

Begging in birds

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ABSTRACT. *Begging in birds.*- Studies of begging in birds are often based upon overly simplistic assumptions. Nestling begging behavior may reflect a variety of factors in addition to short term hunger, and conversely, parents may be able to assess offspring food requirements using cues other than begging. In budgerigars, mothers allocate food according to nestling size, a process that leads to low begging rates but that requires more time for food delivery. Conversely, by allocating food in response to begging behavior, fathers deliver food to nestlings at relatively high rates, but nestlings beg at escalated rates in male-fed nests. Although begging behavior is a promising model system for communication studies, theoreticians need to be aware of the gaps in the empirical literature: it will be difficult to test whether begging is 'honest' without knowing the functional significance of begging behavior.

KEY WORDS. Begging, Birds, Parent-offspring, Provisioning

Introduction

While fascinating in its own right, begging behavior in birds attracts attention because it is often used to study many larger questions in behavioral biology. Begging is relevant to many issues of general theoretical interest, including parent-offspring conflict, the control of parental care, and the evolution of honest communication (Harper, 1986; Godfray, 1991; Godfray & Parker, 1992; Mock & Forbes, 1992) .

However, before plunging ahead to test current theories using begging behavior in birds, we should be aware of what we do or do not know about this system. A primary theme of this paper is that begging behavior in birds may be more complicated

than is commonly supposed. On a more positive note, begging in birds is amenable to elegant observational and experimental studies, so that answers to important, outstanding questions should be available within the next few years.

The simplest possible models of avian begging behavior assume that begging in nestlings increases monotonically as a function of nestling 'hunger', where hunger can be operationally defined by the amount of food in the crop, contractions of the proventriculus, or other physiological indices reflecting short term food requirements (Choi & Bakken, 1990, fig. 1). Conversely, parental feeding rates are assumed to increase monotonically as a function of the rate or intensity of begging in their offspring (fig. 1). The presumed outcome of these two interlocking systems is that food is delivered in

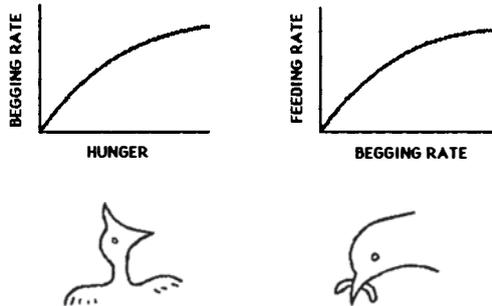


FIGURE 1. A simple model of avian feeding behavior, in which nestling begging rates increase monotonically as a function of hunger, and in which parental feeding rates increase monotonically as a function of nestling begging rates.

[Un modelo simple de comportamiento alimentario en aves, en el que las tasas de llamadas de petición de pollos se incrementan monótonicamente como una función del hambre, y las tasas de alimentación parental lo hacen como una función de las tasas de petición de los pollos.]

the appropriate amounts and at the appropriate intervals to satisfy a nestling's short term food requirements (Ryden & Bengtsson, 1980; Hussell, 1988).

While there is clear evidence that satiety affects nestling begging rates (Choi & Bakken, 1990; Smith & Montgomerie, 1991, but see Welham & Bertram, 1993), this is not the same as saying that hunger is the only factor, let alone the most important factor affecting begging behavior in birds. Over the years, workers have considered a number of other proximate factors that might influence nestling begging rates in one species or another. These factors include attributes of the nestling itself (e.g. its sex, age, size, health and condition), as well as attributes of its nestmates, in particular their sizes, ages and begging rates, relative to those of the focal individual (review in Stamps et al., 1989; see

also Smith & Montgomerie, 1991; Litovich & Power, 1992). In theory at least, all of these factors could have important, independent effects on the begging of individual nestlings.

Of the long list of proximate factors that might influence begging rates, one deserves special mention, because it is often overlooked. This factor is the size or age of a nestling, relative to that of its siblings. Consider a species in which hatching is asynchronous, but in which parents are reluctant or unable to feed fledglings and nestlings at the same time. If successful fledging requires a particular size or stage of maturity, then nestlings that are small relative to their siblings would have to have higher size-specific growth rates in order to fledge successfully along with the rest of the brood (fig. 2). The alternatives are both unattractive: remain in the nest and starve as parents follow the fledglings or fledge immaturely and risk high mortality (e.g. Skutch, 1976). Hence, after controlling for other factors, relatively small nestlings might require more food at a given size than did their larger, older nestmates, when they were the same size. Conversely, this implies that nestlings that are much larger than their siblings should beg at reduced rates, since maximal growth rates would simply lead to their sitting around in the nest, until the rest of the brood was also ready to leave.

The prediction that relative size affects begging rates recently tested in an elegant study by Karen Price, of Simon Fraser University (Price, in prep.). Ms. Price focused on the effects of nestmate hunger and nestmate size on the begging of yellow-headed blackbirds (*Xanthocephalus xanthocephalus*). In this marsh-dwelling species, accelerated growth for relatively small chicks would be advantageous, because small immature nestlings may be left behind after their siblings fledge, or they may fledge prematurely and then drown (Price, pers. comm.). In her laboratory study, all of the subjects were food-deprived for the same period of time, and then their begging responses to artificial stimuli were tested in the presence of four types of nestmates: larger and

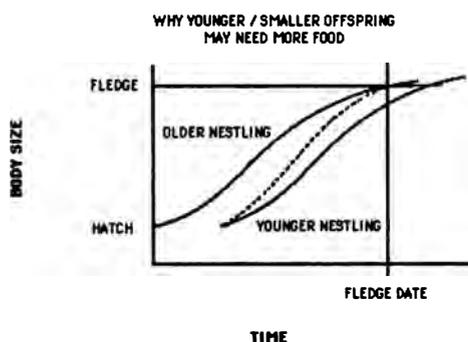


FIGURE 2. Growth trajectories of two nestlings in a species with asynchronous hatching but synchronous fledging. The younger sibling must grow at a higher size-specific rate than its nestmate in order to fledge at the same size and age.

[Trayectorias de crecimiento de dos pollos en una especie con asincronía de nacimiento pero sincrónicas en el momento de abandonar el nido. El más joven debe crecer a una tasa específica de tamaño mayor que su compañero de nido con objeto de volar con el mismo tamaño y edad.]

hungry, larger and satiated, smaller and hungry, and smaller and satiated. Chicks begged more when their nestmate was hungry than when it was satiated, and begged more when their nestmate was larger than when it was smaller; both effects were significant with no interactions in a 2-way Anova (fig. 3). Taken as whole, Karen's study shows that nestling begging rates are determined by at least three factors 1) their own degree of hunger, 2) the hunger and begging rates of their nestmates and 3) their size, relative to that of their nestmates. Hence, relative size is important, even if a nestling is not actively competing with its nestmates for parental attention.

Another lively research area concerns the costs of begging in birds. Recent theoretical studies have suggested that animal communication signals must be costly to be honest (Grafen, 1990; Godfray, 1991). Hence, the race is on to determine the costs of begging behavior in birds. Some workers with a

physiological bent are considering the energetic costs of begging. A recent example of this is provided by John McCarty at Cornell. Mr. McCarty measured resting metabolic rates in tree swallows (*Trachycineta bicolor*), and then compared this to the active metabolic rates of those same birds, when they were stimulated to beg at high rates. He found that the metabolic rate for actively begging nestlings was 1.27 times higher than their resting metabolic rate. Although this ratio was significantly higher than zero, the scope of activity was small, in comparison to the ratios obtained for avian

KAREN PRICE (IN PREP.)
YELLOW-HEADED BLACKBIRDS
(*XANTHOCEPHALUS XANTHOCEPHALUS*)

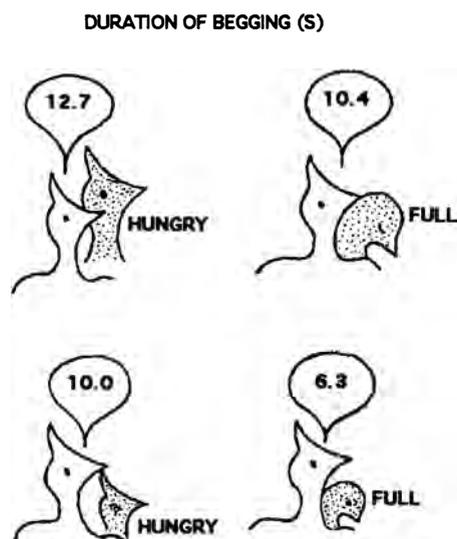


FIGURE 3. Results of an experimental study by Karen Price, showing that both nestmate size and nestmate hunger (begging rates) affect the begging rates of a hungry focal individual.

[Resultados de un estudio experimental de Karen Price, en el que se muestra que el tamaño y el hambre (tasas de petición) del compañero de nido afectan a las tasas de petición de un individuo focal hambriento.]

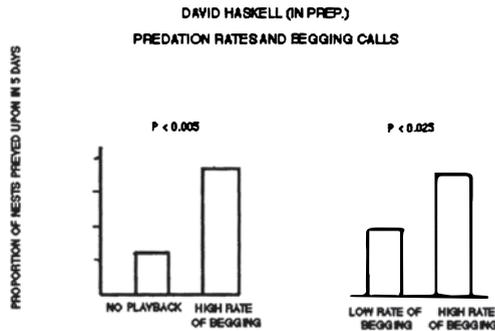


FIGURE 4. Results of an experimental study by David Haskell, in which begging calls were transmitted from artificial nests containing eggs in the field.

[Resultados de un estudio experimental de David Haskell, en el que las llamadas de petición se transmitieron, en el campo, desde nidos artificiales que contenían huevos.]

behaviors that are generally considered to be expensive. For example, activities such as flight or courtship require active metabolic rates that are 3.0 to 16.0 times higher than resting metabolic rates (McCarty, in prep.). McCarty's and other recent studies suggest that the energetic costs of begging may be rather small. If this is true, then many current theoretical models of begging behavior may need to be revised.

Other biologists with a flair for field work have been investigating the effects of begging calls on predation rates under natural conditions (e.g. Redondo & Castro, 1992). In a recent experimental study, David Haskell at Cornell constructed a series of artificial nests, each of which contained a set of quail eggs and a concealed walkie-talkie (Haskell, in prep.), and secreted them in various locations on the ground in natural habitats. In a series of experiments, he found that silent nests had much lower predation rates than nests which continuously played begging calls, and that nests playing begging calls at a low rate suffered less predation than nests

playing the same begging calls at a higher rate (fig. 4). This type of study indicates that begging may increase predation risk. Of course, this type of cost would be borne by the brood as a whole.

To date, more attention has been paid to the behavior of the signalers than to the recipients in the begging-feeding system. However, just as there are a number of factors that can influence offspring begging rates, there are a number of different ways that parent birds might respond to the begging of their offspring. Parents might use begging to discriminate among their offspring on a given visit, and provide more food to the offspring that begs at the highest rate (Smith & Montgomerie, 1991; Litovich & Power, 1992). Alternately, parents might use the overall begging emanating from their nest to determine how much food to allocate to the brood as a whole, versus how much to retain for their own needs. In addition, nestling begging rates at one time might affect the provisioning behavior of the parents at some future time. For instance, parents might forage more actively in the minutes or hours after they experienced high rates of begging at a nest (Haartman, 1953; Litovich & Power, 1992), or high begging rates might maintain levels of parental care over a period of days or weeks, via the priming effects of nestling begging on the hormones that govern parental behavior. At this point, most of the evidence on these questions is anecdotal or observational, so there is plenty of room for further studies of the effects of begging on parental behavior.

In distinct contrast to the recent surge of interest in the costs of begging for nestlings, most workers have ignored the potential costs to parents of relying on begging behavior when assessing the needs of their offspring. However, as was recently pointed out by Dawkins and Guilford (1991), honesty in communication may depend on the costs to recipients of relying on a particular signal, as well as the costs to the individuals that produce the signal. In the case of birds, the salient question is whether parents have ways of assessing offspring

needs other than by relying on begging behavior. If no alternative cues are available, then questions about the costs to recipients are mute. However, if parents do have different options for assessing offspring needs, then one can begin to ask about the relative costs to parents of using begging versus using other ways of assessing offspring food requirements.

The potential costs of different parental care patterns are most obvious in species in which the two parents use different rules when allocating food to their young. Some years ago, my colleagues and I had the opportunity to study one such species, the budgerigar (*Melopsitticus undulatus*). Budgies were studied in captivity, in large flight cages at the University of California, Davis (Stamps et al., 1985, 1987, 1989, 1990).

In both the field and the laboratory, female budgerigars are responsible for incubation and brooding, during which time they are provided with food by their mates. Males continue to feed females after the young hatch, while females remain in the nest hole and allocate food to the nestlings. As we will see below, some males also feed young directly.

Budgerigars are comparable to many parrots, in that they lay eggs at two day intervals, and begin incubation on the first or the second egg. As a result, young hatch out asynchronously, and it is not uncommon for the oldest offspring in a brood of five to be 15 days older than its youngest sibling. The extreme hatch asynchrony in this species sets up a situation in which offspring of very different sizes, motor abilities, and food requirements share the nest at the same time.

Mother budgerigars did not pay much attention to offspring begging. Instead, mothers attended to the size of their offspring, and preferred to feed the smallest offspring first. That size rather than age was important was shown by analysis of maternal feeding rates as a function of offspring size at the same age. There was a strong inverse relationship between size at day 11 and maternal feeding rates

over the following 12 days, a relationship that was significant both within and among families (Stamps et al., 1985). A mother budgerigar often initiated a feeding bout by searching under a squirming pile of begging nestlings until she found a small, naked hatchling. She would then turn it on its back, nibble its head or beak until it accepted food, and then begin to transfer a long series of regurgitations to it while fending off begging older nestlings with her wings.

Paternal feeding behavior was much more variable than that of mothers. In some families, males fed nestlings at relatively high rates, whereas in other families, males almost never fed their offspring directly. Elsewhere we have shown that variation in male provisioning behavior is related to the sex ratio of the brood, with males preferring to feed female-biased broods (Stamps et al., 1987). However, since none of the results discussed below were affected by nestling sex or brood sex ratios, we can ignore offspring sex for the remainder of this paper. Instead, for our purposes we can consider two types of broods: 1) two-parent families, e.g. those in which nestlings received food from both their mothers and their fathers, and 2) one-parent families, in which nestlings received virtually all of their food from their mothers.

In distinct contrast to mothers, father budgerigars paid attention to offspring begging rates (Stamps et al., 1985). Males were most likely to enter nestboxes after hearing begging calls, and once in the box, males responded to offspring begging rates when allocating food to the nestlings. Generally speaking, male budgerigars fed using rules that were comparable to those used by many passerines, in that they tended to jump into the nest, shove food into the closest, most conspicuous mouths, and then leave.

One striking indication of the difference between male and female budgerigars was the way they handled interruptions during a feeding bout. When a female was feeding one offspring and was interrupted by another one, she typically walked around the

nestbox until she found the original offspring, and then resumed feeding it. In the same situation, fathers behaved differently. They were much more easily distracted than mothers, and were more likely to feed the interrupter than go back and feed the original recipient (Stamps et al., 1987).

Based on these results, budgerigars are clearly a species in which there is a viable alternative to relying on begging behavior to assess offspring needs. Mother budgerigars used body size and possibly other visual or vocal cues (e.g. tone of voice, e.g. Redondo & Expósito, 1990) when allocating food to their offspring, while in males, food distribution was determined by offspring begging rates. Hence, this is a species in which we can consider the possible costs to parents of using alternative cues to assess offspring need.

A major result of this study was that parents save time by relying on begging behavior. As one might suspect from the descriptions of male and female feeding behavior, male budgerigars delivered food almost twice as fast as did females within a feeding bout (males: 0.28 regurgitations/sec; females: 0.16 regurgitations/sec; Stamps et al., 1987). Further analyses showed that this difference in feeding rates was due to the costs of discriminating amongst potential recipients, not to a sex difference in feeding behavior per se.

There is one situation in which male budgerigars do discriminate when allocating food to begging individuals. This is when males are simultaneously presented with a begging spouse and begging offspring, in which case, males prefer to feed their offspring. However, when males were confronted with the combination of a begging mate and begging nestlings, their feeding rates declined to those of females, indicating that males as well as females exhibit reduced feeding rates when they discriminate among potential recipients (Stamps et al., 1987).

In the case of female budgerigars, there may not be much point in saving time while provisioning nestlings, since females spend most of their time in

BEGGING RATES (BOUT/HR)		
NESTLING AGE	ONE PARENT FAMILIES	TWO PARENT FAMILIES
 11-12 DAYS OLD	4.4 +/- 1.9	9.4 +/- 4.4
	P < 0.05	
 23-24 DAYS OLD	6.1 +/- 1.9	14.3 +/- 3.8
	P < 0.005	

FIGURE 5. Begging rates for budgerigar nestlings provisioned by the female (one parent families) and by both parents (two parent families) for nestlings in two age categories.

[Tasas de petición de pollos de *Melopsitticus undulatus* provisionados por la hembra (familias de un solo padre) y por ambos padres (familias de dos padres) para pollos de dos categorías de edad.]

the nest in any event. However, there are several reasons why male budgerigars might benefit by reducing time at the nest. As primary food-providers for the family, males spend long periods traveling back and forth from the nest site to foraging areas. Hence, time spent allocating food is time unavailable for foraging. In addition, a bird that flies from bright sunshine into a dark nesthole might require time for its eyes to dark-adapt in order to discriminate offspring using visual cues; perhaps males feed mouths that loom in front of them because that is all they can see! Hence, one possible reason why males rely on begging rather than using the female feeding pattern is that the time required to discriminate among recipients is relatively more expensive for males than for females. In other

words, for males the relative costs of using begging may be lower than the costs of using other cues to assess offspring food requirements.

Of course, variation in parental care tactics in turn has implications for the behavior of their young. From the perspective of a nestling budgerigar, the important question is how parents are likely to respond to its begging behavior. In the case of one-parent budgerigar families, mothers largely ignored begging rates when allocating food to their young, so offspring did not benefit from begging at high rates. However, father budgerigars did pay attention to offspring begging, so the nestlings in two-parent families were often positively reinforced after they begged.

Within a short time after fathers begin to feed, the nestlings in two-parent families begin to beg at high rates, and by the time they were near fledging, they were begging at much higher rates than their counterparts in one-parent families (fig. 5). Hence, young budgerigars seemed able to assess the effects of their begging on their parents, and they only begged at high rates when they were rewarded for this behavior.

Although complicated in detail, the budgerigar story illustrates several points that probably apply to other birds as well. First, parent birds need not always rely on begging behavior when assessing offspring needs; alternative cues may also be available. However, different methods of allocating parental care may lead to different sets of costs and benefits for both parents and their young. In the case of budgerigars, parents who use begging require less time to deliver food, but this parental care pattern leads to escalated begging rates among the nestlings. The use of alternative cues of offspring food requirements requires more time for parental discrimination, but it also results in lower begging rates among the young. Basically, budgerigar parents have two choices...they can feed quickly and end up with a noisy nest, or they can invest more time while provisioning and have a quiet, well behaved family.

Summary

This paper shows that begging behavior in birds may be more complicated than is often supposed. Contra the simplified view of begging and feeding presented in fig. 1, begging in nestlings is likely to be affected by a variety of factors in addition to offspring hunger. In particular, if fledging is synchronous, small/young nestlings may require and request more food at a given body size than their siblings, in order to fledge at the appropriate time and size (fig. 2). In fact, recent experimental studies indicate that nestlings beg more in the presence of relatively larger nestmates, even after controlling for the hunger of the focal individual and its nestmates (fig. 3). We also need to consider the costs of begging to offspring; recent experimental studies suggest that begging may be energetically inexpensive, but that it may increase the risk of predation on the brood as a whole (fig. 4). A largely unexplored topic is the cost to parents who rely on begging, rather than using alternative cues indicative of offspring needs. In budgerigars, parents that rely on begging when allocating food are able to deliver food at a faster rate than those who use other cues for food allocation, but nests in which parents reward begging behavior have escalated begging rates in comparison with nests in which parents use alternative cues of offspring needs (fig. 5). Further empirical (especially experimental) studies of begging in birds are strongly encouraged; these will be essential if we are to determine how this intriguing communication system actually works.

Resumen

Petición en aves.

Este trabajo muestra que el comportamiento de petición en aves puede ser más complicado de lo que a menudo se supone. Contra el punto de vista

simplificado de la petición y la alimentación presentado en la fig. 1, la petición de los pollos está probablemente afectada por una variedad de factores además de por el hambre. En particular, si el emplumarse es sincrónico, los pollos pequeños/jóvenes pueden requerir y pedir más alimento, a un tamaño corporal dado, que sus hermanos, con objeto de emplumarse en el momento y con el tamaño apropiado (fig. 2). De hecho, estudios experimentales recientes indican que los pollos piden más en presencia de compañeros de nido relativamente más grandes, incluso después de controlar el hambre del individuo focal y sus compañeros de nido (fig. 3). También necesitamos considerar los costos de la petición para la descendencia; estudios experimentales recientes sugieren que la petición puede no ser cara energéticamente, pero que puede aumentar el riesgo de depredación de la puesta (fig. 4). Un tópico muy poco investigado es el costo de los padres que se fían de la llamada de petición, en lugar de usar señales alternativas indicativas de las necesidades de la descendencia. En *Melospitticus undulatus*, los padres que se fían de la llamada de petición cuando reparten el alimento son capaces de distribuir el mismo con una tasa más rápida que los que usan otros signos, pero los nidos en que los padres premian el comportamiento de petición tienen mayores tasas de llamadas en comparación con aquellos en que los padres usan rasgos alternativos de las necesidades de las crías (fig. 5). Fomentamos la realización de estudios empíricos (especialmente experimentales) sobre petición en aves, los cuales serían esenciales si tratamos de determinar cómo funciona este intrigante sistema de comunicación.

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