This result is unlikely if stage of breeding influenced flight performance.

Møller and Barbosa note a ''lack of consistency'' between the results reported in Evans (1998) and those reported in Buchanan and Evans (2000), when referring to the effect a 20 mm reduction has on flight performance. There are two important points to note here. First, the nature of the manipulations differed between the two studies; in the earlier study two types of manipulation were used and for both types the original feather was cut and replaced with an appropriate length of feather, following the example set by Møller's work. However, in Buchanan and Evans (2000) the original streamers were reduced in length by trimming the tip without cutting the feather. The difference in the nature of these manipulations will have produced fundamentally different effects on flight performance, but does not negate the conclusions of either study. One of the reasons Buchanan and Evans (2000) used their manipulation method was because Evans (1998) had clearly demonstrated that the type of manipulation carried out had a strong effect on the results obtained and that cutting a tail feather at the base is likely to have fundamental effects on its aerodynamic properties. We would strongly argue that the manipulations carried out by Buchanan and Evans (2000) should be interpreted as having greater biological relevance to the effects of tail length on flight performance in the barn swallow, as in this study the integrity of the feather remained complete. The effect of cutting the feather has been seen in a more recent experiment (Evans MR, Cherry MI and Dowse A, unpublished data). For most flight variables cutting the feather results in a stepwise change in performance. For example, the mean flight velocity of sunbirds (*Nectarinia violacea*) with cut tail feathers was just over 3 m/s faster than that of sunbirds with uncut feathers of the same length. We would suggest that, where possible, cutting tail feathers should be avoided as it disrupts the aeroelastic properties of the feather. However, sometimes it is unavoidable, for example when conducting tail elongation manipulations.

Second, Buchanan and Evans (2000) pointed out in some detail that original streamer length greatly affects the way in which tail reductions affect flight performance. Figure 2 in Buchanan and Evans (2000) demonstrates that for both mean velocity and maximum agility the direction of the change between the control treatment and the 20 mm reduction is dependent on the original tail length of the birds within treatment groups.

We would also like to correct three factual errors made by Møller and Barbosa. It should be noted that while Evans (1998) reports an effect on mean agility, Buchanan and Evans (2000) refer to maximum agility—as such, the results of the two studies cannot be compared. The mean agility of birds in Buchanan and Evans (2000) is 369 ± 12.6 degrees/s, which is very similar to that in Evans (1998). Møller and Barbosa also suggest that in Evans (1998) birds with shortened tails had a mean velocity 10 m/s greater than controls; the real difference is 8.3 m/s (Evans 1998) which compares with a difference of +1.3 m/s for a male with a 120 mm streamer and −1.0 m/s for a male with a 100 mm streamer. Finally, Evans (1998) did not conduct tip manipulations, as suggested by Møller and Barbosa. Two manipulations types were used by Evans (1998); feather was added or removed from the basal portion of the tail feather or from the streamer, but in both cases the feather was cut and rejoined. If this technique had not been used the streamer and basal manipulation types could not have been compared.

We would also like to stress the difference in between the manipulation technique that we have used and that adopted by Møller and his co-workers. We have trimmed the feather while leaving the original feather intact—allowing it to move appropriately. Møller has adopted a technique where the entire feather is cut and rejoined, but this is likely to have negative effects on the aeroelastic properties of the feather. The other unfortunate consequence of Møller's manipulation technique is that it changes the size of the non-sexually dimorphic basal part of the feather while leaving the sexually dimorphic streamer unaffected. We have adopted a technique that allows us to manipulate the streamer itself, rather than the basal part of the feather which is not of interest. Evans (1998) found that the type of manipulation used had large effects on the size and shape of the relation between manipulation and flight. This result has recently been confirmed using doubly labelled water to measure daily energy expenditure. There is little effect of manipulation when basal manipulations are conducted (Cuervo et al., 1996; Hall A, personal communication) while streamer manipulations show pronounced U-shaped relationships (Hall A, personal communication).

Møller and Barbosa suggest that as Buchanan and Evans

(2000) did not report any fitness benefits from the aerodynamic parameters examined, that none exist. We would suggest that this is a rather hasty interpretation of our results. The concept of fitness is defined as "the average per capita lifetime contribution of individuals of that genotype to the population after one or more generations" (Futuyma, 1998). As such, it is probably impossible to measure fitness directly. The majority of field studies tend to assess surrogate measures of fitness for example, the length of the pre-mating period, percent of second clutches, and annual reproductive output (Møller, 1988). None of these variables measure fitness directly, although it is assumed that they vary with fitness. Just as Møller and co-workers have used surrogate fitness measures for the benefits of streamer possession, we were faced with identifying surrogate fitness measures for the costs of streamer possession. Certainly it is true that our study did not attempt to demonstrate that certain flight performance characteristics result in for example, higher reproductive success for individuals. But we would suggest that flight performance is indisputably linked to foraging success, which in turn is likely to have fitness consequences. On a conceptual note it is difficult to see how any experiment to examine the fitness consequences of tail manipulation could be conducted. We assume (under the adaptationist paradigm) that any trait is at its optimum at its current level. So we would assume that swallow streamer length was currently at its equilibrium optimal size for each individual. Therefore, any manipulations are ultimately and inevitably going to have negative effects on fitness. We would like to point out that the theoretical framework for interpreting changes in flight performance with changes in tail length is covered in detail in Evans and Thomas (1997), and this framework assumes that deviations from the optimal tail length would be deleterious in terms of fitness. Møller (1988) demonstrated that streamer elongations improved annual reproductive success. This did not mean that swallows were somehow sub-optimal and should be producing longer streamers. Møller (1989) showed that males given long streamers incurred costs in following seasons—this was taken as evidence that streamers were costly. The negative effect of elongated streamers on the following season could be conceptualized as balancing their positive effect on the current season producing an optimal overall streamer length. Therefore, any experiment that attempted to examine the effect of tail manipulations on fitness would be doomed to failure—negative fitness effects would inevitably be detected with any deviation from the observed value. It is necessary to break down the selective pressures on trait size, to quantify the selection leading to optimal size for each individual. While Møller and his co-workers have focussed on the surrogate measures of the benefits of streamer possession, we have tried to examine surrogate measures of the costs—and we would argue that both are needed for a full understanding of the evolution of the trait. Our results should be regarded as drawing attention to the fact that earlier work has treated aerodynamics as a black box. We feel it is reasonable to assume that differences in for example, the prey caught by swallows with different tail manipulations occur because of changes in flight rather than different food preferences of birds with different tail manipulations.

Additionally, these experiments allowed us to examine the extent to which sexual selection was responsible for streamer elongation, a question that came to prominence with the publication of a plausible mechanism for streamer elongation under natural selection (Norberg, 1994). Examination of variables like annual reproductive output would be unable to distinguish natural and sexual selection, as both hypotheses would predict increased success with increased streamer length. In order to determine the extent of sexual selection

and natural selection the costs have to be examined. Our data strongly suggest that the bulk of the streamer has been produced by natural selection but that sexual selection has extended the streamer beyond the aerodynamic optimum by c15 mm.

Møller and Barbosa suggest that we have been attempting to demonstrate that males benefit from a long tail streamer, when in fact this is an over-simplification of the case. Instead we would argue that our results show that males can benefit from a long tail streamer, depending on their original morphology, but that from an aerodynamic point of view streamers should all be shorter than current lengths. The central aim of our study was, therefore, to demonstrate that both natural and sexual selection have been important in shaping the tail streamer of the barn swallow—not to investigate fitness benefits.

Møller and Barbosa suggest that variation in the time between tail manipulation and the assessment of flight performance could cause major error in the results due to differences in the degree of habituation. We would suggest that if this were the case we would not have found significant repeatabilities (e.g., mean velocity 73.6%, $p < .05$) for the flight parameters measured on different days post-manipulation. However, in an effort to address this issue directly we have re-analyzed the results reported in Buchanan and Evans (2000) including the time between manipulation and filming in each of the glm models determining the effects of manipulation on flight performance. We can confirm that the time between manipulation and filming was not a significant predictor of flight performance for any of the flight variables (mean velocity, $F_{1,34} = 0.76$, $p = .39$; maximum curvature, $F_{1,26} = 0.14$, $p = .714$; maximum agility, $F_{1,29} = 3.82$, $p = .06$; mean xy rate change, $F_{1,26} = 0.02$, $p = .887$; mean acceleration, $F_{1,33} = 3.31$, $p = .078$; PC1, $F_{1,32} = 0.07$, $p = .791$; PC2, $F_{1,44} = 2.21$, $p = .144$). Furthermore, including time between manipulation and filming did not significantly affect any of the model variables for the results originally reported in Buchanan and Evans (2000).

Møller and Barbosa go on to address the optimal flight strategies of birds with different tail lengths, but unfortunately have misinterpreted Figure 3 of Buchanan and Evans (2000). The issue of how original tail length contributes to the effect of tail manipulation on flight is a complex one, but is dealt with in detail in Buchanan and Evans (2000). To take velocity as an example, it is clear that not all birds have the same optimal flight speed. As the sexually selected portion of the tail is removed and the tail is reduced towards its aerodynamic optimum, birds with long tail streamers increase their velocity, whilst birds with short tail streamers decrease their velocity (Buchanan and Evans, 2000: Figure 3). Møller and Barbosa suggest flying faster is beneficial while flying slower is costly—or vice versa. However, the situation is unlikely to be this simple: covariation of morphological characteristics means that individual birds are adapted to fly at a variety of optimal speeds, depending on characteristics such as weight, wing length, and tail fork depth.

Møller and Barbosa are also concerned as to the biological relevance of the flights filmed. Certainly it is true that the birds were not filmed in foraging flight, but observation confirms that swallows have similar flight characteristics during foraging flights and when visiting the nest site (Buchanan et al., unpublished data). We are currently quantifying individual flight characteristics of swallows filmed in foraging flight. However, in defense of our measurements of flight, we find it unlikely that "provisioning nestlings is biologically and aerodynamically irrelevant" as it has been demonstrated that the efficiency of parental provisioning is important for nestling success (de Lope and Møller, 1993) and therefore probably

also for individual fitness. We also suggest that if our results were indeed irrelevant then it would be unlikely that we would have found similar results by using stereo-video of mobbing flight (Allombert S, unpublished data) and in flight mazes (Rowe et al., 2001).

We have now investigated the selection pressures acting on tail morphology in a variety of hirundine species, and obtained highly consistent results (Buchanan and Evans, 2000; Park et al., 2000; Rowe et al., 2001). In particular, a recent study examining the effects of streamer manipulation in barn swallows on flight time through large flight maze has confirmed the U-shaped relationship between tail manipulation and flight performance. This provides additional evidence for the involvement of both natural and sexual selection, in streamer evolution (Rowe et al., 2001). Park et al. (2000) also found that the addition of small streamers to house martins (*Delichon urbica*) resulted in an increase in manoeuvrability during turning flight. Overall, these results suggest that tail streamers are predominantly naturally selected structures improving maneuverability but have been exaggerated by sexual selection in barn swallows resulting in a c15 mm extension beyond the aerodynamic optimum.

In conclusion we would argue that while our data may contain error, it is not systematically biased. Møller and Barbosa have some interesting ideas as to the minimization of any errors included, but this would only increase the strength of the significant relationships detected. We agree that fitness has not been measured by this study—but we would argue that the aim of the study was to demonstrate that both natural and sexual selection have played a role in promoting the evolution of the tail streamer in the barn swallow and to document their relative importance. We would also point out that fitness has not been assessed in any similar study including those of Møller. The exhaustive body of work by Møller and his colleagues confirms the importance of sexual selection for tail exaggeration, however our study confirms that the tail streamer has also evolved under influence from natural selection. Our work has enabled us to quantify the extent of the sexually selected component of streamer length which until recently seemed to be a matter of confusion, for example ''tail ornaments in the . . . swallow have evolved as a result of female choice'' (Møller, 1988); in contrast to ''it is widely accepted that sexual selection cannot on its own be responsible for the elongated tail'' (Hedenström and Møller, 1999). We suggest that the way forward would be to conduct experimental manipulations of the sexually dimorphic trait (i.e., the streamer rather than the basal part of the feather) using manipulations that are smaller than the proposed sexually selected part of the streamer (i.e., <15 mm). This would put studies of the benefits of streamer possession on the same footing as the existing studies of the costs and allow informed discussion of the selective pressures on tail length in this species.

Address correspondence to K.L. Buchanan. E-mail: buchanankl1@cf.ac.uk.

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