Asymmetric Begging Competitions in Red-winged Blackbird *Agelaius phoeniceus* Nestlings

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Abstract

Hatching asynchrony is a mechanism avian parents use to establish competitive handicaps among their progeny. This phenotypic difference creates separate castes of advantaged 'core' offspring and disadvantaged 'marginal' offspring. According to begging models, smaller nestlings should beg harder and receive less for their efforts than their larger nestmates. Here, I examine the begging behaviour of red-winged blackbird (*Agelaius phoeniceus*) nestlings to establish if feeding success is phenotype limited. I compared the relationship between competitive ability and feeding success of core versus marginal nestlings to examine their relative success in begging competitions. I found no difference between core and marginal nestlings in begging intensity or in post-feeding begging length. There was, however, significant differences found between the two broods in neck height. In larger broods, marginal nestlings tended to rank lower in height than their core nestmates. Consistent with begging models, marginal nestlings were shorter (smaller) and received less food, however this difference disappeared in smaller broods. This research also confirmed previous work that indicated neck height as the key determinant in feeding success for red-winged blackbird nestlings. In accordance with these results, it appears that success in begging competitions is phenotype limited.

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Table of Contents

Abstract ii

Acknowledgements iii

Table of Contents iv

List of Tables v

Introduction 1
- The Theory of Begging Behaviour 1
- Phenotype Limitation and Begging Competitions 2
- The Natural History of Red-winged Blackbirds 4

Methods 5
- Field Methods 5
- Data Collection and Analysis 5

Results 9
- Begging Intensity of Core vs. Marginal Nestlings 9
- Neck Height of Core and Marginal Nestlings During Begging Competitions 9
- Post-feeding Begging Duration 10
- Food Acquisition 11

Discussion 13
- Did Marginal Nestlings Beg Harder? 13
- Did Marginal Nestlings Reach the Same Height as Core Nestlings? 13
- Did Marginal Nestlings Beg Longer After Feeding Than Core Nestlings? 14
- Did Marginal Nestlings Obtain as Much Food as Core Nestlings? 15
- Inter-nest Differences in Behaviour 17

Conclusions 18

References 19

List of Tables

Table	Page
Table 1. Begging intensity of nestling red-winged blackbirds in relation to status, nest, brood size, and the interaction between status and brood size, and the per capita feeding rate of nestlings. The mean begging intensity of core nestlings was 2.001 ± 0.090 and for marginal nestlings the mean begging intensity was 2.169 ± 0.117.	9
Table 2. Rank in height of nestling red-winged blackbirds in relation to status, nest, brood size, and the interaction between status and brood size. Core nestlings had a mean rank in height of 2.187 ± 0.079, whereas the mean for marginal nestlings was 2.497 ± 0.098.	10
Table 3. Length of time nestling red-winged blackbirds continued to beg in relation to status, nest, brood size, and the interaction between status and brood size. The mean value of post-feeding begging length for core and marginal nestlings were 9.864 ± 1.431 and 11.712 ± 1.817 respectively.	11
Table 4. Per capita feeding rate of nestling red-winged blackbirds (food items/nestling/h) in relation to nestling status, nest, brood size, and the interaction between status and brood size. The mean values of per capita feeding rate were 0.083 ± 0.005 for core nestlings and 0.058 ± 0.007 for marginal nestlings.	12

Introduction

The Theory of Begging Behaviour

Begging behaviour has been closely examined for its role in communication, parent offspring conflict, sibling competition and evolutionary game theory. Begging behaviour is recognized as a model system for the study of parent-offspring communication (Leonard *et al*., 2003). Begging signals are thought to communicate nestling hunger (or need) and elicit a feeding response, but are they honest or exaggerated (Leonard and Horn 1998; Royle *et al*., 2002)?

There are two major challenges for begging nestlings: (1) indicating hunger level to their parents, and (2) competing with nestmates for parentally delivered food. Game theoretical models have been developed to examine the question of whether begging is honest, and how hard individual nestlings should beg under the influence of sibling competition (reviews in Mock and Parker, 1997; Wright and Leonard, 2002).

Two classes of models have been developed to examine nestling begging behaviour: the honest begging models (Godfray, 1991, 1995), and models of scramble competition (Parker *et al*., 1989; Parker *et al*., 2002). Under the honest begging models, parents are assumed to control food allocation and inspect offspring signals of need to determine who gets fed. The system is kept honest by the cost of the signal produced by the offspring, i.e. begging is energetically expensive and/or elevates the risk of predation. Under the scramble model of begging competition, the relative begging effort of individual nestlings determines food allocation, i.e. the offspring rather than the parents effectively control it. Despite key differences between the honest begging and scramble models of begging, competitions in both yield such similar predictions that it will be difficult for empiricists to differentiate (Royle *et al*., 2002).

Both sets of models make similar predictions about the behaviour of strong and weak individual nestlings in asymmetric competitions. A robust prediction of both honest signaling and scramble models is that stronger sibs should get more food with less begging effort, weaker nestmates the opposite (how should stronger siblings share food with their weaker counterparts and how hard should each work to obtain food). The basic prediction is that weaker sibs should beg harder but receive less food than stronger nestmates (Parker *et al*., 2002; Rodríguez-Gironés *et al*., 2002).

Empirical evidence supporting this prediction has been found in yellow-headed blackbirds (*Xanthocepahlus xanthocephalus*) (Price and Ydenberg, 1995; Price *et al*., 1996), barn swallows (*Hirundo rustica*) (Lotem, 1998) and European starlings (*Sturnus vulgaris*) (Cotton *et al.*, 1999). Smiseth *et al*. (2002) found that in broods of asynchronously hatched bluethroat (*Luscinia svecica svecica),* the senior nestlings obtained a greater share of the resources when food was limited. However, there was not a significant difference between junior and senior nestlings in behavioural measures (positioning in the nest or begging posture). This same study found a significant difference in the length of time nestlings continued to beg post-feeding. The authors proposed that junior nestlings may need to increase this post-feeding behavior to induce parents to increase provisioning rates which would potentially reduce the competition among nestmates and allow junior nestlings to access more food (Smiseth and Amundsen, 2002).

Phenotype Limitation and Begging Competitions

These phenotypic differences (older vs. younger) are competitive handicaps (phenotype limitations) that are expected to have profound effects on the outcome of begging competitions. As begging competitions are most often won by the nestling that is able to stretch its neck the

farthest, the larger, older nestlings tend to have a significant advantage. Older nestlings are usually able to stretch their neck into the highest ranked positions or across the entire nest to out compete nestlings that would have otherwise been positioned closest to the parent (Smiseth and Amundsen, 2002).

A phenotypic handicap arises when parental manipulation, such as hatching asynchrony, impairs an individual's competitive status among its brood mates. Other examples result from manipulations in egg size and hormonal complement. However, the effect of hatching asynchrony is more influential than the effects of differential egg size, although a larger marginal egg may partially close the competitive gap between core and marginal offspring (Forbes, 2005). Hatching asynchrony occurs because the incubation period begins before the last egg is laid (Clark and Wilson, 1981). The first laid eggs are incubated sooner and therefore the nestlings of these eggs hatch sooner. Eggs that are laid after the incubation period has commenced hatch later resulting in asynchronously hatched broods. This behaviour creates competitive asymmetries among nestlings. Those nestlings that hatch first and simultaneously (within a few hours) are referred to as the core brood; nestlings that hatch one or more days later than the core brood are referred to as the marginal brood (Mock and Forbes, 1995; Forbes *et al*., 1997). The first marginal nestlings tend to hatch approximately twenty-four hours after the core brood and consecutively hatched marginal nestlings may differ in age by more than one day. Hatching asynchrony imposes a competitive handicap upon marginal nestlings that are younger and smaller than their core nestmates. As a consequence, they grow more slowly and suffer higher mortality (Forbes *et al*., 1997; Forbes and Glassey, 2000; Forbes *et al*., 2001). Forbes and Glassey (2000) found that the growth and survival of older (=core) nestling red-winged blackbirds was higher and less variable than that of their marginal nestmates.

Here, I examined the begging behaviour of core and marginal red-winged blackbird (*Agelaius phoeniceus*) nestlings, to determine if success in begging competitions is phenotype limited. I tested the hypothesis that marginal nestlings expend greater effort on begging than their core nestmates to obtain a lower food reward. I have considered measures that are consistently observed in begging literature such as begging intensity, neck height and post-feeding begging length. These measures were examined in relation to feeding success.

The Natural History of Red-winged Blackbirds

Red-winged blackbirds are abundant altricial, passerine birds found throughout much of North America (Jarmillo and Burke, 1999). Their range extends from Alaska and the Yukon in the north, to Mexico, Costa Rica, and the Bahamas in the south (Beletsky, 1996). During the breeding season, red-winged blackbirds mainly occupy *Typha sp.* and *Scirpus* sp. dominated marshes, although they are also found in other wetlands and in upland sites (Jaramillo and Burke, 1999).

Male red-winged blackbirds arrive in Manitoba in early spring to establish and defend a territory as large as two km^2 (Jaramillo and Burke, 1999). After a territory is established as many as 15 arriving females may choose to nest within one male's territory (Beletsky, 1996; Jaramillo and Burke, 1999). Female red-winged blackbirds construct their own nests and are responsible for the majority of the parental care (incubating, brooding and feeding) (Beletsky, 1996; Beletsky and Orians, 1996). The female usually lays 3-5 eggs, rarely 2 to 6 (Jaramillo and Burke, 1999).

Methods

Field Methods

Professor Scott Forbes from the University of Winnipeg along with a crew of summer field assistants collected data on the red-winged blackbirds nesting in man-made wetland habitats on the outskirts of the City of Winnipeg, Manitoba. The field data used in this project were collected from 1993 to 2004. At the beginning of each field season these marshes were visited, nests were found, mapped and numbered. Nests were visited daily and eggs and nestlings were marked with non-toxic felt markers for individual identification. Mass and presence of feathers were recorded along with the time of visit until nestlings were depredated or fledged.

Data Collection and Analysis

Video recordings were made of red-winged blackbird broods ranging in age (of core nestlings) from one to eleven days under fair weather conditions. The video camera was placed one to three feet from the nest. At most nests the presence of the camera appeared to have no discernible effect on parental behaviour (similar findings in Glassey, 2000). The parent was flushed from the nest when the video camera was set up but they usually returned within approximately ten minutes and resumed feeding at a rate that appeared to be consistent among all nests. Videotape sessions lasted from two to six hours, with interruptions during inclement weather. To avoid pseudoreplication (Hurlbert, 1984), only one videotaping session per nest was used in the analyses reported below.

From the library of video observations, I selected all usable videotape. Of the 40 useable videos, 32 contained nests with both core and marginal nestlings, whereas the other eight contained only core nestlings. Due to the nature of this study (video observation) there was a

high degree of variation among nests, which may have been controlled for had this been an experimental study. Nests consisted of one to three core nestlings and zero to two marginal nestlings. Videos were excluded where: swapping experiments had been conducted, cowbirds were present in the nest, nestlings were undistinguishable or where parents blocked the view of feeding activities.

From the videos, I recorded the height and begging intensity of each nestling. For the relative measure of height, nestlings were ranked on an ordinal scale that began with one representing first place, followed by a two for second place and a three for third place. Nestlings that were not begging were assigned the last place position; therefore, if there were four nestlings and the three begging nestlings achieved different heights the nestling that was not begging was assigned a value of four. In a case where there was a tie the average of two ranks would be assigned to each nestling. For example, if one nestling achieved first place it would be assigned a one, if there were two nestlings tied for second place they would each be assigned two and a half and the last ranked nestling would received a four.

I measured begging intensity based on an absolute scale, where each number represented a specific action or sequence of actions. In this case zero = not begging, one = gaping, two = gaping and neck stretching, three = gaping, neck stretching and wing flapping, four = all of the first three measures plus standing. These values were recorded for all feedings that occurred where data could be gathered with at least ten feedings per nest. A stopwatch was used to measure the amount of time that each nestling continued to beg after the last feeding occurred. Using a random numbers table generated in Excel (Microsoft Inc.), a minimum of ten feedings per nest was selected for analysis of post-feeding begging time.

All of the raw data collected during video observation were entered into Excel spreadsheets. All values for begging measures (height, begging intensity and the time nestlings continued to beg after the last feeding occurred) were averaged for each nestling. These values were then divided by the size of the core and marginal broods thereby giving an average value for each brood. For the feeding analysis I calculated the total number of feedings that each core nestling received, and then calculated a sum for the total brood. This value was divided by the total number of core nestlings in the brood and further divided by the total number of video minutes. This gave a percentage for the number of feedings that an average core nestling received per time period. The same calculations were conducted for the marginal nestlings to compare the feeding rate between core and marginal nestlings.

Data were analyzed using Statistical Package for the Social Sciences (SPSS). I conducted a General Linear Model – Univariate analysis where the begging measure was the dependent variable, core or marginal were the fixed factor and nest number the random factor; covariates included brood size and interaction between core or marginal nestlings and brood size. For begging intensity (dependent variable), an additional covariate, feeding frequency (the number of times a nestling was fed per total number of video minutes) was added. For all statistical analyses a custom model was designed to include the above-mentioned variables. A custom model is a selection that can be made in SPSS to define a model containing certain variables and interactions chosen specifically for the analysis. The differences between core and marginal nestlings were the primary focus of this research; specific dependent variables (height, begging intensity, number of food items received) were examined in relation to core vs. marginal nestlings. The core-marginal status was the key variable while nest number, and brood size were included as “nuisance variables” as they were not of direct interest but accounted for variation in

begging behaviour and are well known for their influence on begging behavior (Scott Forbes pers. comm., 2007).

Results

Begging Intensity of Core vs. Marginal Nestlings

There was no significant effect of nestling status on begging intensity (Table 1) as core and marginal nestlings begged at similar intensities. In this model the random 'nest' factor was significant, indicating significant inter-nest variation in begging intensity. There was also a significant effect of per capita feeding rate – begging was more intense at nests where the rate of food delivery was higher. Brood size had no significant affect on begging intensity.

Table 1. Begging intensity of nestling red-winged blackbirds in relation to status, nest, brood size, and the interaction between status and brood size, and the per capita feeding rate of nestlings. The mean begging intensity of core nestlings was 2.001 ± 0.090 and for marginal nestlings the mean begging intensity was 2.169 ± 0.117.

Independent variable	F	Degrees of freedom	P
Nestling status	0.418	1,28	0.523
Nest factor	7.518	39,28	0.000
Brood size	0.000	1,28	0.988
Nestling status x Brood size interaction	0.117	1,28	0.734
Per capita feeding rate	13.162	1,28	0.001

Neck Height of Core and Marginal Nestlings During Begging Competitions

There was a significant effect of nestling status on neck height in begging competitions (Table 2). Core offspring reached higher than marginal offspring, an expected result given that core offspring are older and larger. In this model the random 'nest' factor was not significant – given that neck height is a ranked variable, this result is expected (Table 2). Brood size had a

significant effect on rank in neck height which was expected because the dependent variable was ordinal – larger broods have more nestlings to rank and this variable was included mainly to correct for this variation statistically. There was an interaction between brood size and nestling status (Table 2), indicating that in larger broods, marginal nestlings tended to rank lower in neck height.

Table 2. Rank in height of nestling red-winged blackbirds in relation to status, nest, brood size, and the interaction between status and brood size. Core nestlings had a mean rank in height of 2.187 ± 0.079, whereas the mean for marginal nestlings was 2.497 ± 0.098.

Independent variable	F	Degrees of freedom	P
Nestling status	5.617	1,29	0.025
Nest factor	1.161	39,29	0.341
Brood size	7.289	1,29	0.011
Nestling status x Brood size interaction	9.391	1,29	0.005

Post-feeding Begging Duration

Core and marginal nestlings did not differ significantly in how long they continue to beg following feeding (Table 3). In this model the dependent variable was begging length post feeding, the random factor (nest number) was significant and the co-variates (brood size and status x brood size) were not significant (Table 3). This indicates that inter-nest variation is the most influential factor on the dependent variable.

Table 3. Length of time nestling red-winged blackbirds continued to beg in relation to status, nest, brood size, and the interaction between status and brood size. The mean value of post-feeding begging length for core and marginal nestlings were 9.864 ± 1.431 and 11.712 ± 1.817 respectively.

Independent variable	F	Degrees of freedom	P
Nestling status	0.848	1,28	0.365
Nest factor	2.012	39,28	0.028
Brood size	0.116	1,28	0.735
Nestling status x Brood size interaction	0.551	1,28	0.464

Food Acquisition

The relationship between per capita feeding success of core and marginal nestlings was complex. The main factor (nestling status) was not significant, but there was an interaction between brood size and status (Table 4). This means that in small broods, there was no difference in the feeding success of core and marginal offspring, but that in large broods, marginal offspring fared worse than core offspring. There was also a significant nest effect, as per capita feeding rate differed significantly across nests.

Table 4. The per capita feeding rate of nestling red-winged blackbirds (food items/nestling/h) in relation to nestling status, nest, brood size, and the interaction between status and brood size. The mean values of per capita feeding rate were 0.083 ± 0.005 for core nestlings and 0.058 ± 0.007 for marginal nestlings.

Independent variable	F	Degrees of freedom	P
Nestling status	1.716	1,29	0.200
Nest factor	1.888	39,29	0.039
Brood size	1.648	1,29	0.209
Nestling status x Brood size interaction	4.274	1,29	0.048

Discussion

Did Marginal Nestlings Beg Harder?

Hungrier nestlings are expected to beg more intensely and smaller nestlings are expected to be hungrier as a result of being out competed by their larger, stronger nestmates (Budden and Wright, 2001; Kilner and Johnstone, 1997). Therefore I expected that marginal nestlings would beg more intensely than core nestlings. Contrary to expectation, marginal nestlings did not beg harder overall, nor was there any interaction with brood size – i.e., marginal nestlings did not beg harder than core nestlings in larger broods. There was, however, an influence of per capita feeding rate on begging intensity; chicks that received *more* food begged harder (Table 1).

Parker *et al*. (1989) predicted that the associated costs of begging would be less of a burden for stronger nestlings. Perhaps on a small temporal scale, feeding makes stronger nestlings, which are able to beg harder despite their phenotypic handicap. Therefore as long as there are enough resources to sustain all brood members and as long as they each participate in begging competitions, at some time, each nestling will likely receive a share of these resources. Fed nestlings may beg more intensely, however, they will most likely become satiated at some point and beg slightly less thereby creating an opportunity for the next beggar.

Did Marginal Nestlings Reach the Same Height as Core Nestlings?

Due to hatching asynchrony, marginal nestlings are placed at a considerable size disadvantage compared to their older nestmates. Even when experimentally comparing core and marginal nestlings at the same number of days post hatch, size differences are

likely as these two castes of nestlings are born into different competitive environments. The lack of competition experienced by first-hatched nestlings provides them with a growth advantage over a marginal nestling of the same age (Forbes and Glassey, 2000). Marginal nestlings always have to 'share' with older, larger nestmates whereas core nestlings may have enjoyed being the sole recipient of parentally delivered resources or at least benefited from contest with equally competitive nestmates. This difference in size gives core nestlings a substantial advantage over marginal nestlings in reaching highest to obtain food. Consistent with both expectation and previous research, on the same study system (Glassey, 2000), marginal nestlings did not achieve the same height as core nestlings. Moreover, I found a significant interaction between nestling status and brood size (Table 2), indicating that marginal nestlings ranked lower in neck height in larger broods.

Did Marginal Nestlings Beg Longer After Feeding Than Core Nestlings?

Previous work with asynchronously hatched bluethroat (*Luscinia svecica svecica)* found that, although senior and junior nestlings did not differ in any pre-feeding begging measures, juniors continued to beg for longer after feeding (Smiseth and Amundsen, 2002). As previously discussed, the explanation was that juniors had little to gain from increasing their pre-feeding begging effort due to their inferior competitive ability and that juniors may have resorted to this post-feeding behaviour to encourage parents to increase their feeding rates.

My results differ from Smiseth and Amundsen (2002), as I found no difference between core and marginal red-winged blackbird nestlings in post-feeding begging effort.

By applying the rational of Smiseth *et al*. (2002), and following the suggestion of Glassey and Forbes (2002), red-winged blackbird nestlings may use post-feeding begging tactics to influence future feeding rates, however, this behaviour does not appear to be unique to marginal nestlings.

Did Marginal Nestlings Obtain as Much Food as Core Nestlings?

According to both types of begging models (honest and scramble competition), handicapped (marginal) nestlings should receive less food than their core counterparts (Parker *et al*., 1989, 2002; Rodriguez Girones *et al*., 1996). In my study, this result was obtained only in large broods of red-winged blackbirds. Marginal nestlings did not receive less food in small broods. This effect appears from the significant interaction between nestling status and brood size (Table 4). As discussed above, this interaction was also significant for height, suggesting that in larger broods marginal nestlings did not reach as high as core nestlings and as a result received less food.

Previous work has shown that neck height is the strongest determinant of feeding success in nestling red-winged blackbirds (Teather, 1992; Glassey, 2000), and similarly important in other avian systems (Leonard *et al*., 2003). Earlier work on the red-winged blackbird system showed that last-hatched nestlings were only half as likely as first-hatched nestlings to achieve the highest neck rank (Glassey, 2000). That study, however, did not explicitly examine the role of brood size. Here, last hatched nestlings only received less when brood size increased.

Leonard *et al*. (1999) similarly found a negative relationship between increased brood size and feeding rate per nestling. However, they also found a positive relationship

between increased brood size and begging intensity. Although begging intensity of red-winged blackbird nestlings did not appear to be affected significantly by brood size, height and feeding success were. Marginal nestlings did not reach as high and they were fed less when they were in larger broods but these differences disappeared in small broods.

If height is the key determinant in feeding success for red-winged blackbird nestlings as has been previously suggested (Glassey and Forbes, 2002), perhaps there is no reason for core and marginal nestlings to differ in begging intensity. Begging intensity was not affected by brood size and there was no difference found between core and marginal nestlings. Only nestlings that were fed begged harder. Therefore, neither core nor marginal nestlings appeared to increase their begging effort (begging intensity) until they were fed. A feeding may act as a down payment for effort, making it worthwhile for a nestling to beg harder only after it has been fed. Also, a marginal nestling may choose to expend less energy on begging intensity in larger broods and instead direct its energy into stretching its neck and counting on a feeding opportunity to arise when the larger nestlings choose not to exert their full begging potential, i.e. when satiated.

In small broods, food may be evenly distributed among fewer nestlings allowing them to achieve similar size despite their hatching order. This similar size results in the ability to achieve similar heights and therefore similar feeding success. In crimson rosella (*Platycercus elegans)*, neither food distribution nor the growth rates of chicks changed with increasing hatching asynchrony and food was evenly distributed to nestlings even in broods with large size differences (Krebs *et al*., 1999). Interestingly,

the mean brood size was 5.3 nestlings, which would be considered the maximum brood size for red-winged blackbird nestlings and correspondingly, where the largest differences would be expected. However, crimson rosella nestlings do not fledge for approximately 35 days after hatching and the parents appear to display complex patterns of parental food allocation, whereas red-winged blackbird nestlings fledge approximately twelve days after hatching. The large differences that exist between these two species make them difficult to compare, however, it does help to reveal an important conclusion that continues to surface in begging literature. Begging behaviour is complex, often involving multiple signaling components, and it is highly malleable and context or species dependent (Royle *et al*., 2002).

Inter-nest Differences in Behaviour

In all of the analyses reported above, there were strong differences across nests (the nest number variable treated as a random factor in the models). The source of this variation is not known, though it is potentially related to differences in brood size. Surprisingly, brood size did not register as a significant covariate in three of the four analyses reported here (neck height being the exception). It is possible that variation in behaviour attributable to brood size was accounted for by the nest variable.

Conclusions

1. These results are not consistent with expectations set forth in conventional begging models.
2. Marginal nestlings did not beg harder for less reward, in fact there was no difference between core and marginal nestlings in begging intensity.
3. Feeding success rather than phenotypic differences lead nestlings to increase their begging effort.
4. As expected, marginal nestlings had lower neck heights than core nestlings, which correspond to the size difference found among asynchronously hatched nestlings.
5. Nestlings may beg after feedings to induce parents to return to the nest with more food, but this behavior is not unique to marginal nestlings as there was no difference between the core and marginal broods in post-feeding begging effort.
6. In large broods, marginal nestlings did not reach as far as core nestlings therefore they were not fed as much as core nestlings, however, this difference was not apparent in smaller broods.
7. Based on these results, success in begging competitions is phenotype limited; the difference exists for neck height and not other begging measures, and it appears to be somewhat dependent on brood size.

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