Resource Competition among Nestling Red-winged Blackbirds

(*Agelaius phoeniceus*)

By:

Barb C. Glassey

A Thesis
Submitted to the Faculty of Graduate Studies
In Partial Fulfillment of the Requirements
For the Degree of

Doctor of Philosophy

Department of Zoology
University of Manitoba
Winnipeg, Manitoba

THE UNIVERSITY OF MANITOBA

FACULTY OF GRADUATE STUDIES
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A Thesis/Practicum submitted to the Faculty of Graduate Studies of The University

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Dedicated to my mother, Barbara Glassey-Partridge,

who provided the motivation.

General Abstract

Red-winged blackbird (*Agelaius phoeniceus*) females hatch their offspring asynchronously, creating mixed-aged broods comprising first-hatched "core" nestlings and later-hatched "marginal" offspring. Nestlings communicate their requirements to the parents using a combination of vocal and visual behaviours. Other studies of begging have focused solely on the need for food; here I incorporate thermal care as a resource. I begin by outlining the ontogeny of begging by red-winged blackbird nestlings using data collected from video-taped nests. My results indicate that parents use the collective begging efforts of the brood to assess both the thermal and nutritional requirements of the brood - the female parent responds to a weak collective effort by increasing nest attentiveness whereas a strong effect stimulates foraging. I compare the begging behaviour of core vs. marginal offspring at three phases of brood development, to determine whether developmental disparities influence the outcome of begging competitions. My results indicate that the outcome of begging competitions is primarily determined by size. Consequently, larger nestlings consistently receive more food. I develop a novel, non-surgical technique to mute nestlings temporarily in order to separate vocal from visual begging displays. My results indicate that food allocation is determined principally on the basis of visual displays, but that the foraging is regulated by the cumulative vocalizations of the brood. A secondary effect of the muting treatment is to reduce the length of time that nestlings beg, to which parents respond by increasing nest attentiveness. Finally, I compare parent-offspring interactions in unparasitised broods of red-winged blackbirds, to broods parasitised by the brown-headed cowbird

(*Molothrus ater*) across the nestling period. Cowbird nestlings differ from host nestlings by maintaining a consistent begging effort, and by begging for a lengthy period of time, particularly following the allocation of food. Host nestlings increase their begging efforts in response to the presence of the cowbird, but as they are unable to sustain the effort, parents do not increase foraging.

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I would like to thank my committee, Drs. Evans, Abrahams, Kenkel, and Wiens, for their valuable input and accessability. Special thanks to the late Dr. Evans, who encouraged me to find a way to mute nestlings; Dr. Abrahams, for having an open door;

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General Introduction

Nestlings of altricial birds are confined to the nest where they are dependent on the parent to supply their nutritional and thermal requirements. Studies of passerine communication have focused almost exclusively on the roles of vocal and visual signals in the allocation of food and scheduling of parental provisioning. However parental brooding is also essential to passerine species, as nestlings are ectothermic for the first half of the nestling period. A stable thermal environment optimises nestling growth, metabolism (Olson 1992), food assimilation and begging abilities (Choi and Bakken 1990). The relative benefits derived from the supply of heat and food change over the nestling period, as offspring are transformed from small, nearly helpless, naked ectotherms to fully feathered, active endotherms. Although much attention has focused on how size differences within broods influence the outcome of begging competitions, the potential role of differential developmental has been overlooked.

My research focuses on the communication systems of red-winged blackbirds (*Agelaius phoeniceus*), as a model for passerine birds generally. The general questions that lay the foundation for my doctoral research are: (1) how do nestlings communicate their need for food and heat, both critical resources? (2) what is the role of hatching asynchrony in food competition among nestlings? (3) what are the functions of vocal and visual nestling behaviours? and (4) how does the presence of a brood parasite, unrelated to the host species, modify parent-offspring interactions?

In Chapter 1, I present an ethogram based on observations compiled from unmanipulated broods. As in most passerines, red-winged blackbird broods make the transition to homeothermy midway through the nestling period, and until then, rely upon

the parent for warmth (Hill and Beaver 1982). Because the female is in most cases the sole provider of both heat and food early in the nestling period (Whittingham and Robertson 1993, Yasukawa *et al.* 1993), brooding and feeding are mutually exclusive activities. That passerine nestlings use begging behaviour to communicate hunger and nutritional needs to parents is well established. But by what means do offspring communicate their thermal needs? I assess parent and offspring behaviour in broods videotaped over the nestling period, in order to identify the behaviours which alert the female parent to the need for increased nutritional care, supplied at the expense of brooding.

In Chapter 2, I examine the influence of size and developmental disparities in relation to the outcome of begging competitions by nestling red-winged blackbirds. Blackbird nestlings hatch asynchronously, resulting in broods of mixed ages. Consequently physiological thermoregulation is initiated by first-hatched "core" offspring (*sensu* Mock and Forbes 1995) while their later-hatched "marginal" siblings are still ectothermic. Sensory maturation and the initiation of endothermy enhance motor skills and response time, both important determinants of begging performance (Khayutin 1985, Holcomb and Twiest 1971, Olson 1994). Unlike the size differential imposed by hatching asynchrony, these physiological changes are initiated midway through the nestling period, which may further disadvantage younger nestlings.

Using the age of the of the core nestlings relative to the age of the marginal nestlings, I assign each brood to one of three categories, shown previously to correspond to three phases of brood developmental in this species (Hill and Beaver 1982): (i) all nestlings younger than five days old, and all assumed to be ectothermic (inertial phase);

(ii) core nestlings at least five days old, and assumed to have initiated endothermy; marginal nestlings younger than five days old, and assumed to be still ectothermic (transitional phase); and (iii) all nestlings at least five days old, and all assumed to have inititiated endothermy (regulatory phase). Begging performance and feeding success of nestlings were assessed from videotaped broods. Core and marginal nestlings did not differ with respect to begging response when the parent arrived at the nest. However, as larger offspring were frequently more successful at stretching their necks the highest when in direct competition with other nestlings for food, they were more successful than their smaller siblings. My results indicate that size is the most important determinent of food reception.

Nestling birds use a combination of vocal and visual signals to solicit food from parents. These signals serve at least two discrete functions: (i) to induce parents to bring more food; and (ii) to influence how food is allocated among brood members. Playback experiments have shown that vocal cues serve function i (Henderson 1975, Harris 1983, McLean and Griffin 1988, Price 1998, Wright 1998). But do they also function to influence intra-brood allocation, as contemporary begging theory suggests (e.g. Parker 1985, Harper 1986, Parker et al.1989), or is that governed chiefly by the non-vocal components of begging (neck-stretching, gaping, jockeying for position within the nest)? I test that the latter alternative is correct in Chapter 3, using a novel non-surgical muting procedure to decouple the vocal and visual components of begging in nestling red-winged blackbirds. I muted a single nestling within the brood temporarily (1 h) and compared its behaviour to a sham-muted nestling and to its own behaviour prior to muting. I address the functional roles of vocal and visual displays by measuring the contribution of each to

individual feeding success and overall parental provisioning.

In Chapter 4, I explore the impact of a brood parasitic brown-headed cowbird (*Molothrus ater*) nestling on nestlings by comparing the behaviour of host nestlings in parasitised and unparasitised broods, using as a guide the ethogram outlined in Chapter 1. Red-winged blackbirds and cowbirds are similar in morphology, but growth rates, thermal development, and vocalisations differ between the two species (Nice 1939, Gochfeld 1979, Eastzer *et al.* 1980, Fiala and Congdon 1983, Woodward 1983, Broughton *et al.* 1987, Weatherhead 1989). Until very recently, the majority of studies which have assessed cowbird behaviour have focused on older, endothermic broods (Nice 1939, Gochfeld 1979, Eastzer *et al.* 1980, Woodward 1983, Broughton *et al.* 1987, Briskie *et al.* 1994, but see Dearborn *et al.* 1998, Lichtenstein and Sealy 1998). Little is known regarding the ontogeny of begging by cowbirds, as continuous monitoring of parasitised broods has been lacking. I assess how the presence of a cowbird affects the behaviour of host parents and offspring across the nestling period by measuring nestling begging behaviour, feeding success, parental provisioning rates, and parental attentiveness from videotaped broods.

References

Broughton, K.E., A.L. Middleton and E.D. Bailey. 1987. Early vocalizations of the brown-headed cowbird and three host species. Bird Behaviour 7: 27-30.

Bugden, S. C. and R. M. Evans. 1997. Vocal solicitation of heat as an integral component of the developing thermoregulatory system in young domestic chickens. Can. J. Zool. 75: 1949-1954.

Choi, I.-H. and G.S. Bakken. 1990. Begging response in nestling red-winged blackbirds (*Agelaius phoeniceus*): effect of body temperature. Physiol. Zool. 63:965-986

Eastzer, D., P.R. Chu and A.P. King. 1980. The young cowbird: average or optimal nestling? Condor 82: 417-425.

Espira, A. and R. M. Evans. 1996. Energy savings from vocal regulation of ambient temperature by 3-day-old domestic chicks. Can. J. Zool. 74: 599-605.

Evans, R. M. 1994. Cold-induced calling and shivering in young American white pelicans: honest signalling of offspring need for warmth in a functionally integrated thermoregulatory system. Behav. Ecol. Sociobiol. 36: 17-23.

Fiala, K. L. and J.D. Congdon. 1983. Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. Ecology 64: 642-647.

Gochfeld, M. 1979. Begging by nestling shiny cowbirds: adaptive or maladaptive? Living Bird 17: 41-50.

Harper, A.B. 1986. The evolution of begging: sibling competition and parent-offspring conflict. Am. Nat. 128: 99-141.

Harris, M.P. 1983. Parent-young communication in the Puffin *Fratercula arctica*. Ibis 125: 109-114.

Henderson, B.A. 1975. Role of the chick's begging behaviour in the regulation of parental feeding behaviour of *Larus glaucescens*. Condor 77: 488-492.

Hill, R.W. and D.L. Beaver. 1982. Inertial thermostability and thermoregulation in broods of redwing blackbirds. Physiol. Zool. 55: 250-260.

Holcomb, L. C. and G. Twiest. 1971. Growth and calculation of age for red-winged blackbird nestlings. Bird-Banding 42: 1-78.

Khayutin, S.N. 1985. Sensory factors in the behavioral ontogeny of altricial birds. Advances in the Study of Behaviour 15: 105-152.

McLean, I. G. and J. M. Griffin. 1988. Structure, function and mimicry in begging calls of passerines and cuckoos. Acta XX Congr. Int. Ornithol.: 1273-1284.

Mock, D.W., and L.S. Forbes. 1995. The evolution of parental optimism. Trends Ecol. Evol. 10: 130-134.

Nice, M.M. 1939. Observations on the behaviour of a young cowbird. Wilson Bull. 51: 233-239.

Olson, J. M. 1992. Growth, the development of endothermy, and the allocation of energy in red-winged blackbirds (*Agelaius phoeniceus*) during the nestling period. Physiol. Zool. 65: 124-152.

Olson, J. M. 1994. The ontogeny of shivering thermogenesis in the red-winged blackbird (*Agelaius phoeniceus*). J. Exp. Biol. 191: 59-88.

Parker, G.A. 1985. Models of parent-offspring conflict. V. Effects of the behaviour of the two parents. Anim. Behav. 33: 519-533.

Parker, G.A., D.W. Mock and T.C. Lamey. 1989. How selfish should stronger sibs be? Am. Nat. 133: 846-868.

Price, K. 1998. Benefits of begging for yellow-headed blackbird nestlings. Anim. Behav. 56, 571- 577.

Weatherhead, P.J. 1989. Sex ratios, host-specific reproductive success, and impact of Brown-headed Cowbirds. Auk 106: 358-366.

Wiebe, M. O. and R. M. Evans. 1994. Development of temperature regulation in young birds: evidence for a vocal regulatory mechanism in two species of gulls (Laridae). Can. J. Zool. 72: 427-432.

Whittingham, L. A. and R. J. Robertson. 1993. Nestling hunger and parental care in red-winged blackbirds. Auk 110: 240-246.

Woodward, P.W. 1983. Behavioural ecology of fledgling brown-headed cowbirds and their hosts. Condor 85: 151-163.

Wright, J. 1998. Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. Behav. Ecol. Sociobiol. 42: 423-429.

Yasukawa, K., F. Leanza, and C.D. King. 1993. An observational and brood-exchange study of paternal provisioning in the red-winged blackbird (*Agelaius phoeniceus*). Behav. Ecol. 4: 78-82.

Chapter 1: Parent-offspring communication in red-winged blackbirds: balancing conflicting demands during the transition to endothermy

Abstract

Nestlings of altricial birds are confined to the nest where they are dependent on the parent to provide two critical resources: food and heat. That nestlings use begging behaviour to communicate hunger and nutritional needs to parents is well established. But by what means do offspring communicate their thermal needs? As in most passerines, red-winged blackbird (*Agelaius phoeniceus*) broods make the transition to homeothermy midway through the nestling period, and until then, rely largely upon parents for warmth. Because the parent female is in most cases the sole provider of both heat and food, brooding and feeding are mutually exclusive activities. Here I show that the collective begging effort of the brood determined how long the parent remains at the nest. A weak collective effort, characteristic of young broods, stimulated increased nest attentiveness. Females responded to an abrupt increase in brood demand midway through the nestling period by spending less time at the nest. Parents appear to derive information regarding both the nutritional and thermal requirements of the brood by assessing the strength of the collective begging response, and supplying the needs of the majority.

Introduction

Altricial birds begin life as ectotherms, but undergo large-scale and rapid morphological, physiological and behavioural remodeling prior to departing the nest. Red-winged blackbirds (*Agelaius phoeniceus*), for example, increase tenfold in mass and are transformed from naked and near-helpless hatchlings into fully-feathered homeotherms in the span of ten days (Holcomb and Twiest 1971, Olson 1994). Nestlings must acquire and assimilate large quantities of food while completing the developmental process, and also require heat from a brooding parent in the period before they can fully regulate their own body temperature (Yarbrough 1970, Hill and Beaver 1982, Westerterp *et al.* 1982). In many altricial birds, including red-winged blackbirds, during the first half of the nestling period the female both forages on behalf of the brood, and also provides thermal care, two mutually exclusive activities (Hill and Beaver 1982, Haggerty 1992, Weathers 1992, Lozano and Lemon 1995, Verbeek 1995).

Red-winged blackbird females can either initiate incubation with the last egg, creating synchronously hatched broods of uniform age, or commence incubation with the first-laid egg(s), creating asynchronously hatched broods of mixed-aged nestlings. Hill and Beaver (1982) describe two phases of development for broods of red-winged blackbirds that hatch synchronously. The first is the inertial phase, which extends from hatch to day four. Maternal heat transfer is the primary source of warmth during this phase, requiring frequent and lengthy brooding by the parent. The inertial phase is characterized by the inability of nestlings to thermoregulate when isolated, necessitating huddling for the maintenance of body temperature during parental absences. The initiation of incipient endothermy by all individuals within the brood ("brood

homeothermy" Hill and Beaver 1982), marks the regulatory phase (day five to fledge). During the regulatory phase heat is produced metabolically, requiring a larger intake of food (Olson 1994), begging is initiated more quickly due to improvements in sensory and motor control (Marsh and Wichler 1982, Choi and Bakken 1990, Olson 1992), and feather growth reduces the benefits of brooding by impairing conductive heat transfer between parent and offspring (Webb and King 1983). Thermal care is generally not provided to broods in the regulatory phase (Hill and Beaver 1982).

The inertial phase is delimited from the regulatory phase by a significant reduction in the length of the parental feeding visit, and a concomitant increase in foraging rates (Hill and Beaver 1982), although offspring behaviours that alert parents to the onset of brood homeothermy are as yet undetermined.

The inertial and regulatory phases of development also occur in asynchronously hatched broods, however they are separated by a third, interim phase, during which the needs of the first-hatched, or "core" nestlings (Mock and Forbes 1995), and later-hatched "marginal" offspring begin to diverge. I call this the "transitional phase". Core nestlings in transitional phase broods have initiated endothermy, and are physiologically similar to nestlings in regulatory phase broods, while ectothermic marginal offspring are more similar to nestlings in inertial phase broods (Hill and Beaver 1982).

Considerable attention has focused on parent-offspring communication in altricial birds and the role that brood begging plays in manipulating parental foraging (von Haartman 1953, Henderson 1975, Bengtsson and Ryden 1983, McLean and Griffin 1988, Stamps *et al.* 1989, Redondo and Castro 1992, Whittingham and Robertson 1993, Price and Ydenberg 1995). Recent work spanning a variety of species (domestic chickens,

Gallus gallus - Bugden and Evans 1997, Espira and Evans 1996; ring-billed gull *Larus delawarensis*, and herring gulls *L. argentatus* - Wiebe and Evans 1994; American white pelican, *Pelecanus erythrorhynchos* - Evans 1992, 1994) suggests that offspring begging may also communicate thermal need.

In this paper I examine the development of parent-offspring interactions over the nestling period and identify how parents assess the energetic requirements of the brood. The objective of this study is three-fold: (i) to describe the generalized pattern of parent-offspring interactions throughout the red-winged blackbird nestling period; (ii) to relate this to the transition from parental brooding to feeding that occurs with the onset of endothermy; and (iii) to identify the proximate mechanism(s) cueing parents to brood homeothermy.

Methods

I studied red-winged blackbirds in wetlands near Winnipeg, Manitoba, from late May to early July from 1993 to 1996. In this population, female red-winged blackbirds lay an average clutch of 3.95 eggs (n = 722 clutches), and incubate the eggs for 11-13 days. The nestling period spans 9-11 days, during which time females continue to provide all of the care, by brooding or shading the young. The average brood size at hatch is 3.52 nestlings (n = 541 broods). However, partial brood loss, which often results from starvation of the last-hatched nestling, means that broods are smaller later in the nestling period (average day 8 brood size = 2.75 nestlings, n = 366 broods).

Broods were surveyed daily, and the behaviour of nestling and parent blackbirds was

studied by collecting videotaped observations of 30 different broods aged from 2 - 9 days (hatch day = 0), representing 95 nestlings. Broods contained either two (n = 3), three (n = 15) or four (n = 11) nestlings, with an average hatch spread of 1.07 ± 0.69 (s.d.) days. The female parent was the sole provider of both thermal and nutritional care for most of these broods. At five older broods (average age 7.6 ± 0.51 days), males contributed roughly 1/6th of the food to the brood (i.e., 18.4 % of the feeding visits). Because of high rates of depredation, I were unable to collect data from the same broods every day, precluding the use of repeated-measures analysis.

Video cameras were set up 1.5 - 3 m from nests, and 2 h of videotape was gathered at each nest. Observations were collected between 9:00 AM and 3:00 PM CST. Nestling behaviour from all visits during a one-hour span from the latter half of the taping session was analyzed from each videotaped brood on a frame-by-frame basis, and the mean from each nest used for analysis.

Parental behaviour

Parental behaviour was gauged using three measures: i) visit frequency (foraging rate); ii) visit duration; and iii) absence duration. Hourly parental effort was assessed using the formula:

Parental effort/h = (number of visits x length of visit) + (number of foraging absences x length of absence).

Visits were subdivided into two phases: i) the food distribution phase, which spanned the interval between the parent's arrival and when the last food item was allocated; and ii) the non-feeding phase, which extended from allocation of the last food item until the

departure of the parent. Non-feeding activity included behaviours associated with regulating the temperature of the brood (brooding, shading), sanitation (removal of fecal sacs and debris), and/or guarding.

Nestling behaviour

For each visit during a one-hour span I measured four indices of "primary begging response" (*sensu* M. L. Leonard and A. Horn, Department of Biology, Dalhousie University, Halifax, Nova Scotia, pers. comm.). The primary begging response refers to the begging behaviour of nestlings initiated in response to the arrival of a parent at the nest, and can be divided into a number of components. First, the latency of begging was defined as the amount of time between the arrival of the parent on the nest rim and the initiation of begging. A negative latency indicates that begging commenced before the parent's arrival at the nest, and a positive latency indicates that begging began after the parent arrived at the nest. Secondly, the frequency of begging was defined separately for periods before and after food allocation as the number of visits per hour on which a nestling begged, and the number of visits per hour on which a nestling continued to beg following the allocation of food. Thirdly, the duration of begging was defined as the total length of time that a nestling begged during a visit. Begging duration was subdivided into two measurements: the length of time that nestlings begged while food was being allocated; and the length of time nestlings continued to beg after the last food item was dispensed. Fourthly, the intensity of begging was scored and recorded as follows when the parent arrived at the nest: 0 (not begging), 1 (gaping), or 2 (gaping with neck stretched) (e.g. Cotton *et al.* 1999). The sides of the nest cup often blocked leg and wing activity, so the scoring system could not include measures of these. To avoid temporal

pseudoreplication (Hurlbert 1984), I used different broods, and averaged the values for each behavioural variable for each nestling over the entire one hour observation period.

I identified the begging indices that contributed to the length of the feeding and non-feeding phases using linear regression. I then computed the correlations among the selected variables for each nestling using principal components analysis, a process that generates a single factor score based on the collective strength of the correlational relationship between the components. I used this score as a measure of overall begging effort. Scores ranged between –3.0 and + 3.0. A negative score indicated low effort, which meant that the nestling had responded slowly, begged at low intensity, seldom continued to beg following the allocation of food, or if they did, begged for a short duration. A positive score, indicating high effort, meant that the nestling had immediately initiated high intensity begging in response to the arrival of the parent, and frequently continued to beg for an extended period following the allocation of food.

Brood behaviour

The behaviour of the brood as a whole was assessed by calculating the average for each index of primary begging response (latency, frequency, duration and intensity) from all nestlings within a brood. I used principal components analysis to generate a factor score using the same correlated variables as for nestlings. The factor score generated for each brood was used as a measure of the collective begging effort of the brood.

The first principal component score explained 70.22% of variance, with factor loadings of –0.84 (latency), 0.76 (duration of continued begging), 0.09 (intensity) and 0.86 (proportion of visits on which the nestling continued to beg).

Given that many nests were lost to predation, preventing continuous monitoring of the videotaped broods, I used the population data to compute the instantaneous growth rate $(R = g \cdot d^{-1})$, (Holcomb and Twiest 1971).

Using the age of the core nestlings relative to the age of the marginal nestlings, I assigned each brood to one of three categories, shown previously to correspond to three phases of brood developmental in this species (Hill and Beaver 1982): i) core and marginal nestlings less than five days old, and all assumed to be ectothermic (inertial phase); ii) core nestlings at least five days old and assumed to have initiated endothermy; marginal nestlings younger than five days old, and assumed to be still ectothermic (transitional phase); iii) core and marginal nestlings at least five days old, and all assumed to have inititiated endothermy (regulatory phase).

Results

Parental behaviour

Parents increased delivery rates as broods aged, although the effect was non-significant $(F_{1,28} = 3.51, P = 0.072;$ Fig. 1.1a). There was, however, a significant effect of brood stage (ANOVA: $F_{2,27} = 3.673, P = 0.039$). Whereas the number of visits to broods between the inertial and transitional phases of development remained essentially constant $(P = 1.000)$, there was a slight, albeit non-significant, increase in the frequency of visits between the inertial and regulatory phases $(P = 0.069)$.

Figure 1.1. Mean (± SE) red-winged blackbird parental behaviour over the nestling

period. Three measures of parental behaviour were used: a) the foraging rate (visits per

hour), b) the length of foraging absences (min), and c) the length of visits (min).
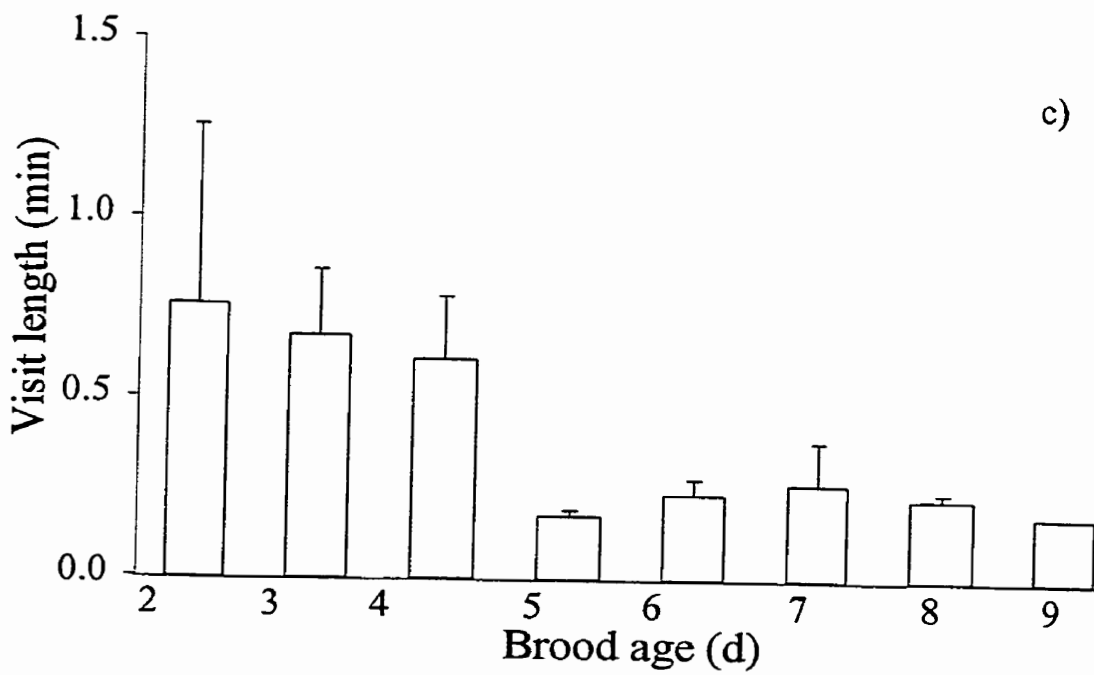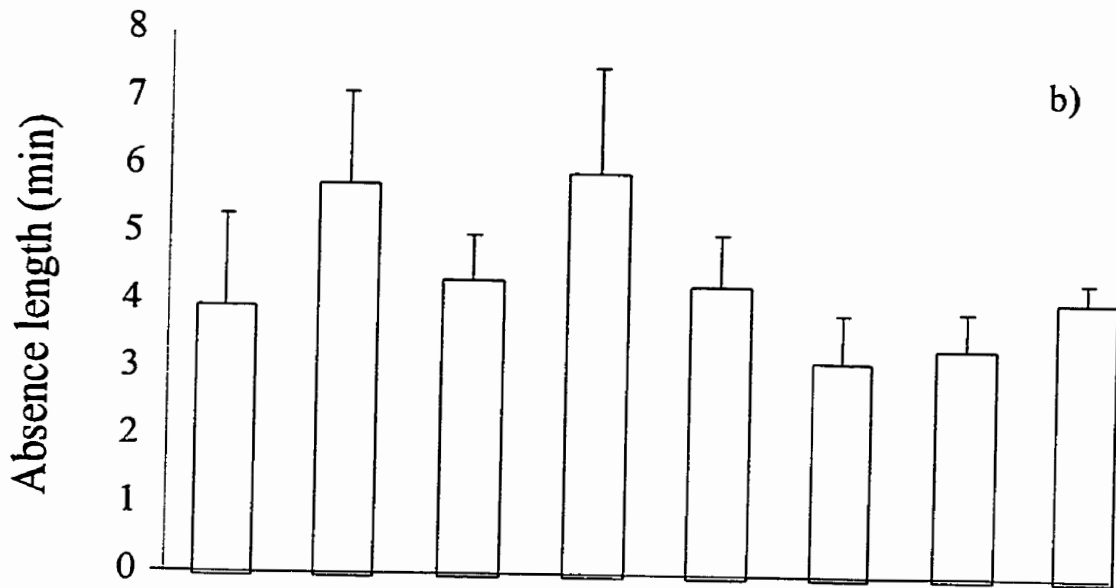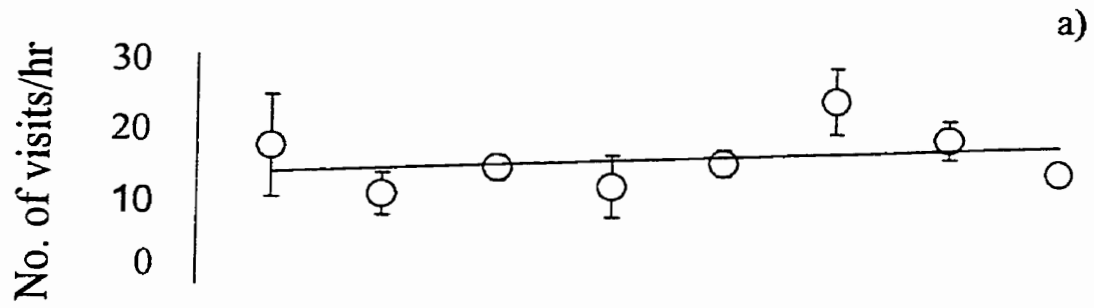
Similarly, although there was no significant relationship between the length of the foraging absence and brood age ($F_{1,28}$ = 2.99, P = 0.095; Fig. 1.1b). Consequently, there was little variation across development stages (ANOVA: $F_{2,27}$ = 2.96, P = 0.069).

In contrast to visit frequency and absence length, the effect of brood age on visit length was highly significant ($F_{1,28}$ = 13.32, P = 0.001; Fig. 1.1c). Parents significantly reduced the amount of time that they spent at broods in the later phases of development (ANOVA: $F_{2,27}$ = 9.93, P = 0.001). After day four, the length of time parents spent at the nest during a visit fell sharply, resulting in significantly longer visits to broods in the inertial phase of development relative to the transitional (P = 0.002) or regulatory (P = 0.002) phases.

Nestling behaviour

Begging is composed of numerous correlated behaviours related to age and development. Four behavioural indices best described the mean collective brood begging effort: intensity, latency, continued begging and proportion continuing to beg (Table 1.1). In other words, a brood begging at maximum effort could be described as one in which intense begging was consistently initiated by the majority of nestlings prior to the arrival of the parent, and where begging by the majority continued for an extended period after the allocation of food.

Within broods, nestling effort increased over the first four days, and then remained high for the remainder of the nestling period ($F_{1,94}$ = 19.17, P < 0.001; Fig. 1.2), reflecting the developmental pattern of the primary begging response indices, all of which reached a local maximum (or minimum, in the case of latency) at about day five

Table 1.1. The strength of the correlational relationships among the indices of primary begging response. Results were determined by principal components analysis and presented as the correlation matrix, accompanied by one-tailed P-values in brackets. The PC1 scores accounted for 69.76% of variance with factor loadings of −0.293 (latency), 0.268 (duration of continued begging), 0.325 (intensity) and 0.308 (proportion of visits on which the nestling continued to beg).

Principal component loadings	Total length of continued begging (min)	Latency (min)	Proportion that continue begging
Intensity	0.547 (0.001)	-0.667 (0.000)	0.777 (0.000)
Total length of continued begging (min)		-0.506 (0.002)	0.502 (0.002)
Latency (min)			-0.560 (0.001)

Figure 1.2. The relationship between red-winged blackbird nestling begging effort (calculated as a factor score) and nestling age.
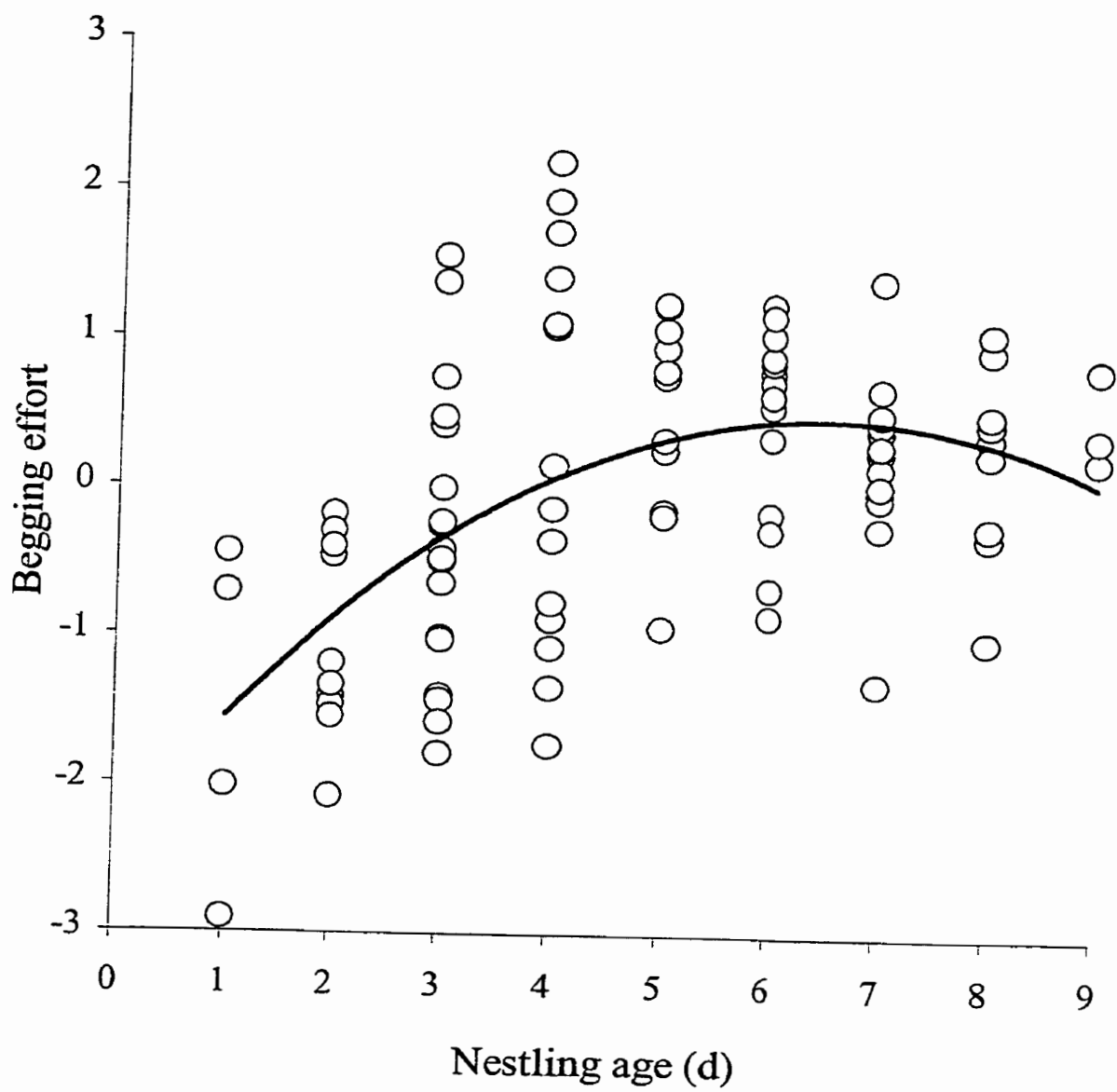
Figure 1.3. The ontogeny of begging behaviour by red-winged blackbird nestlings. The mean (± SE) of the primary begging response indices are shown: a) begging latency, a measure of response relative to the arrival of the parent; b) begging intensity, scored as 0 (not begging), 1 (gaping), or 2 (gaping with neck stretched); c) proportion of visits on which nestlings begged before and after food allocation (all proportions arcsine square root transformed); d) the duration of time that nestlings begged before and after food allocation.
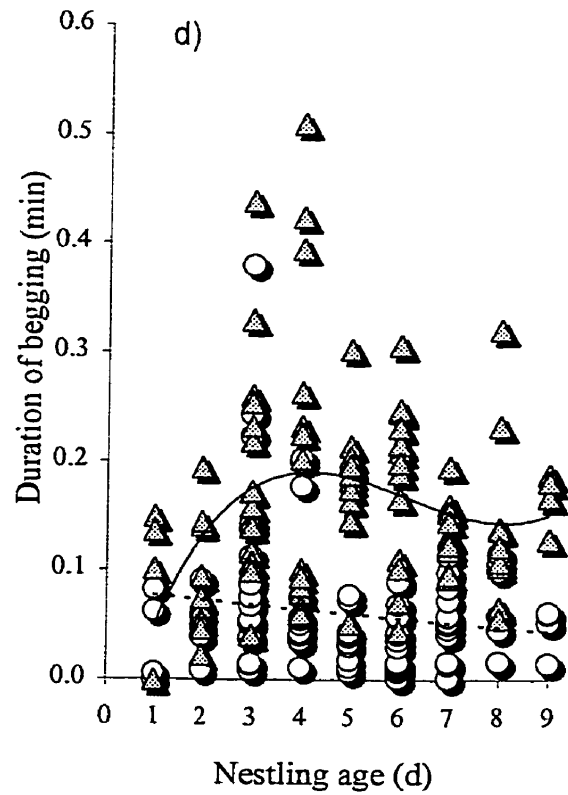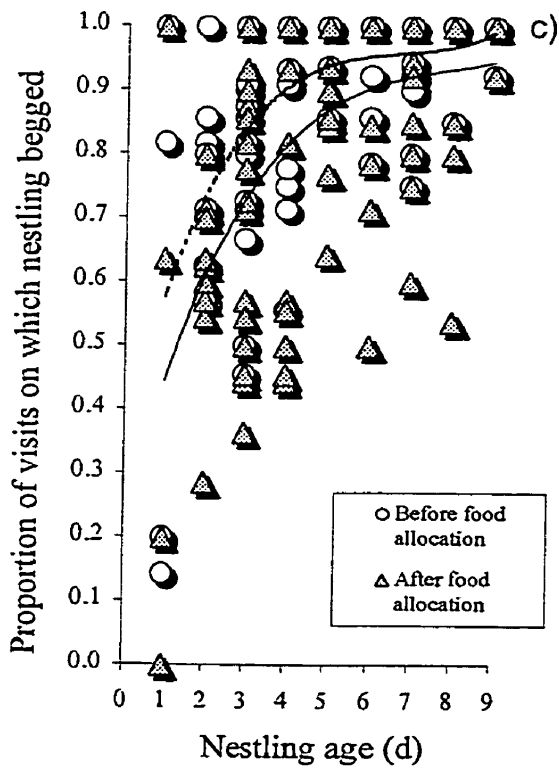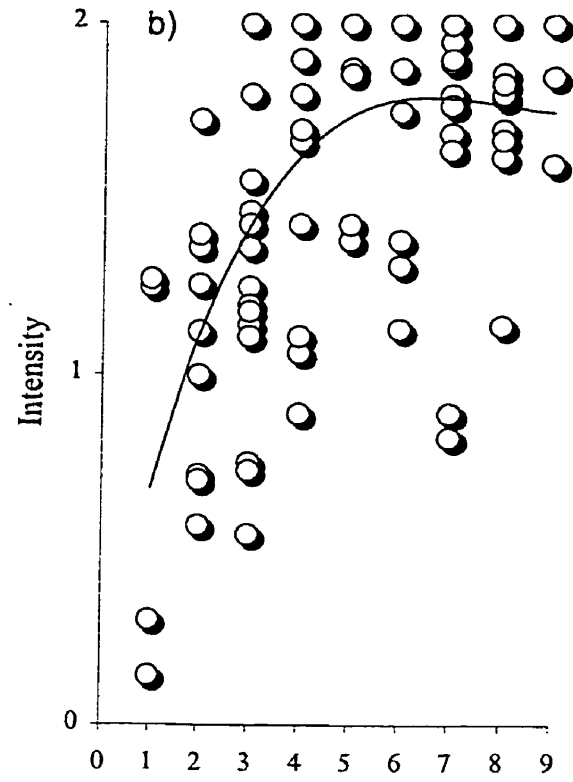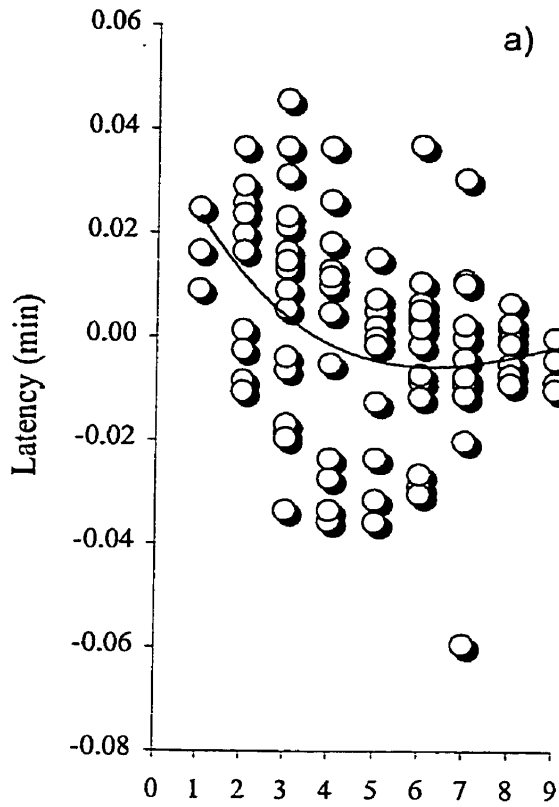
(Figs. 1.3a-d). Younger nestlings consistently delayed begging until after the arrival of the parent ($F_{1,94} = 7.46$, P = 0.001; Fig. 3a), and begged at lower intensities ($F_{1,94} = 29.34$, P < 0.001; Fig. 1.3b). Younger nestlings were less likely to continue to solicit after food was allocated ($F_{1,94} = 20.92$, P < 0.001; Fig. 1.3c) and stopped begging earlier ($F_{1,94} = 3.77$, P = 0.027; Fig. 1.3d).

The duration and frequency of begging differed within visits before and after the allocation of food. Significantly less time was spent begging before food allocation than after (paired-t: $t_{97} = 8.48$, P = 0.001; Fig. 1.3d), and begging was more frequently initiated prior to the arrival of the parent than it was sustained following food allocation (paired-t: $t_{97} = 6.41$, P < 0.001; Fig. 1.3c).

Nestling begging efforts were lowest during the first three days post-hatch, the interval with the highest instantaneous rate of growth (Table 1.2).

Brood behaviour

Changes in both parent and offspring behaviour were apparent midway through the nestling period (Fig. 1.4). The abrupt reduction in the length of the feeding visit on day five coincided with the beginning of the transitional phase, and continued for the remainder of the nestling period, encompassing the regulatory phase.

The length of time that the parent remained at the nest was inversely related to the collective begging effort of the brood ($F_{1,28} = 3.60$, P = 0.042, Fig. 1.4). Negative scores, characteristic of broods younger than five days old (inertial phase), were associated with extended visits at the nest, and positive scores, which occurred after day four (hereafter "older broods", to include both the transitional and regulatory phases) were associated with relatively brief visits. During a visit, the lengths of the feeding and non-feeding

Table 1.2. The mean ($\pm$ SE) instantaneous rate of growth ($R = g \cdot d^{-1}$), and the overall begging effort (derived from principal components analysis), of red-winged blackbird nestlings from day 1 to 9 of the nestling period.

Age (d)	Instantaneous growth rate (n = 997)	Begging effort (n = 95)
1	0.419 ± 0.015	-1.514 ± 0.576
2	0.375 ± 0.014	-1.031 ± 0.205
3	0.362 ± 0.016	-0.359 ± 0.242
4	0.254 ± 0.014	0.234 ± 0.352
5	0.193 ± 0.011	0.493 ± 0.209
6	0.159 ± 0.090	0.457 ± 0.181
7	0.127 ± 0.010	0.213 ± 0.157
8	0.060 ± 0.009	0.230 ± 0.217
9	0.061 ± 0.012	0.560 ± 0.160

Figure 1.4. The mean ($\pm$ SE) length of time that a red-winged blackbird parent spent at the nest during a feeding visit, the mean ($\pm$ SE) begging effort of the brood, and brood age.
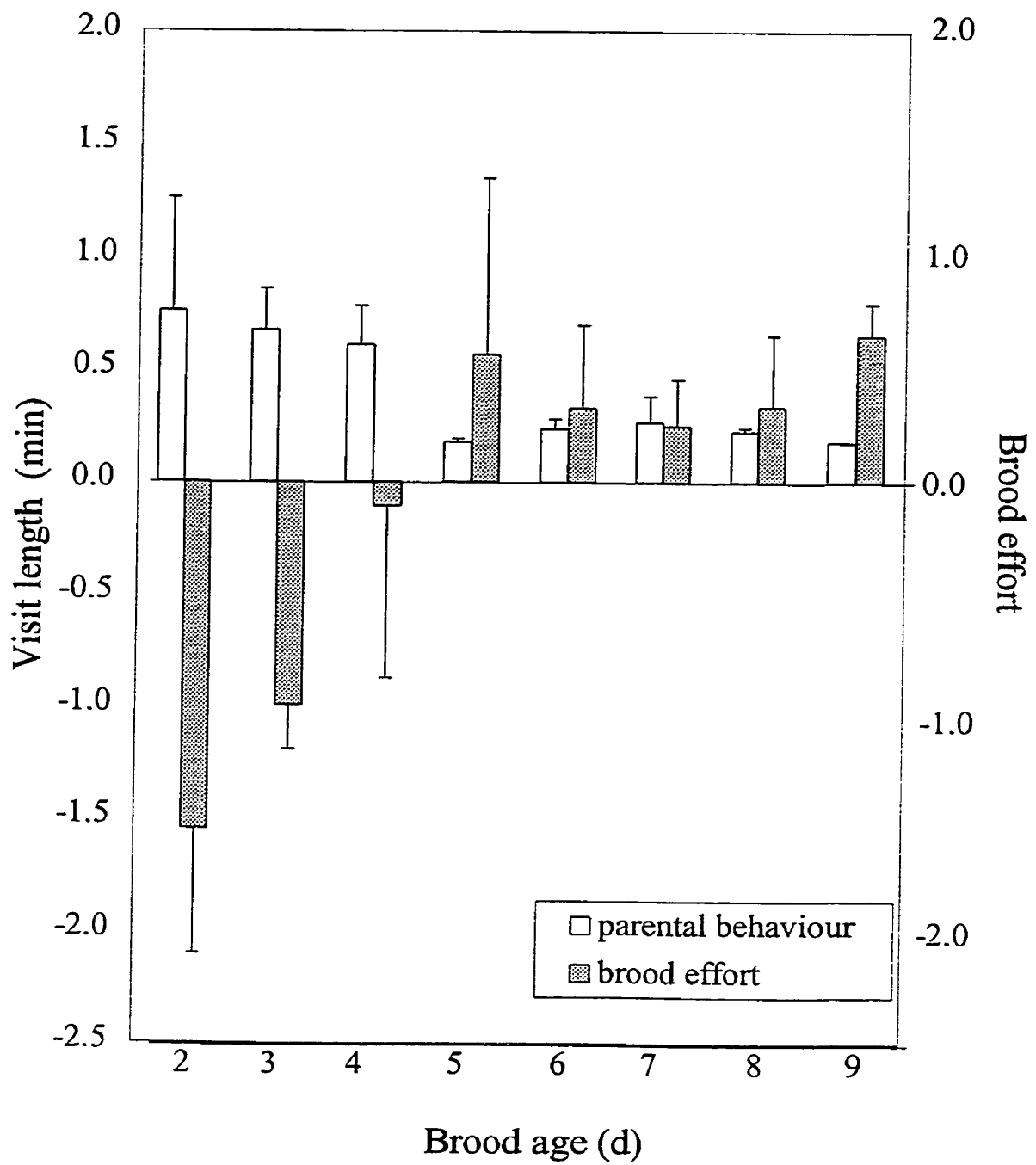
stages were affected by different components of begging. A rapid and intense begging response by the brood expedited food allocation, which reduced the length of the feeding phase (Table 1.3a). Continued begging by the majority of the brood following food allocation reduced the length of the non-feeding phase (Table 1.3b).

I assessed differences in parent and offspring behaviour between younger and older broods using an independent-samples t-test. Despite consisting of fewer nestlings than younger broods, older broods were heavier and exerted a greater collective effort (Table 1.4). Visits to younger broods were significantly longer because more time was required to distribute food, and parents were significantly more attentive, remaining at the nest for an extended period following food allocation (Table 1.4).

The female provided thermal care (brooding or shading) to eight broods, the majority (71%) of which were in the inertial phase of development. However, two older broods, a day-six brood in the transitional phase of development, and a day-seven brood in the regulatory phase, both exhibited a low collective begging effort (< 0), and were also provided with thermal care (Fig. 1.5).

Discussion

Nestlings of altricial birds are confined to the nest where they are dependent on the parent to supply their nutritional and thermal requirements. Midway through the nestling period, parents begin to spend less time at the nest, and more time foraging (Eisner 1963, Hill and Beaver 1982, Haggerty 1992, Verbeek 1995). The balance between provisioning and brooding in altricial birds has previously been studied in relation to brood age, size, and environmental parameters (Johnson and Best 1982, Bedard and

Table 1.3. Results of multiple regression analysis to determine which behavioural indices (proportion that beg, intensity, latency) contributed to: a) the length of the feeding phase (overall adjusted $R^2 = 0.111$, $P = 0.111$; best fit adjusted $R^2 = 0.144$, $P = 0.047$), and which behavioural indices (proportion that continue begging, duration of continued begging, intensity) contributed to b) the length of the non-feeding phase (overall adjusted $R^2 = 0.256$, $P = 0.013$; best fit adjusted $R^2 = 0.273$, $P = 0.005$).

a)

Begging behaviour	B (slope)	SE	t	P
Intensity	-0.039	0.033	-1.177	0.249
Latency (min)	0.747	0.807	0.926	0.363

b)

Begging behaviour	B (slope)	SE	t	P
Duration of continued begging (min)	1.333	0.592	2.251	0.033
Proportion that continue begging	-0.560	0.148	-3.774	0.001

Table 1.4. The behaviour of redwinged-blackbird parents, measured as the mean ($\pm$ SE) length of the feeding visit, feeding phase and non-feeding phase, and mean ($\pm$ SE) measures of brood characteristics, assessed as the begging effort, age (d), number of nestlings and collective mass. Measurements from younger (< day five; inertial phase) and older ($\geq$ day five; transitional and regulatory phase) broods are compared.

Variable	Younger Broods (n=10)	Older Broods (n=20)	P (2-tailed)
Parental Behaviour			
Visit length (min)	0.515 ± 0.128	0.224 ± 0.035	0.008
Feeding phase (min)	0.100 ± 0.024	0.043 ± 0.007	0.007
Non-feeding phase (min)	0.415 ± 0.123	0.174 ± 0.031	0.018
Cleaning and assessment	0.273 ± 0.046	0.172 ± 0.033	0.087
Thermal care (min)	0.142 ± 0.057	0.002 ± 0.040	0.052
Brood characteristics			
Brood effort	-0.749 ± 0.353	0.375 ± 0.157	0.002
Brood age (d)	3.200 ± 0.249	6.850 ± 0.274	<0.001
Brood size (no.of nestlings)	3.800 ± 0.133	3.000 ± 0.126	<0.001
Brood mass (g)	10.516 ± 0.773	25.622 ± 1.302	<0.001

Figure 1.5. The relationship between the mean (± SE) length of time that the parent red-winged blackbird remained at the nest during a visit to provide thermal care (brooding or shading/hour), and brood age.
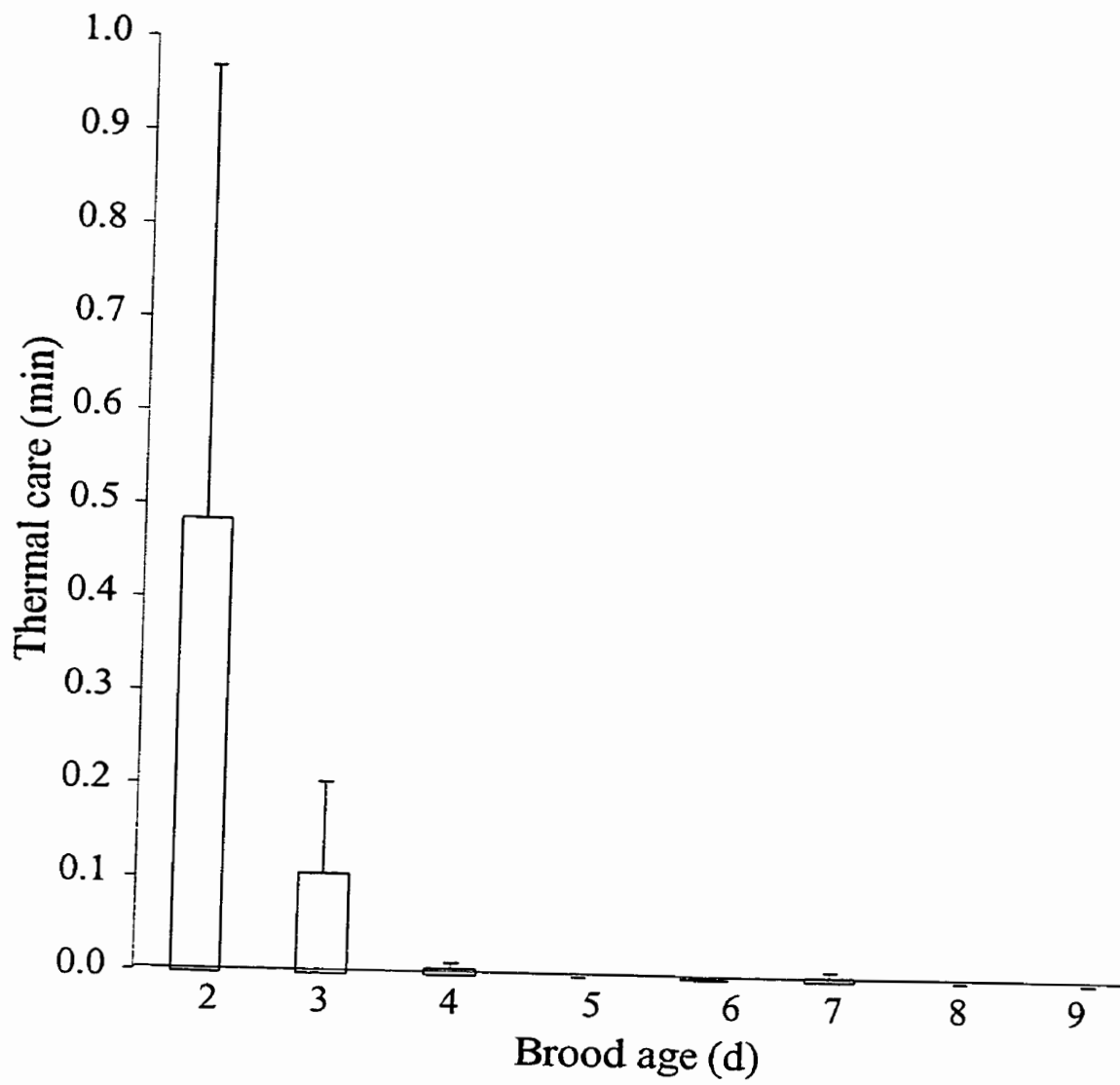
Meunier 1983, Heagy and Best 1983, Carey 1990, Weathers 1992, Haggerty 1992, Lozano and Lemon 1995, Verbeek 1995). Many of these authors note the importance of the thermal status of offspring, which changes over the nestling period, but do not examine this effect explicitly. Hill and Beaver (1982) provide an important exception. They describe their results in relation to brood thermoregulation and provide correlational evidence that parents adjust the amount of time spent at the nest in relation to the thermoregulatory ability of the brood. Here I focus on the behavioural rules that govern the balance between parental brooding and provisioning in relation to the age and developmental phase of the brood.

During the first three days after hatching, red-winged blackbird nestlings are physiologically ectothermic. Metabolic costs are low, and because the bulk of energy is allocated to tissue production, the instantaneous rate of growth is high (Olson 1992). Beginning on day four, nestlings must increase their energetic intake in order to cover the additional metabolic costs associated with the onset of endothermy. Consequently, the initially rapid rate of growth slows as more energy is diverted to maintenance, digestion and thermoregulation (Holcomb and Twiest 1971, Olson 1992). These basic tradeoffs in large part explain the typical growth curve of nestling passerine birds. Intriguingly, the ontogeny of nestling begging follows the same pattern. Begging effort increases rapidly in young broods, and reaches a maximum on day five, coincidentally, I assume, with the onset of the initiation of incipient thermoregulation by core nestlings (see Hill and Beaver 1982, Olson 1992).

After day five, there is a sharp reduction in the length of parental visits with two components: first, a decrease in the length of the food distribution phase, and second, a

reduction in the length of the non-feeding phase. Upon arriving at the nest, parents assess individual begging effort to allocate food. Following the food distribution phase, parents appear to evaluate the thermal requirements of the brood. Shorter visits to older broods resulted from both faster food dispersal and diminished nest attentiveness, both of which reflect changes in nestling begging behaviour. Unlike broods at the inertial phase of development where nestlings respond slowly and sporadically to the arrival of the parent, transitional and regulatory phase broods are characterized by an immediate, intense begging response by the majority of the brood which continues for an extended period following food allocation.

The female parent reduced brooding on day five in response to an increase in the collective begging effort of the brood (demand). However, contrary to predictions (Hussell 1988) and Hill and Beaver's (1982) observations of synchronously hatched broods of red-winged blackbirds, there was no corresponding shift in foraging rate (supply). Earlier work on this, and other red-winged blackbird systems (see Chapter 1, Holcomb and Twiest 1971, Caccamise 1976, Cronmiller and Thompson 1980) indicate that partial brood loss is highest midway through the nestling period. My results suggest that the period of peak brood demand may have been offset by a reduction in brood size, which would account for the very gradual increase in supply observed.

Studies of three other passerines have identified changes in offspring behaviour and parental response that correspond to phases of nestling development associated with the transition to endothermy. Leonard and Horn (1996) observed that a lower proportion of tree swallow (*Tachycineta bicolor*) nestlings begged in younger (day 1 to day 4) compared to older broods (day 9 to day 11), and suggested that brood responsiveness and

parental foraging rates are affected by nestling development, especially between these phases. Similarly, the initially unsynchronized and irregular begging response observed by young great tit (*Parus major*) and European blackbird (*Turdus merula*) broods improved gradually during the first half of the nestling period (Bengtsson and Ryden 1981). An abrupt change in the feeding procedure, associated with developmental changes occurring around day four, expedited food transfer in older broods. Nestlings became better at retaining food items, and at directing begging toward the feeding parent, and broods exhibited faster and more synchronized responses. Yasukawa *et al.* (1993) achieved similar results by experimentally switching younger red-winged blackbird broods with older broods. An immediate increase in parental foraging rates resulted from the higher nutritional demands of older broods.

The collective begging effort of the brood appears to communicate both thermal and nutritional needs, the former passively and the latter actively. A weak begging effort, characteristic of, but not restricted to, inertial phase broods, appeared to signal that nestlings did not require immediate feeding, and below a given threshold, that they required warmth. Conversely, a strong collective effort, both characteristic of and restricted to older broods, appeared to signal a preference for immediate nutritional care. My results suggest that a weak collective effort signals thermal need, to which parents respond by brooding or shading, irrespective of brood age or phase of development.

Provision of thermal care fluctuates on a number of temporal scales: over the nestling period, as the thermal and energetic needs of the developing brood change (Dawson and Evans 1957, Yarbrough 1970, Hill and Beaver 1982, Johnson and Best 1982); periodically, in response to both unseasonably hot (Morton and Carey 1971, Johnson and

Best 1982, Murphy 1985) and cold (Hill and Beaver 1982) weather; and hourly, in conjunction with the diurnal solar cycle (Gotie and Kroll 1973, Heagy and Best 1983). Choi and Bakken (1990) identified a link between begging and body temperature in red-winged blackbirds that indicates that vocal and non-vocal behaviours are temperature-sensitive. Outside a fairly narrow "temperature tolerance zone", defined as a range of ambient temperatures across which nestlings are able to solicit food, panting and loss of coordination inhibit begging, hunger contractions virtually cease, and nestlings are unable to assimilate food (Choi and Bakken 1990). Thus foraging for broods too hot or cold is unproductive. Evaluating brood activity throughout the feeding visit appears to provide parents with the opportunity to adjust their behaviour in order to meet the fluctuating nutritional and thermal needs of the brood.

My results suggest that the passive communication of the need for heat precedes active demands for food, supporting the hypothesis that non-signalling is the precursor to signalling (Rodriguez-Girones *et al.* 1996). Rather than leaving the nest after feeding, a common parental response to inactive, sated broods (Bengtsson and Ryden 1981, Litovitch and Power 1982, Leonard and Horn 1996, 1998), parents responded to a low collective effort by extending visits and increasing attentiveness. Begging behaviour in broods at the inertial phase was coordinated with parental feeding activity, and stopped once the external stimulus was removed. In contrast, in transitional and regulatory phase broods, the majority of competitors responded when they detected the parent approaching, and continued to solicit after food had been dispensed. Parents appear to derive information regarding the nutritional and thermal requirements of the brood by assessing the strength of the begging response, and respond by supplying the needs of the

majority.

References

Bedard, J. and Meunier, M. 1983. Parental care in the Savannah sparrow. Can. J. Zool. 61: 2836-2843.

Bengtsson, H. and Ryden, O. 1981. Development of parent-young interaction in asynchronously hatched broods of altricial birds. Z. Tierpsychol. 56: 255-272.

Bengtsson, H. and Ryden, O. 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major*. Behav. Ecol. Sociobiol. 12: 243-251.

Bugden, S. C. and Evans, R. M. 1997. Vocal solicitation of heat as an integral component of the developing thermoregulatory system in young domestic chickens. Can. J. Zool. 75: 1949-1954.

Caccamise, D.F. 1976. Nesting mortality in the red-winged blackbird. Auk 93: 517-534.

Carey, M. 1990. Effects of brood size and nestling age on parental care by male field sparrows (*Spizella pusilla*). Auk 107: 580-586.

Choi, I.-H. and Bakken, G. S. 1990. Begging response in nestling red-winged blackbirds (*Agelaius phoeniceus*): effect of body temperature. Physiol. Zool. 63: 965-986

Cotton, P. A., Wright, J. and Kacelnik, A. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. Am. Nat. 153: 412-420.

Cronmiller R.R. and C.F. Thompson. 1980. Experimental manipulation of brood size in red-winged blackbirds. Auk 97: 559-565.

Dawson, W. R. and Evans, F. C. 1957. Relation of growth and development to temperature regulation in nestling field and chipping sparrows. Physiol. Zool. 30: 315-327.

Eisner, E. 1963. A quantitative study of parental behaviour in the Bengalese finch. Behaviour 20: 134-206.

Espira, A. and Evans, R. M. 1996. Energy savings from vocal regulation of ambient temperature by 3-day-old domestic chicks. Can. J. Zool. 74: 599-605.

Evans, R. M. 1992. Embryonic and neonatal vocal elicitation of parental brooding and feeding responses in American white pelicans. Anim. Behav. 44: 667-675.

Evans, R. M. 1994. Cold-induced calling and shivering in young American white pelicans: honest signalling of offspring need for warmth in a functionally integrated thermoregulatory system. Behav. Ecol. Sociobiol. 36: 17-23.

Gotie, R. F. and Kroll, J. C. 1973. Growth rate and ontogeny of thermoregulation in nestling great-tailed grackles *Cassidix mexicanus prosopidicola* (Icteridae). Condor 75: 190-199.

Haggerty, T. H. 1992. Effects of nestling age and brood size on nestling care in the Bachman's sparrow (*Aimophila aestivalis*). Am. Midl. Nat. 128: 115-125.

Heagy, P.A. and Best, L. B. 1983. Factors affecting feeding and brooding of brown thrasher nestlings. Wilson Bull. 95: 297-303.

Henderson, B. A. 1975. Role of the chick's begging behavior in the regulation of parental feeding behavior of *Larus glaucescens*. Condor 77: 488-492

Hill, R. W. and Beaver, D. L. 1982. Inertial thermostability and thermoregulation in broods of redwing blackbirds. Physiol. Zool. 55: 250-260.

Holcomb, L. C. and Twiest, G. 1971. Growth and calculation of age for red-winged blackbird nestlings. Bird-Banding 42: 1-78.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Hussell, D. J. T. 1988. Supply and demand in tree swallow broods: a model of parent-offspring food-provisioning interactions in birds. Am. Nat. 131: 175-202.

Johnson, E. J. and Best, L. B. 1982. Factors affecting feeding and brooding of gray catbird nestlings. Auk 99: 148-156.

Leonard, M. L. and Horn, A. 1996. Provisioning rules in tree swallows. Behav. Ecol. Sociobiol. 38: 341-347.

Leonard, M. L. and Horn, A. 1998. Need and nestmates affect begging in tree swallow. Behav. Ecol. Sociobiol. 42: 431-436.

Litovich, E. and Power, H. W. 1982. Parent-offspring conflict and its resolution in the European starling. Ornith. Monogr. No. 47. American Ornithologist's Union. Washington, D.C. 71 pp.

Lozano, G. A. and Lemon, R. E. 1995. Food abundance and parental care in yellow warblers (*Dendroica petechia*). Behav. Ecol. Sociobiol. 37: 45-50.

Marsh, R. L. and Wichler, S. J. 1982. The role of muscle development in the transition to endothermy in nestling bank swallows, *Riparia riparia*. J. Comp. Biol. B 149: 99-105.

McLean, I. G. and Griffin, J. M. 1988. Structure, function and mimicry in begging calls of passerines and cuckoos. Acta XX Congr. Int. Ornithol.: 1273-1284.

Mock, D.W. and Forbes, L. S. 1995. The evolution of parental optimism. Trends Ecol. Evol. 10: 130-134

Morton, M. L. and Carey, C. 1971. Growth and the development of endothermy in the mountain white-crowned Sparrow (*Zonotrichia leucophrys oriantha*). Physiol. Zool. 44: 177-189.

Murphy, M. T. 1985. Nestling Eastern Kingbird growth: effects of initial size and ambient temperature. Ecology 66: 162-170.

Olson, J. M. 1992. Growth, the development of endothermy, and the allocation of energy in red-winged blackbirds (*Agelaius phoeniceus*) during the nestling period. Physiol. Zool. 65: 124-152.

Olson, J. M. 1994. The ontogeny of shivering thermogenesis in the red-winged blackbird (*Agelaius phoeniceus*). J. Exp. Biol. 191: 59-88.

Price, K. and Ydenberg, R. 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. Behav. Ecol. Sociobiol. 37: 201-208.

Redondo T, and Castro, F. 1992. Signalling of nutritional need by magpie nestlings. Ethology 92: 192-204.

Rodriguez-Girones, M. A., Cotton, P. A. and Kacelnik, A. 1996. The evolution of begging: signalling and sibling competition. Proceedings of the National Academy of Sciences of the USA 93: 14637-14641.

Stamps, J., Clark, A., Arrowood, P. and Kus, B. 1989. Begging behavior in budgerigars. Ethology 81: 177-192.

Verbeek, N. A. M. 1995. Body temperature and growth of nestling northwestern crows, *Corvus caurinus*. Can. J. Zool. 73: 1019-1023.

von Haartman, L. 1953. Was reizt den Trauerfliegenschnäpper zu füttern? Die Vogelwarte 16: 157-164.

Weathers, W. W. 1992. Scaling nestling energy requirements. Ibis 134: 142-153.

Webb, D. R. and King, J. R. 1983. Heat-transfer relations of avian nestlings. J. Therm. Biol. 8: 301-310.

Westerterp, K., Gortmaker, W., and Wijngaarden, H. 1982. The energetic optimum in brood-raising in the starling *Sturnus vulgaris*: an experimental study. Ardea 70: 153-162.

Wiebe, M. O. and Evans, R. M. 1994. Development of temperature regulation in young birds: evidence for a vocal regulatory mechanism in two species of gulls (Laridae). Can. J. Zool. 72: 427-432.

Whittingham, L. A. and Robertson, R. J. 1993. Nestling hunger and parental care in red-winged blackbirds. Auk 110: 240-246.

Yarbrough, C. G. 1970. The development of endothermy in nestling gray-crowned rosy finches, *Leucosticte tephrocotis griseonucha*. Comp. Biochem. Physiol. 34: 917-925.

Yasukawa, K., Leanza, F. and King, C.D. 1993. An observational and brood-exchange study of paternal provisioning in the red-winged blackbird (*Agelaius phoeniceus*). Behav. Ecol. 4: 78-82.

Chapter 2: Differential begging behaviour in red-winged blackbird (*Agelaius phoeniceus*) broods

Abstract

Red-winged blackbird (*Agelaius phoeniceus*) nestlings begin life as ectotherms, and make the transition to endothermy during early development. Sensory maturation and the initiation of endothermy impart improved motor skills and faster response time, which are known to enhance begging performance. Unlike the size handicap imposed by hatching asynchrony, these physiological changes are initiated midway through the nestling period, potentially conferring an additional handicap on younger nestlings. I examined the influence of size and developmental disparities in relation to performance in intrabrood begging competitions of nestling red-winged blackbirds. Broods were assessed at three phases: (i) all nestlings assumed to be ectothermic (inertial phase); (ii) first-hatched nestlings assumed to have initiated endothermy, last-hatched nestlings still ectothermic (transitional phase); (iii) all nestlings assumed to have initiated endothermy (regulatory phase). Differential development did not exaggerate the gap in competitive ability between first- and last-hatched nestlings at the transitional phase of brood development. Core nestlings were consistently able to access more food than marginal nestlings by neck stretching, a size-related behaviour. Unequal resource investment resulting from the phenotypic handicap of hatching asynchrony contributed to increased mortality of last-hatched nestlings midway through the nestling period.

Introduction

Altricial birds routinely hatch their broods asynchronously, creating initial inequalities in nestling size and development (Lack 1947, Clark and Wilson 1981, Mock 1984, Magrath 1990). The phenotypic handicap of hatching asynchrony exerts a profound influence on the outcome of sibling competitions. As with most passerine birds, sibling rivalry in red-winged blackbird (*Agelaius phoeniceus*) broods is described as a scramble competition, which means that an individual's success in begging competitions is determined by its performance relative to its nestmates (Parker *et al.* 1989). Recent work on this system has shown that brood reduction results from insufficient resources and differential resource allocation, the latter attributed to the phenotypic handicap of hatching asynchrony (Forbes and Glassey in press). Numerous studies have shown that older, first-hatched nestlings consistently make better competitors by virtue of their larger size (Lockie 1955, Ricklefs 1965, Ryden and Bengtsson 1980, Greig-Smith 1985, Mead and Morton 1985, McCrae *et al.* 1993, Kacelnik *et al.* 1995, Price and Ydenberg 1995, but see Stamps *et al.* 1985, Gottlander 1987, Leonard and Horn 1996). Less attention has focused on how developmental disparities influence the outcome of begging competitions.

Differential begging behaviour is assumed to occur in mixed age broods, when the feeding response of older and younger nestlings varies due to divergent sensory and physiological abilities (Bengtsson and Ryden 1981, Pijanowski 1992). This assumption is based on the fact that first-hatched nestlings acquire and improve motor skills ahead of their later-hatched siblings, and reach key developmental landmarks, such as the acquisition of sight and the initiation of physical thermoregulation, sooner (Dawson and

Evans 1957, Marsh and Wichler 1982, Olson 1992, Choi and Bakken 1990). In nestlings of the red-winged blackbird, an altricial passerine, endothermy and vision both begin to develop around day four and improve until day eight, when eyes are wide open and nestlings are physiologically endothermic (Holcomb and Twiest 1971, Olson 1994). Sensory maturation governs which cues will elicit begging behaviour, and motor activation determines the speed at which nestlings can respond to these cues (Khayutin 1985). The acquisition of sight, in combination with enhanced auditory sensitivity, shortens the interval between signal reception (e.g., a parent returning with food) and begging response during the latter half of the nestling period (Khayutin 1985). Similarly, enhanced motor unit recruitment begins midway through the nestling period, imparting greater strength to the neck and gastrocnemius muscles which are used to initiate and maintain begging (Marsh and Wichler 1982, Olson 1994). Consequently, the begging response of older, endothermic nestlings is faster than the response of younger, ectothermic nestlings (Dawson and Evans 1957, Choi and Bakken 1990).

Unlike the size differential imposed by hatching asynchrony, physiological changes associated with development are initiated midway through the nestling period, potentially conferring additional advantage(s) on older, larger nestlings, and widening the competitive gap between the larger, first-hatched "core" offspring (*sensu* Mock and Forbes 1995), and smaller, later-hatched "marginal" offspring.

Female red-winged blackbirds lay a clutch of two to five eggs (mode = 4) and begin to incubate prior to laying the last egg (Forbes *et al.* 1997), creating mixed-aged broods composed of first-hatched or core nestlings, and one or two later-hatched marginal nestlings that are smaller in size (Mock and Forbes 1995). The size hierarchy,

initiated when the oldest nestling(s) hatch (hatch = day 0), is maintained throughout the nestling period, suggesting that if size alone is the principal determinant of begging success, the outcome of begging competitions (food reception) should be skewed consistently to larger, core offspring. Furthermore, if development influences the outcome of begging competitions, I expect an increased magnitude of difference in food reception by core nestlings midway through the nestling period (differential resource investment), a corollary of which is expected to be a higher mortality of marginal nestlings (brood reduction).

Methods

I conducted field studies on red-winged blackbirds near Winnipeg, Manitoba, from May to July from 1994 to 1998. Nests were censused daily, nest contents were recorded, and nestlings were weighed using an Ohaus electronic balance. I recorded the nestling behaviour of 18 broods between 9:00 AM and 3:00 PM CST using 6 - 24x zoom VHS videocameras placed 1.5 – 6 m from nests under fair weather conditions. Down tracts on the head and back of nestlings were coloured with non-toxic felt markers to facilitate individual recognition. Taping sessions normally lasted 2 h, and in most cases, parents resumed feeding of nestlings within minutes of the camera being set up near the nest. In a minority of cases, the female parent was camera-shy and the taping session was discontinued. These data are not included here.

A feeding visit was defined as the arrival of a parent carrying food to the nest. Food loads comprised an average of 1.4 ± 0.11 s.e. items, and were usually made up of one large, or primary item, and a second, smaller prey item or a fragment that had broken

off from the primary item. I did not attempt to identify prey qualitatively. As nestling begging effort was most intense during the distribution of the primary food item, I used acquisition of the primary item, as opposed to total food items, as a standardised measure of feeding success.

Absolute measures of begging

For each visit during a one-hour span I measured the behaviour of nestlings in response to the arrival of the parent at the nest. The "primary begging response" (*sensu* M. L. Leonard and A. Horn, Department of Biology, Dalhousie University, Halifax, Nova Scotia, pers. comm.) refers to the begging behaviour of nestlings initiated in response to the arrival of a food-bearing parent at the nest.

Four indices of primary begging response were scored. First, the latency of begging was defined as the amount of time between the arrival of the parent on the nest rim, and the initiation of begging. A negative latency indicates that begging commenced before the parent's arrival at the nest, and a positive latency indicates that begging began after the parent arrived at the nest. Secondly, the frequency of begging was defined as the number of visits per hour on which a nestling begged. Thirdly, the duration of begging was defined as the total length of time that a nestling begged during a visit. Fourthly, the intensity of begging was scored and recorded as follows when the parent arrived at the nest: 0 (not begging), 1 (gaping), or 2 (gaping with neck stretched) (e.g. Cotton *et al.* 1999). The sides of the nest cup often blocked leg and wing activity, so the scoring system could not include measures of these. To avoid pseudoreplication

(Hurlbert 1984), I averaged the values for each behavioural variable for each nestling over the entire one hour observation period.

In order to identify assess whether core and marginal nestlings differed in begging response, and if so, at what phase(s) differential begging occurred, I used a MANOVA with hatch rank (core vs. marginal) and brood phase (inertial, transitional or regulatory) as fixed factors, and the four indices of begging response as dependent variables. All tests were two-tailed, and *post hoc* pairwise comparisons were made using a Bonferonni multiple comparisons test. The high rate of predation in the population prevented me from using the same broods at every phase of development, and thus from using the preferred method of repeated-measures ANOVA.

Relative measures of begging

I randomly selected ten feeding visits on which more than one nestling begged from each videotaped brood for a more in-depth analysis of competitive behaviour by core and marginal nestlings. For each feeding visit I recorded: i) which nestling within the brood commenced begging first (Begin); ii) the location of each nestling in relation to the position of the feeding adult, usually the female (Body position); iii) the relative height to which competing nestlings stretched their necks (Neck height); and iv) the beak-to-beak distance between the competing nestling and the feeding adult (Head position).

In order to determine whether core and marginal nestlings could enhance food reception behaviourally, I examined the disparity between how often a nestling was fed first when it ranked first in one of the four behavioural categories, and how often it was fed first when it did not rank first in that same category. A large gap between the two

indicated that performance in that behavioural category is important to feeding success. The data associated with the begging variables (Begin, Body position, Head position, Neck height) were not normally distributed, so the means of two samples were compared using a two-sample approximate randomization test based on 25,000 shuffles (Manly 1991). Using a Bonferroni correction, the appropriate alpha value for this series of tests was assessed as ($\alpha = 0.003$).

Tapes were analysed on a frame-by-frame basis, and for the behavioural variable of interest, I used the mean from all of the feeding visits on which a nestling begged first as the unit of statistical analysis to avoid pseudoreplication. The small data set required me to pool the data from all phases of brood development.

Brood phases

I based my analysis on a modification of Hill and Beaver's (1982) classification system for red-winged blackbirds. All individuals within inertial phase broods are characterised by the inability to thermoregulate when isolated, which necessitates huddling in order to maintain the body temperature and metabolic rate during parental absences (Hill and Beaver 1982). After the fourth day of the nestling period, synchronous broods enter the regulatory phase, characterised by improved individual thermogenesis. In contrast to the inertial phase, where all nestlings are ectothermic, in the regulatory phase all nestlings have initiated thermoregulation.

Hill and Beaver (1982) describe a third phase of brood development - an interphase between the inertial and regulatory phases - characterised by intrabrood differences in nestling physiology. This phase, which I refer to as the transitional phase,

only occurs in asynchronously hatched broods. Here core nestlings have initiated

thermoregulation, and are therefore more like nestlings in regulatory phase broods, while

later-hatched marginal offspring are still physiologically ectothermic, and more similar to

nestlings in the inertial phase of brood development (Hill and Beaver 1982).

In the present study, I used the age of the of the core nestlings relative to the age of

the marginal nestlings, and assigned each brood to one of three categories, shown

previously to correspond to three phases of brood developmental in this species (Hill and

Beaver 1982): i) core and marginal nestlings less than five days old, and all assumed to

be ectothermic (inertial phase broods; n = 8); ii) core nestlings at least five days old and

assumed to have initiated endothermy; marginal nestlings younger than five days old, and

assumed to be still ectothermic (transitional phase broods; n = 5); iii) core and marginal

nestlings at least five days old, and all assumed to have inititiated endothermy (regulatory

phase broods; n = 7). Within each brood, I paired a randomly selected marginal nestling

with a randomly selected core nestling and classified the pair according to the phase of

the brood from which they came.

Mortality

To assess the degree of intrabrood variation associated with differential mortality

I used the census data to track changes in brood structure (degree of age spread, number

of core and marginal competitors) and total brood size over the nestling period. Broods

escaping predation were assessed at the inertial, transitional and regulatory phases of

development and analysed using a repeated-measures ANOVA. A Kaplan-Meier analysis

(Kaplan and Meier 1958) was used to assess the probability of nestling survival.

Variation in survival between phases was assessed using a pairwise log-rank test (Lawless 1982). After day seven, nestling disappearance is often linked to fledging, as opposed to death, so I restricted survival analysis to broods seven days old or younger (Forbes *et al.* 1997).

Results

Absolute measures of begging

There was no significant effect of hatch rank within broods on any of the indices of primary begging response, and no indication of differential begging behaviour between core and marginal nestlings at any phase of brood development (latency: $F_{1,34} = 0.151$, P = 0.700, duration: $F_{1,34} = 0.138$, P = 0.713, frequency: $F_{1,34} = 0.323$, P = 0.573, intensity: $F_{1,34} = 0.775$, P = 0.385; Table 2.1).

There was, however, a significant main effect of the overall developmental phase of the entire brood on the frequency (brood phase: $F_{2,34} = 7.876$, P = 0.002, interaction: $F_{2,34} = 0.943$, P = 0.399; Table 2.1), and intensity of begging response (brood phase: $F_{2,34} = 10.514$, P < 0.001, interaction: $F_{2,34} = 0.903$, P = 0.415; Table 2.1). Nestlings from inertial phase broods responded significantly more slowly to the arrival of a food-bearing parent, and begged at lower intensity than those from broods in either the transitional (frequency: P = 0.027, intensity: P = 0.007), or regulatory phases of development (frequency: P = 0.027, intensity: P < 0.001).

I used exploratory regression analysis to assess the relationship between reception of the primary food item, nestling mass and the indices of begging response at each phase

Table 2.1. Mean (± SE) brood size, hatch spread and number of core and marginal competitors from broods in the inertial (n = 8), transitional (n = 5) and regulatory (n = 7) phases of development.

Behaviour	Hatch rank	Inertial phase	Transitional phase	Regulatory phase
Frequency (proportion)	Core	0.769 ± 0.065	0.971 ± 0.082	0.955 ± 0.070
	Marginal	0.694 ± 0.065	0.873 ± 0.065	0.978 ± 0.065
Duration (min)	Core	0.232 ± 0.036	0.227 ± 0.045	0.206 ± 0.038
	Marginal	0.192 ± 0.036	0.213 ± 0.045	0.223 ± 0.038
Latency (min)	Core	0.007 ± 0.007	-0.010 ± 0.009	0.000 ± 0.008
	Marginal	0.014 ± 0.007	-0.004 ± 0.009	-0.006 ± 0.008
Intensity	Core	1.329 ± 0.141	1.886 ± 0.179	1.786 ± 0.151
	Marginal	1.118 ± 0.141	1.630 ± 0.179	1.912 ± 0.151

of brood development. In broods at the inertial and regulatory phases of development, both size and behaviour registered as strongly significant predictors of feeding success (Table 2.2). Larger, faster nestlings received food more often at the inertial phase, reducing the length of time that nestlings begged (overall adjusted $R^2 = 0.404$, P = 0.064, best fit adjusted $R^2 = 0.436$, P = 0.019; Table 2.2). Large size, in combination with frequent, high intensity begging, contributed to food reception by nestlings in broods at the regulatory phase (overall adjusted $R^2 = 0.556$, P = 0.035, best fit adjusted $R^2 = 0.574$, P = 0.009; Table 2.2). In contrast, there was little evidence of a behavioural effect at the transitional phase, where size was the principal determinent of feeding success (overall adjusted $R^2 = 0.351$, P = 0.265, best fit adjusted $R^2 = 0.552$, P = 0.008; Table 2.2).

Relative measures of begging

There was a strong tendency for all nestlings, regardless of hatch rank, to improve food reception by ranking first in a behavioural category (Fig. 2.1). In particular, nestlings were able to almost treble their food share by ranking first in neck height ($D_{marginal} = 0.399$, P = 0.002; $D_{core} = 0.450$, P < 0.001; Fig. 2.1). Commencing begging first greatly increased a nestling's food share, although the data for marginal offspring fell short of significance ($D_{marginal} = 0.271$, P = 0.017; $D_{core} = 0.303$, P = 0.001; Fig. 2.1). Nestlings were able to access a non-significantly larger food share by reducing the distance between their own and the parent's head ($D_{marginal} = 0.240$, P = 0.033; $D_{core} = 0.141$, P = 0.187; Fig. 2.1). Body position relative to the parent was the least important determinant of feeding success, particularly for core nestlings who received essentially the same

Table 2.2. Results of multiple regression analysis to determine the degree to which size (mass) and begging response (latency, duration and frequency) contributed to the reception of the primary food item by nestlings in broods at the inertial (n = 8), transitional (n = 5) and regulatory (n = 7) phases of development.

Brood phase	Variable	B (slope)	SE	t	P
Inertial	Begging duration prior to food allocation	2.016	7.485	0.269	0.793
	Begging latency (min)	-25.320	23.157	-1.093	0.298
	Proportion of visits on which nestling begs	-0.367	1.418	-0.259	0.800
	Mass (g)	0.245	0.100	2.452	0.032
Transitional	Begging duration prior to food allocation	71.404	53.121	1.344	0.237
	Begging latency (min)	64.217	102.837	0.624	0.560
	Proportion of visits on which nestling begs	-0.488	7.276	-0.067	0.949
	Mass (g)	0.410	0.157	2.610	0.048
Regulatory	Begging duration prior to food allocation	-30.861	27.409	-1.126	0.289
	Begging latency (min)	-52.007	35.130	-1.480	0.173
	Proportion of visits on which nestling begs	-6.590	3.305	-1.994	0.077
	Mass (g)	0.179	0.070	2.258	0.031

Figure 2.1. Food reception (mean (± SE) proportion of primary food items) vs. performance in begging competitions of: core and marginal nestlings. Four behavioural performance are shown: Begin (order in which nestlings began begging; Head (beak-to-beak distance between the nestling and feeding adult; Body (the position of the body relative to that of the feeding adult; Neck (vertical neck height). Data represented by light bars are from those visits during which a nestling ranked first in a given behavioural category; data represented by dark bars are from those visits during which a nestling did not rank first in a given behavioural category.
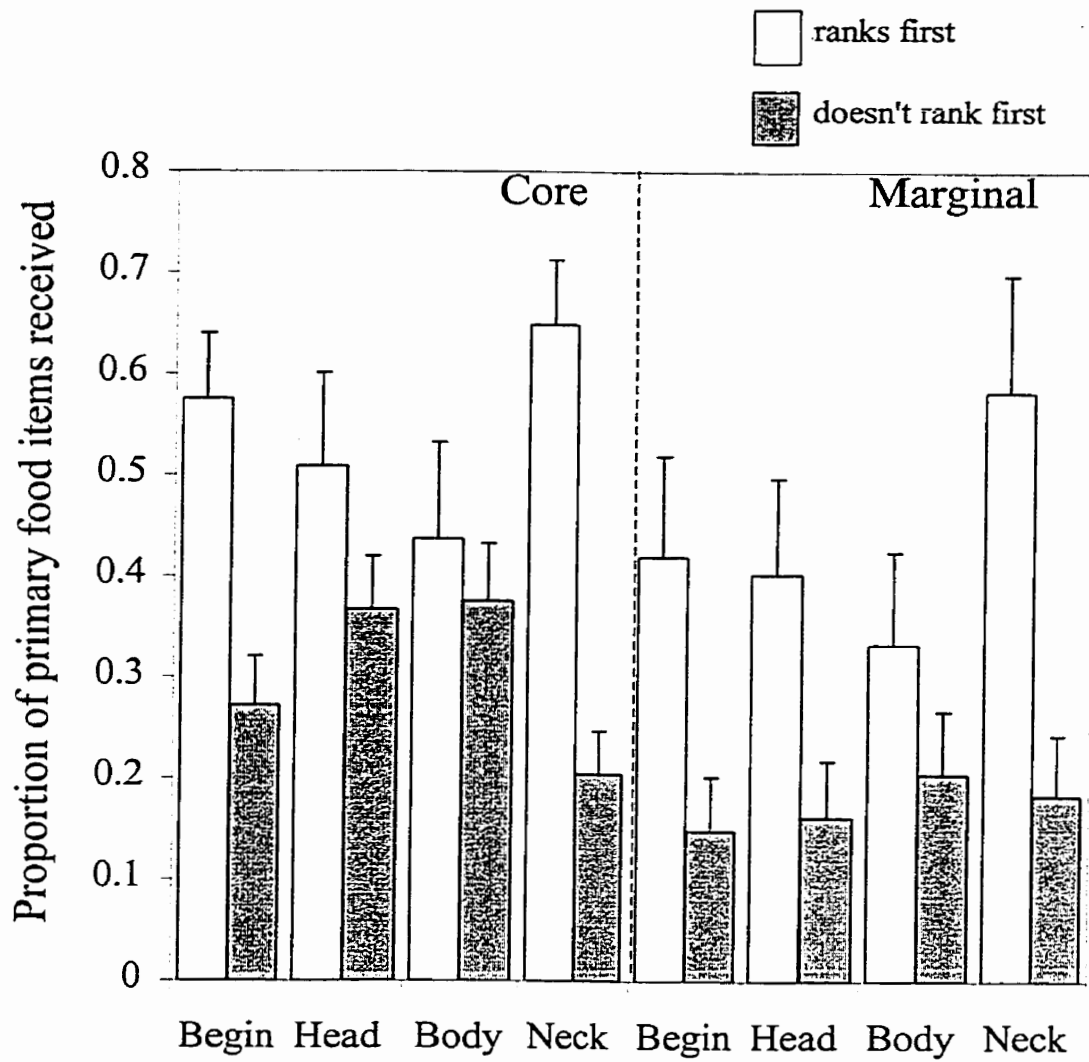
amount of food, regardless of their location relative to the parent ($D_{marginal}$ = 0.128, P = 0.253; D_{core} = 0.614, P = 0.566; Fig. 2.1).

I assessed whether the frequency with which core and marginal nestlings ranked first in a behavioural category differed, using a MANOVA with hatch rank (core vs. marginal) and brood phase as variables. Proportions were $\sin^{-1} \sqrt{x}$ transformed prior to analysis, and a *post-hoc* Bonferonni multiple comparisons correction factor was applied. The proportion of visits on which core and marginal nestlings began to beg first (P = 0.465), positioned their heads nearest to the parent (P = 0.967), and situated their bodies closest to the parent (P = 0.821) did not differ significantly between nestlings (Fig. 2.2). However, core nestlings ranked first in neck height significantly more often than marginal nestlings at every phase of brood development (hatch rank: $F_{1,32}$ = 4.725, P = 0.037, brood phase: $F_{2,32}$ = 1.474, P = 0.244, interaction: $F_{2,32}$ = 0.018, P = 0.892; Fig. 2.2). The results of a MANOVA, using brood phase and nestling hatch rank as fixed factors revealed that the frequency difference in neck height was consistent across phases ($F_{2,32}$ = 0.906, P = 0.414).

Size

Nestling size increased across phases, and core nestlings were consistently larger than marginal nestlings (hatch rank: $F_{1,34}$ = 23.824, P < 0.001, brood phase: $F_{2,34}$ = 43.192, P < 0.001, interaction: $F_{2,34}$ = 0.696, P = 0.505; Table 2.3). Both core and marginal nestlings grew quickly between the inertial and regulatory phases. Since all nestlings roughly doubled in mass during this interval, the size ratio was maintained, with marginal nestlings about two-thirds as large as core. However, whereas core nestlings increased a

Figure 2.2. Mean (± SE) proportion of visits on which core and marginal nestlings ranked

first in a behavioural category (Begin, Head, Body, Neck).
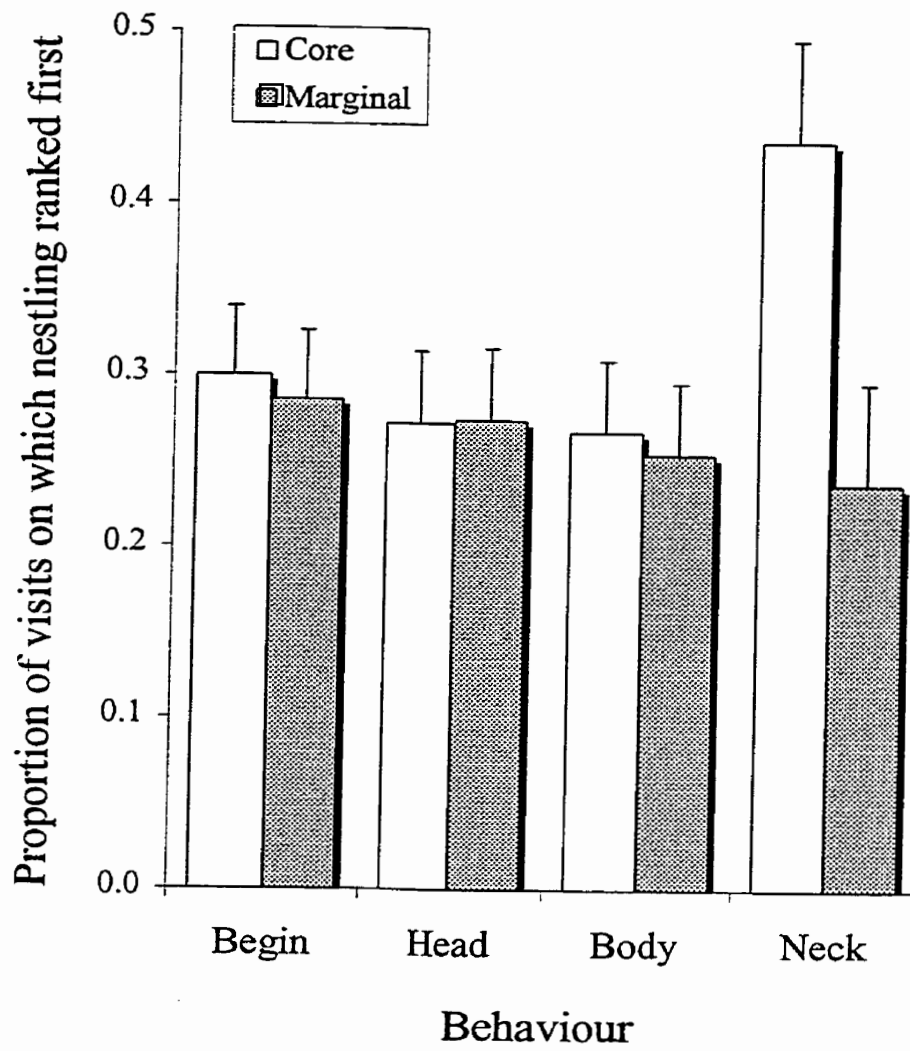
Figure 2.3. Mean ($\pm$ SE) growth of core and marginal nestlings measured as

$Mass_{marginal}/Mass_{core}$.
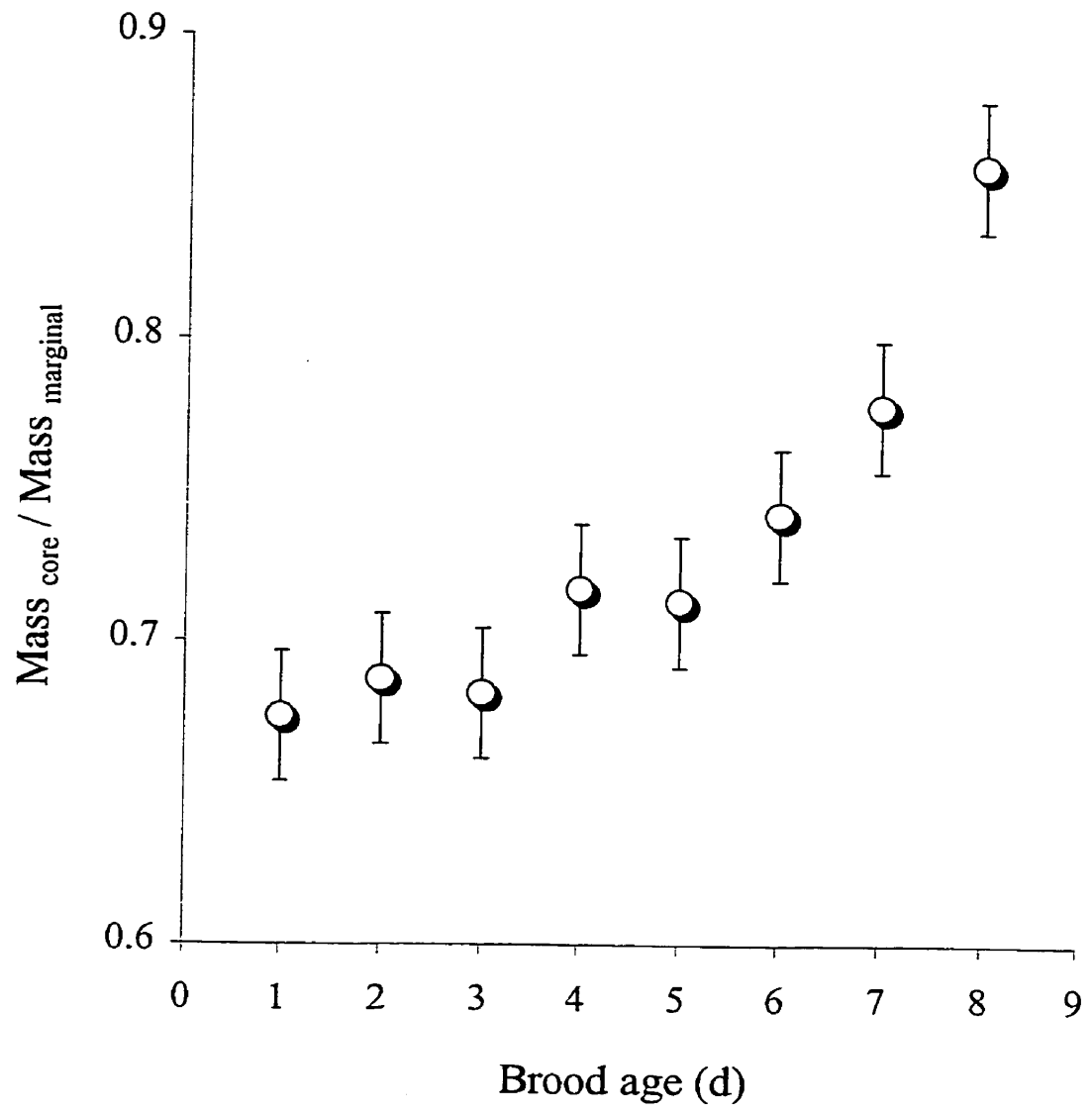
Table 2.3. Mean (± SE) mass (g) and consumption of primary food items by core and marginal nestlings from broods in the inertial (n = 8), transitional (n = 5) and regulatory (n = 7) phases of development.

Variable	Brood phase	Core nestlings	Marginal nestlings	Difference ($mass_c$/ $mass_{m)}$	Ratio ($mass_m$/ $mass_c$)
Mass (g)	Inertial	13.325 ± 1.693	8.212 ± 1.693	5.112 ± 2.221	0.616
	Transitional	24.660 ± 2.142	15.360 ± 2.142	9.330 ± 2.889	0.623
	Regulatory	31.071 ± 1.810	22.871 ± 1.810	8.200 ± 2.374	0.736
Primary food items/h	Inertial	2.625 ± 0.565	1.000 ± 0.378	1.625 ± 0.905	0.381
	Transitional	5.000 ± 1.225	1.800 ± 1.114	3.200 ± 0.735	0.360
	Regulatory	6.571 ± 0.812	3.857 ± 0.800	2.714 ± 1.304	0.587

further one-third in size between the transitional and regulatory phases, marginal nestlings grew at a faster rate, reducing the size differential to one-quarter (Table 2.3). Changes in the mass ratio between core and marginal nestlings were first initiated midway through the nestling period (Fig. 2.3).

Food acquisition

Nestling intake increased across phases, and core nestlings consistently received more food items during a one-hour span than marginal nestlings (hatch rank: $F_{1,34} = 15.271$, P < 0.001, brood phase: $F_{2,34} = 10.861$, P < 0.004, interaction: $F_{2,34} = 0.547$, P = 0.584; Table 2.3). Marginal offspring in broods at the inertial and transitional phases received 38% and 36% of core intake respectively. Food reception by marginal nestlings increased to 60% of the core share in broods at the regulatory phase (Table 2.3).

Mortality

Mortality was attributed to starvation if a nestling suffered reduced mass and slowed growth before death. The probability of a core nestling surviving until day eight was significantly higher than that of a marginal nestling (core = 0.95, marginal = 0.80, $\chi^2 = 14.14$, df = 2, P < 0.001). Unlike the risk to core offspring, which remained consistently low across phases ($\chi^2 = 4.30$, df = 2, P = 0.117, Fig. 2.4), marginal offspring survival was much more variable ($\chi^2 = 18.80$, df = 2, P < 0.001). The greatest disparity between core and marginal survival occurred at the transitional phase ($\chi^2 = 8.55$, P = 0.004), where marginal deaths accounted for all of the nestling mortality. Generally, the smallest, last-hatched marginal nestlings died first. As a result, broods in the regulatory phase were

Figure 2.4. Kaplan-Meier cumulative survival estimates (mean ± SE) for core (white box) and marginal (black box) nestlings from broods in the inertial, transitional, and regulatory phases of development: n = 469 nestling days.
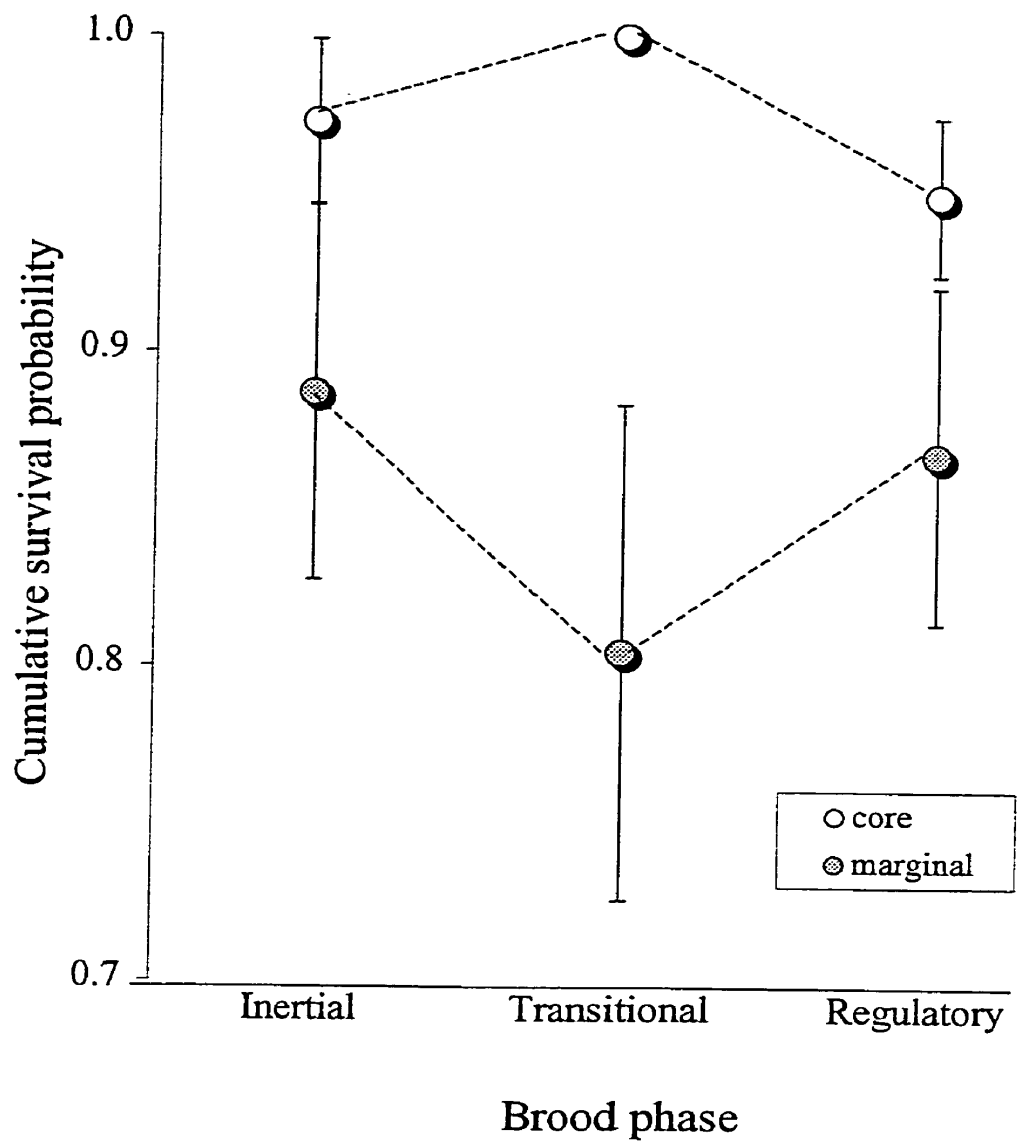
Table 2.4. Mean (± SE) brood size, number of core and marginal nestlings, and age difference between core and marginal nestlings from broods in the inertial (n = 8), transitional (n = 5) and regulatory (n = 7) phases of development.

Brood stage	Brood Size			Age difference (d)
	Total no. of nestlings	No. of core nestlings	No. of marginal nestlings	
Inertial	3.76 ± 0.14	2.06 ± 0.18	1.71 ± 0.14	1.47 ± 0.12
Transitional	3.65 ± 0.12	2.00 ± 0.19	1.65 ± 0.19	1.35 ± 0.15
Regulatory	2.94 ± 0.10	1.94 ± 0.18	1.00 ± 0.17	0.88 ± 0.15

both smaller (Repeated-measures ANOVA, $F_{2,32} = 20.54$, $P < 0.001$; Table 2.4), and more synchronous (Repeated-measures ANOVA, $F_{2,32} = 15.31$, $P < 0.001$).

Discussion

First-hatched (core) red-winged blackbird nestlings experienced substantial survival advantages over their later-hatched (marginal) nestmates. I assessed whether this was attributable chiefly or solely to differences in size that result from asynchronous hatching, or whether behavioural differences that arise from developmental asynchrony played an additional important role. If the latter is important, I would expect competitive differences between core and marginal offspring to widen during the transitional phase, when the physiological advantage is assumed to be greatest for core offspring.

Contrary to earlier assumptions (e.g. Bengtsson and Ryden 1981, Pijanowski 1992), I found no evidence of a differential begging response between core and marginal nestlings at any phase of brood development. However, despite matching the begging response of core offspring, marginal nestlings consistently received less food for their efforts. When in competition, any nestling, regardless of size, that ranks first in a behavioural category (Begin, Neck height, Body position, Head position) improves its chances of receiving food. However, the larger size of core nestlings makes neck stretching a more effective strategy, particularly in the early phases of brood development (inertial, transitional) when the size differential is greatest.

Begging by nestling red-winged blackbirds is initiated by the arrival of the feeding parent at the nest (the physical jostling) and/or the feeding call of the parent

immediately prior to arriving at the nest. Although the response to these tactile and auditory cues is related to motor development, which improves with age, hunger or social stimulation (e.g. jostling by nestmates) may stimulate younger marginal nestlings to match the efforts of their older siblings.

Body position relative to the parent is dependent on the arrival location of the feeding parent. Feeding parents normally use certain locations on the nest more than others, but variation exists, meaning that even the smallest nestlings can access the closest position. Head position again contains an element of chance, and is again partially under parental control. Minimising beak-to-beak distance contains vertical (neck stretching) and horizontal spatial dimensions (reaching across the nest to the feeding adult). Large nestlings on the opposite side of the nest possess an advantage in that they can reach over smaller nestlings, but smaller offspring close to the feeding parent can rank first in these competitions since they do not have as far to reach.

Neck height is the only behaviour directly related to physical size. The largest nestlings can stretch their necks highest, and thus marginal nestlings can only win this dimension of competition if core nestlings do not exert their full advantage. That the success of neck stretching is conditional upon size is consistent with a phenotypic-limited begging strategy (Parker 1982). Core nestlings use their size advantage in broods at all phases of development to access a greater food share than their smaller, younger nestmates. Thus, the high feeding success and low mortality of core nestlings reflects the fact that they faced few real competitors. This type of unequal resource allocation, referred to as "despotic" (Forbes 1993), is closer to a sibling dominance hierarchy than a true scramble (Parker *et al.* 1989). That food is not distributed equitably is consistent with

studies of a variety of other passerine nestlings. Despite begging more than their larger nestmates, smaller nestlings generally receive less food (Ryden and Bengtsson 1980, Bengtsson and Ryden 1981, Smith and Montgomerie 1991, Price and Ydenberg 1995, Redondo and Castro 1992, Lotem 1998).

There was an increased risk to marginal nestlings at the transitional phase, clearly indicated by their higher mortality. However, within the scope of this study, I was unable to determine how much of this risk was sustained during the transitional phase *per se*, or how much may have resulted from earlier food shortfalls. Red-winged blackbirds carry only small lipid reserves over the nestling period (Ricklefs 1967). Death by starvation occurs in 9 to 13 h in food-deprived nestlings (Fiala and Congdon 1983); less extreme food deprivation presumably would take longer. Consistent with my results, partial brood loss commonly occurs midway through the nestling period in this species (see also Holcomb and Twiest 1971, Caccamise 1976, Cronmiller and Thompson 1980). Consequently, broods in the regulatory phase are smaller and more synchronous, when the thermal benefits derived from an extra body are lowest and the metabolic requirements of the brood are at their peak.

Although core nestlings in regulatory phase broods continued to receive the greatest proportion of primary food items, the discrepancy between food shares was smallest. The effects of hatching asynchrony are felt least strongly in broods at the regulatory phase, where the difference in mass between core and marginal offspring is smallest. The growth pattern characteristic of red-winged blackbird nestlings, in combination with the death of the youngest, smallest competitors at earlier phases, likely accounted for much of the reduced size effect that I observed. When fitted to a logistic

equation, the inflection point occurs around day four, and an asymptote is reached just prior to fledging (Olson 1992).

My results show that unequal resource investment results from the phenotypic handicap of hatching asynchrony, and leads to brood reduction, as predicted by Forbes and Glassey (in press). Under resource allocation theory, a brood hierarchy ensures the survival of core offspring, so that marginal offspring are reared only once the needs of the core nestlings have been met. My results suggest that the degree to which the phenotypic handicap influences the outcome of begging competitions varies, depending on the phase of development. However, variation is primarily attributable to a reduction in the size differential between core and marginal offspring in broods at the regulatory phase, as opposed to differential development during the transitional phase. Core offspring appear to succeed because they have a size advantage that can be called upon to access more food whenever they need it, either to meet their own changing energetic requirements, or during periods of food shortfall.

References

Bengtsson, H. and O. Ryden. 1981. Development of parent-young interaction in asynchronously hatched broods of altricial birds. Z. Tierpsychol 56: 255-272.

Caccamise, D.F. 1976. Nesting mortality in the red-winged blackbird. Auk 93: 517-534.

Choi, I.-H. and G.S. Bakken. 1990. Begging response in nestling red-winged blackbirds (*Agelaius phoeniceus*): effect of body temperature. Physiol. Zool. 63: 965-986.

Clark, A.B. and D.S. Wilson.1981. Avian breeding adaptations: hatching asynchrony, brood reduction and nest failure. Q. Rev. Biol. 56: 253-277.

Cotton, P.A., J. Wright and A. Kacelnik. 1999 Chick begging strategies in relation to brood hierarchies and hatching asynchrony. Am. Nat. 153: 412-420.

Cronmiller, R.R. and C.F. Thompson. 1980. Experimental manipulation of brood size in red-winged blackbirds. Auk 97: 559-565.

Dawson, W.R. and F.C. Evans. 1957. Relation of growth and development to temperature regulation in nestling field and chipping sparrows. Physiol. Zool. 30: 315-327.

Fiala, K.L. and J.D. Congdon. 1983. Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. Ecology 64: 642-647.

Forbes, L.S. 1993. Avian brood reduction and parent-offspring "conflict". Am. Nat. 142: 82-117.

Forbes, L.S., S. Thornton, B. Glassey, M.J. Forbes and N. Buckley. 1997. Why parent birds play favourites. Nature (London) 390: 351-352.

Forbes, S. and B. Glassey. In press. Asymmetric sibling rivalry and nestling growth in red-winged blackbirds. Behav. Ecol. Sociobiol.

Gottlander, K. 1987. Parental feeding behaviour and sibling competition in the pied flycatcher Ficedula hypoleuca. Ornis. Scand. 18: 269-276.

Greig-Smith, P. 1985. Weight differences, brood reduction, and sibling competition among nestling stonechats Saxicola torquata (Aves: Turdidae). J. Zool. Lond. A 5: 453-465.

Hill, R.W., D.L. Beaver. 1982. Inertial thermostability and thermoregulation in broods of redwing blackbirds. Physiol. Zool. 55: 250-266.

Holcomb, L.C.and G. Twiest.1971. Growth and calculation of age for red-winged blackbird nestlings. Bird-Banding 42: 1-78.

Hurlbert, S.H. 1984 Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Kacelnik, A., P.A. Cotton, L. Stirling and J. Wright. 1995. Food allocation among nestling starlings: sibling competition and the scope of parental choice. Proc. Royal Soc. Lond. B 259: 259-263.

Kaplan, E.L. and P. Meier. 1958. Nonparametric estimation from incomplete observations. J. Am. Stat. Assoc. 53: 457-481.

Khayutin, S.N. 1985. Sensory factors in the behavioral ontogeny of altricial birds. Advances in the Study of Behaviour 15: 105-152.

Lack, D. 1947. The significance of clutch size. Ibis 89: 302-352.

Lawless, J.F. 1982. Statistical Models and Methods for Lifetime Data. John Wiley and Sons, New York.

Leonard, M.L. and A. Horn. 1996. Provisioning rules in tree swallows. Behav. Ecol. Sociobiol. 38: 341-347.

Lipar, J.L., E.D. Ketterson and V. Nolan, Jr. 1999. Intraclutch variation in testosterone content of red-winged blackbird eggs Auk 116: 231-235.

Lockie, J.D. 1955. The breeding and feeding of jackdaws and rooks with notes on carrion crows and other Corvidae. Ibis 97: 341-369.

Lotem, A. 1998. Higher levels of begging behavior by small nestlings: a case of a negatively correlated handicap. Israel J. Zool. 44: 29-45.

Magrath, R.D. 1990. Hatching asynchrony in altricial birds. Biol. Rev. 65: 587-622.

Manly, B.F.J. 1991. <u>Randomization and Monte Carlo Methods in Biology.</u> Chapman and Hall, New York.

Marsh, R.L. and S.J. Wichler. 1982. The role of muscle development in the transition to endothermy in nestling bank swallows, *Riparia riparia*. J. Comp. Biol. B: 149: 99-105.

McRae, S.B., P.J. Weatherhead and R. Montgomerie. 1993. American robin nestlings compete by jockeying for position. Behav. Ecol. Sociobiol. 33: 101-106.

Mead, P.S. and M.L. Morton. 1985. Hatching asynchrony in the mountain white-crowned sparrows (*Zonotrichia leucophrys oriantha*): a selected or incidental trait? Auk 102: 781-792.

Mock, D.W. 1984. Siblicidal aggression and resource monopolization in birds. Science 225: 731-733.

Mock, D.W. and L.S. Forbes.1995. The evolution of parental optimism. Trends Ecol. Evol. 10: 130-134.

Olson, J.M. 1992. Growth, the development of endothermy, and the allocation of energy in red-winged blackbirds (*Agelaius phoeniceus*) during the nestling period. Physiol. Zool. 65: 124-152.

Olson, J.M. 1994. The ontogeny of shivering thermogenesis in the red-winged blackbird (*Agelaius phoeniceus*). J. Exp. Biol. 191: 59-88 .

Parker, G.A. 1982. Phenotype limitedevolutionarily stable strategies. In <u>Current problems in sociobiology</u> (ed. B.R. Bertram, T.H. Clutton-Brock, R.I.M. Dunbar, D.I. Rubenstein, and R. Wrangham), pp. 173-201. Cambridge University Press, Cambridge.

Parker, G.A., D.W. Mock and T.C .Lamey. 1989. How selfish should stronger sibs be? Am. Nat. 133: 846-868.

Pijanowski, B.C. 1992. A revision of Lack's brood reduction hypothesis. Am. Nat. 139: 1270-1292.

Price, K. and R. Ydenberg. 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. Behav. Ecol. Sociobiol. 37: 201-208.

Redondo, T. and F. Castro. 1992. Signalling of nutritional need by magpie nestlings. Ethology 92: 192-204.

Ricklefs, R.E. 1965. Brood reduction in the Curve-billed Thrasher. Condor 67: 505-519.

Ryden, O. and H. Bengtsson. 1980. Differential begging and locomotory behaviour by early and late hatched nestlings affecting the distribution of food in asynchronously hatched broods of altricial birds. Z. Tierpsychol. 53: 209-224.

Schwabl, H. 1996. Maternal testosterone in the avian egg enhances postnatal growth. Comp. Biochem. Physiol. A. 114: 217-276.

Schwabl, H., D.W. Mock and J.A. Gieg. 1997. A hormonal mechanism for parental favouritism. Nature 386: 231.

Smith, H. G. and R. Montgomerie 1991. Nestling American robins compete with siblings by begging. Behav. Ecol. and Sociobiol. 29: 307-312.

Stamps, J.A. Clark, P. Arrowood and B. Kus. 1985. Parent-offspring conflict in budgerigars. Behaviour 94: 1-40.

Chapter 3: The functions of vocal and visual signals in nestling begging

Abstract

Nestling birds use vocal and visual behaviours when soliciting food from parents. Such behaviours serve at least two discrete functions: (i) to induce parents to bring more food; and (ii) to influence how food is allocated among brood members. Playback experiments have shown that vocalizations serve function i. But do they also function to influence intra-brood allocation, as contemporary begging theory suggests, or is that governed chiefly by the non-vocal components of begging (neck-stretching, gaping, jockeying for position within the nest)? I tested this hypothesis using a novel non-surgical muting technique to decouple the vocal and visual components of begging in nestling red-winged blackbirds (*Agelaius phoeniceus*). Single chicks that were muted temporarily (1h) continued to be fed at roughly the same rate as either the same individual prior to muting or sham-muted nestlings in the same brood. Parents reduced provisioning rates by increasing nest attentiveness in response to changes in the begging behaviour of the brood following treatement. These included less time spent begging (visual and vocal), accompanied by a reduction in the collective vocalizations of the brood. My results suggest that vocalizations function primarily to regulate parental foraging rates, and visual begging displays function primarily to access food (competition).

Introduction

Theoreticians explain the familiar and conspicuous begging signals of nestling birds as manifestations of sibling rivalry and parent-offspring conflict (Trivers 1972, Mock and Parker 1997). The theory of intrabrood conflict predicts that parents will award resources based upon the relative solicitation effort of individual nestlings, leading to exaggerated offspring demands (Macnair and Parker 1978, Parker 1985, Harper 1986, Parker *et al.*1989). Siblings compete for parentally-provided resources in many birds and mammals, and success in intrabrood competitions is a powerful determinant of offspring growth and survival (Mock and Parker 1997). In the scramble competitions characteristic of passerine birds, an individual's success is a function of its begging intensity relative to that of its competitors (Parker 1985, Harper 1986, Mock and Parker 1997, Parker *et al.* 1989). Begging consists of both visual (e.g., wing-flapping, gaping, neck-stretching, jostling) and vocal elements (Henderson 1975, Macnair and Parker 1978, Smith and Montgomerie 1991, Kacelnik *et al.*1995, Cotton *et al.* 1996, Lotem 1998a). Accumulating evidence suggests that the influence of these behaviours on the allocation of food within the brood and on the overall foraging rate are not equal.

Nestlings can influence food reception by virtue of their competitive abilities. The most effective strategy appears to be minimizing the beak-to-beak distance between the offspring and parent, either by securing the position closest to an established distribution point (Ryden and Bengtsson 1980, Bengtsson and Ryden 1981, Greig-Smith 1985, Gottlander 1987, Stamps *et al.* 1989, Smith and Montgomerie 1991, Litovitch and Power 1992, McRae *et al.* 1993, Kacelnik *et al.* 1995, Kilner 1995), or by reaching highest (Teather 1992). Although visual begging influences within-brood food allocation

(Litovitch and Power 1982, Price and Ydenberg 1995, Redondo and Castro 1992, Price 1996, Kilner 1995, Cotton *et al.* 1996, Leonard and Horn 1996, Kolliker 1998, Lotem 1998a), these behaviours do not appear to provide sufficient stimulation for the parent to change overall provisioning levels (e.g. von Haartman 1953, Miller and Conover 1979). By using mirrors, von Haartman (1953) "doubled" brood size while maintaining vocal solicitations at the level of a two-chick brood. Parents did not increase foraging rates, despite the silent visual displays of an additional two "chicks". Similarly, silent pecking by very young (<3 day old) surgically muted ring-billed gull, *Larus delawarensis*, chicks provided insufficient stimulus to initiate parental provisioning (Miller and Conover 1979).

In contrast, an increase in parental foraging rates is associated with elevated vocal solicitations by the brood in response to experimental food deprivation (von Haartman 1953, Bengtsson and Ryden 1983, Whittingham and Robertson 1993) or playback of recorded begging calls (Henderson 1975, Harris 1983, McLean and Griffin 1988, Burford *et al.* 1998, Price 1998, Wright 1998, but see Clark and Lee 1998).

Although theoretical models assume a positive relationship between the intensity of individual vocal solicitations and feeding success (Motro 1989, Redondo and de Reyna 1988, Harper 1986, Briskie *et al.* 1994), at least two empirical studies indicate that vocalizations may play an auxiliary role relative to non-vocal behaviour in the competition for food. The outcome of begging competitions among yellow-headed blackbird, *Xanthocephalus xanthocephalus*, nestlings was determined chiefly by size-related visual signals (Price and Ydenberg 1995). Following experimental food deprivation, the pattern of within-brood food allocation was maintained, despite longer

and more intense vocalisations by hungry offspring (Price and Ydenberg 1995). As well, neck stretching by large nestlings in asynchronously hatched great tit, *Parus major*, broods enabled them to procure food that was initially brought to the nest in response to the vocal begging of their smaller, hungrier nestmates (Bengtsson and Ryden 1983). These results suggests that vocalising may not be necessary for food reception.

I used a novel experimental procedure to mute individual nestlings temporarily, in order to separate the effects of vocal and visual signals and to examine the role of each in determining overall levels of brood provisioning and within-brood allocation of resources. I predicted that: (1) the collective vocal solicitations of the brood serve primarily to increase the amount of food delivered to the nest through an increase in parental foraging rates; and (2) the visual, as opposed to vocal, component of begging is used in competition by broodmates, in order to increase food reception by an individual.

Methods

I muted individual nestlings temporarily in seven- to nine- day-old broods (hatch = day 0 of oldest nestling) of red-winged blackbirds, *Agelaius phoeniceus*, during June and July of 1997 and 1998 in a population near Winnipeg, Manitoba. Female red-winged blackbirds in this population lay three to five eggs ($\bar{x}$ = 3.95, n = 722 clutches), and incubate the eggs for 11-13 days. The nestling period spans 9-11 days, during which time females provide nearly all of the care. The average brood size at hatch is 3.52 nestlings (n = 541 broods). Partial brood loss, often involving starvation of the last-hatched nestling, means that fewer nestlings survive to fledge (day eight brood size = 2.75 nestlings, n = 366 broods).

I matched two nestlings, within two- or three-chick broods, for size (muted = 29.71 ± 2.13 g, sham = 29.64 ± 2.36 g, Paired t test: t_9 = 0.030, P = 0.977) and age (muted = 7.40 ± 0.34 d, sham = 7.60 ± 0.27d, Paired t test: t_9 = -0.802, P = 0.443), and assigned them randomly for muting or sham-muting treatments. One nestling in a brood was muted via a topical application of ~0.08 ml, gel-based Xylocaine^R (lidocaine hydrochloride 2%) oral anaesthetic, which was applied to the internal surface of the syrinx. I used the same procedure with the sham-muted individual except that a petroleum gel of comparable consistency was substituted for the anaesthetic. After treatment, nestlings were returned to their original position within the nest. I monitored nestling behaviour under fair weather conditions with the aid of 6-24x zoom video cameras placed two to four metres from nests. Nestlings were marked for individual identification and I monitored the rate of brood provisioning and food allocation within broods before and after treatment. Control observations for the effects of the experimental procedure were then obtained from each experimental nestling itself (before treatment) as well as from a sham-muted control. Since the muting effect of the lidocaine began to wear off after about one hour, the analysis was restricted to behavioural data gathered for one hour before and after treatment.

Ethical Note

The experimental devocalization of passerines has been employed principally as a tool to determine the contribution of male song to mating and territory acquisition. To date, all experimental muting techniques used on passerines have involved surgery, and have been restricted to adult birds (e.g. Smith 1977, Smith 1979, Dufty 1986). The application of

these techniques to nestlings has two major drawbacks: (1) the birds remain mute for 13-14 days, a span encompassing the entire nestling period; and (2) the procedures require a lengthy postoperative recovery period, leaving nestlings vulnerable to infection, starvation and infanticide. In addition, the small size of passerine nestlings precludes the use of a surgical procedure. The experimental technique I have developed circumvents these problems. "Temporary" is defined by hours rather than days, and the use of a non-surgical, minimally invasive technique reduces significantly both the risk of infection and the recovery period. However the success of the muting procedure was variable, and highly temperature-dependent. When successful, muting was almost immediate, but the technique failed if sufficient quantity of the anaesthetic did not reach the syrinx. Failures were high during cold weather when nestlings were more likely to react to handling by calling and to be in poor condition. I suspect that absorption was also slower. Of the 52 muting attempts, 31 (59.6 %) were unsuccessful, and 5 (9.6 %) resulted in nestling mortality. Mortality was associated with underweight individuals, or nestlings that attempted to call during the procedure, thereby exposing the bronchus. Parents continued to provision all broods, regardless of the outcome of the treatment. The methods used in this study were approved by the Animal Care Committee of the University of Winnipeg, and complied with Canadian Council of Animal Care guidelines.

Nestling Behaviour

I assessed nestling begging activity at the beginning of each feeding visit using three measures of "primary begging response" (sensu M. L. Leonard and A. Horn, Department of Biology, Dalhousie University, Halifax, Nova Scotia, pers. comm.), defined as

begging initiated in response to the arrival of a food-bearing parent at the nest. First, the duration of begging, was subdivided into: i) the length of time that nestlings begged while food was being allocated (pretotal); and ii) the length of time nestlings continued to beg after the last food item was dispensed (total continued). Secondly, begging intensity was recorded when the parent arrived at the nest. Begging intensity was scored as 0 (not begging), 1 (gaping), or 2 (gaping with neck stretched) (e.g., Cotton *et al.* 1999). The sides of the nest cup often blocked leg and wing activity, precluding the use of additional behavioural variables. Thirdly, the latency of begging response measures the interval between the arrival of the parent on the nest rim and the initiation of begging. A negative latency indicates that begging commenced before the parent's arrival at the nest, whereas a positive latency indicates that begging began after the parent arrived at the nest. To avoid pseudoreplication (Hurlbert 1984), I averaged the values for each behavioural variable for each nestling over the entire one-hour observation period. I also generated a single, average value per brood for each behavioural index. Visits on which the body of the parent blocked the nestlings were excluded from the in-depth behavioural analysis.

Brood participation, measured as the proportion of the brood begging, was recorded once when the parent arrived at the nest, and again after the last food item was allocated. Per capita provisioning was estimated from the number of primary food items, representing the majority of the food load, consumed by each nestling during a visit. Mass gain was positively correlated with the intake of primary food items ($F_{1,46} = 8.52$, P $= 0.005$).

Parental Behaviour

I assessed three measures of parental feeding effort: (1) visit frequency (foraging rate); (2) visit duration; and (3) absence duration. Hourly parental effort was assessed using the formula:

Parental effort/h = (number of visits x length of visit) + (number of foraging absences x length of absence).

The length of the feeding visit is dependent on parental activity at the nest. Food was provided on all visits, but, in addition to feeding, parents often remained either to clean the nest by removing a fecal sac or to regulate the temperature of the brood by shading or brooding. The order in which these tasks were performed during a visit seldom varied (nutrition, followed by nest cleaning, brooding or shading), although not all types of care were provided on every visit. Specifically, parents often departed after allocating food without cleaning the nest or providing thermal care. The female virtually never brooded or shaded after finding a fecal sac, but flew away with the fecal sac.

I categorised feeding visits on the basis of the type of care that was provided: food only (nutrition visit); food provided and fecal sac removal (sanitation visit); food and shading or brooding provided (thermal visit). During each visit I assessed the length of: (1) the food distribution phase, encompassing the interval between when the parent arrived and when the last food item was allocated; and (2) the non-feeding phase, extending from allocation of the last food item until the departure of the parent. Non-feeding activity included assessment, nest cleaning, shading and brooding.

Results

Differences in provisioning among entire broods

Foraging rates fell significantly after a single nestling was muted (Paired t test: $t_9 = 2.36$, $P = 0.043$), primarily because parents remained at the nest for a. longer period of time, extending the length of the visit (Paired t test: $t_9 = -2.98$, $P = 0.0015$). Parental absences were also slightly longer (Paired t test: $t_9 = -2.11$, $P = 0.064$).

The length of time that parents spent at broods containing a muted nestling was highly correlated with non-feeding activity (non-feeding activity: $F_8 = 1075.0$, $P < 0.001$, feeding activity $F_8 = 2.46$, $P = 0.156$). The majority of feeding visits, both before and after treatment, were strictly nutritional - parents generally departed after allocating food and assessing the brood (MANOVA: visit type $F_{2,54} = 71.61$, $P = 0.014$, before vs. after $F_{1,54} = 0.022$, $P = 0.895$, interaction $F_{2,54} = 1.10$, $P = 0.339$; Fig. 3.1).

Following treatment, parents spent more time at the nest, although the effect was dependent on the type of visit (MANOVA: visit type $F_{2,34} = 12.186$, $P < 0.001$, before vs. after $F_{1,34} = 24.390$, $P < 0.001$, interaction $F_{2,34} = 9.201$, $P = 0.001$; Table 3.1). The removal of a fecal sac shortened feeding visits slightly, as parents departed immediately upon finding one, but these visits did not differ in length from those in which only food was provided (nutrition vs. sanitation: $P = 0.330$). There was no change in the length of sanitation visits following treatment, where the presence of a fecal sac continued to be the primary stimulus for departure (Table 3.1). In contrast, the length of

Figure 3.1. The mean (±SE) proportion of hourly feeding visits in which nutrition (nutrition visit), nutrition and fecal sac removal (sanitation visit), and nutrition and thermal care was provided (thermal visit).
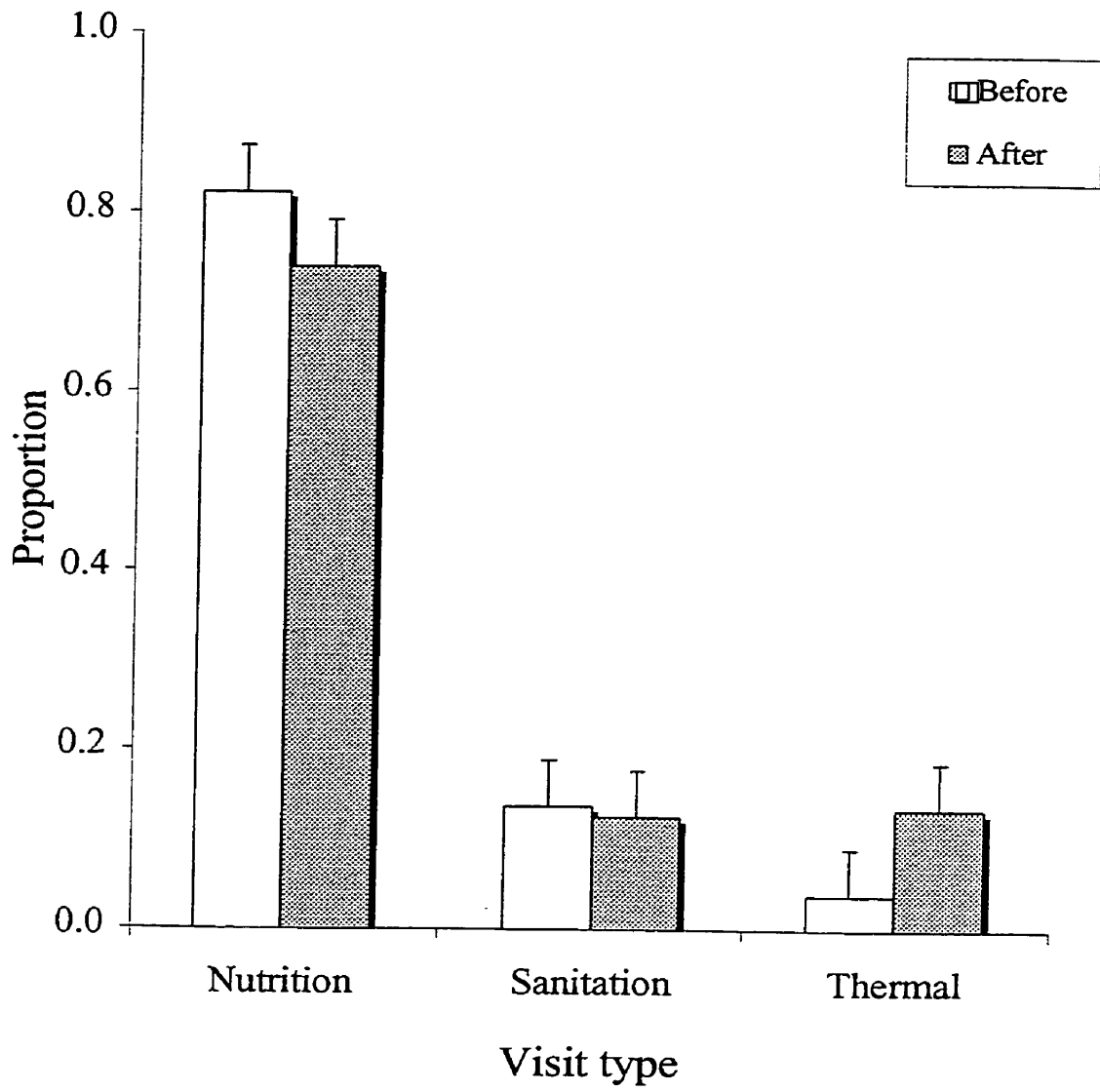
Table 3.1. The mean (± SE) duration of feeding visits devoted to each type of care at

broods before and after muting a single nestling: nutrition; nutrition and cleaning

(sanitation); nutrition and brooding or shading (thermal). Visits are divided into feeding

and non-feeding phases, and the duration of time spent brooding or shading (thermal

care) during the non-feeding phase is presented for the thermal visit.

Visit type	Before treatment (min)	After treatment (min)	t	df	P
Nutritrition	0.305 ± 0.116	0.591 ± 0.116	-2.162	9	0.059
Feeding phase	0.059 ± 0.013	0.062 ± 0.012	-0.367	9	0.722
Non-feeding phase	0.244 ± 0.069	0.530 ± 0.154	-2.307	9	0.046
Sanitation	0.195 ± 0.129	0.280 ± 0.149	-1.391	12	0.189
Feeding phase	0.054 ± 0.015	0.141 ± 0.011	-0.484	12	0.637
Non-feeding phase	0.067 ± 0.023	0.215 ± 0.164	-1.261	12	0.231
Thermal	0.335 ± 0.269	1.977 ± 0.183	-2.861	4	0.046
Feeding phase	0.040 ± 0.020	0.130 ± 0.051	-1.158	4	0.311
Non-feeding phase	0.295 ± 0.025	1.848 ± 0.371	-2.786	4	0.050
Thermal care	0.155 ± 0.105	1.300 ± 0.267	-2.818	4	0.048

time that parents spent at the nest during nutritional visits nearly doubled at treated broods, although the increase fell short of significance (t_{12} = -2.162, P = 0.059). Lengthier visits were attributable to a longer period of assessment by the parent following the allocation of food (non-feeding phase), as opposed to more time spent allocating food (feeding phase) (Table 3.1).

Thermal visits were significantly longer than those during which food alone (P = 0.001) or food and cleaning (P < 0.001) were provided. Again, an increase in the length of thermal visits following treatment (t_4 = -2.86, P = 0.046, Table 1) resulted from more time spent at the nest during the non-feeding phase.

Following treatment, the visual behaviour of the brood differed in only one way - there was a significant reduction in the length of time that treated broods begged during the non-feeding phase (Table 3.2). Brood participation, begging intensity, and the latency of response were all maintained at pretreatment levels (Table 3.2).

Food was allocated immediately following the arrival of the parent; however, as offspring continued to beg after its distribution, the bulk of solicitations (~70%) occurred during the non-feeding phase. The latency of response influenced the length of the feeding phase (Table 3.3), while the duration of continued visual and vocal displays influenced the length of the non-feeding phase, and by extension, the overall visit length (Table 3.4). The length of time that nestlings continued to solicit following food allocation, combined with the collective vocalisations of the brood, together explained 53.8% of the variance in visit length (ANOVA: $F_{2,17}$ = 12.08, P = 0.001).

Table 3.2. Multiple regression model assessing the relationship between non-feeding activity and various components of brood begging effort: intensity, proportion begging, vocal effort, and duration of continued begging (min).

a)

	B (slope)	SE	t	P
Intensity	-0.262	0.300	-0.875	0.396
Proportion begging	0.100	0.371	0.269	0.791
Collective vocalizations	-0.348	0.149	-2.330	0.034
Total duration of continued begging (min)	-3.822	1.823	-2.097	0.053

b)

	B (slope)	SE	t	P
Vocal	-0.310	0.136	-2.283	0.036
Total duration of continued begging (min)	-4.409	1.362	-3.238	0.005

Table 3.3. Multiple regression model assessing the relationship between parental feeding activity and various components of brood begging effort: intensity, proportion begging, vocal effort, and latency of response.

Brood behaviour	B (slope)	SE	t	P
Intensity	-0.003	0.024	-0.110	0.914
Proportion begging	0.080	0.034	0.579	0.572
Collective vocalizations	-0.003	0.008	-0.338	0.740
Length of begging prior to food allocation (min)	0.890	0.106	8.402	<0.001
Latency	1.892	0.559	3.385	0.004

Table 3.4. Mean (± SE) begging effort (latency, intensity, continued begging, proportion begging) before and after muting a nestling.

Behaviour	Before treatment	After treatment	t	df	P
Total duration of continued begging (min)	0.138 ± .016	0.110 ± .050	2.276	9	0.049
Length of begging prior to food allocation (min)	0.050 ± .011	0.051 ± .013	-0.084	9	0.935
Latency (min)	0.002 ± .003	0.000 ± .003	-0.527	9	0.611
Intensity	1.650 ± .104	1.670 ± .077	-0.245	9	0.812
Proportion that continue to beg following food allocation (min)	0.885 ± .043	0.818 ± .039	1.569*	9	0.151
Proportion that beg while food was being allocated	0.904 ± .031	0.887 ± .028	1.542*	9	0.157

* analysis performed on $\sin^{-1} \sqrt{x}$ transformed data

Differences in provisioning among nestings within broods

There was a slight, albeit non-significant reduction in food shares by muted and sham-muted nestlings following treatment (Repeated-measures ANOVA: mute vs. sham: $F_{1,18}$ = 1.641, P = 0.216; before vs. after: $F_{1,18}$ = 1.054, P = 0.318; interaction $F_{1,18}$ = 0.061, P = 0.808; Fig. 3.2). Thus the shortfall in food associated with the reduction in overall levels of provisioning to broods containing a muted nestling appears to have affected muted and non-muted nestlings roughly equally. Being mute did not place an experimental nestling at a particular disadvantage.

There was a trend, albeit non-significant, for both muted and sham-muted nestlings to beg for less time following treatment (Repeated-measures ANOVA: muted vs. sham-muted $F_{1,18}$ = 6.760, P = 0.018; before vs. after $F_{1,18}$ = 1.280, P = 0.273, interaction $F_{1,18}$ = 0.083, P = 0.776; Fig. 3.3a). Despite being matched for size and age, muted nestlngs initially begged for less time than sham-muted nestlings. I was unable to determine what may have contributed to this difference. However, following treatment all nestling reduced the duration of time that they begged, and the magnitude of the reduction was as large for sham-muted nestling as muted nestling (paired t-test: t = 0.255, df = 9, P = 0.805).

Muted nestlings reduced the intensity of their begging efforts following treatment, which resulted in a significant overall reduction (Repeated-measures ANOVA: muted vs. sham-muted $F_{1,18}$ = 1.739, P = 0.204, before vs. after $F_{1,18}$ = 0.445, P = 0.024, interaction $F_{1,18}$ = 2.561, P = 0.127, [1 - β = 0.329]; Fig. 3.3b). An interaction effect was not discernable, most likely due to the small sample size and resulting low power.

Figure 3.2. The mean (± SE) proportion of primary food items received by treated and

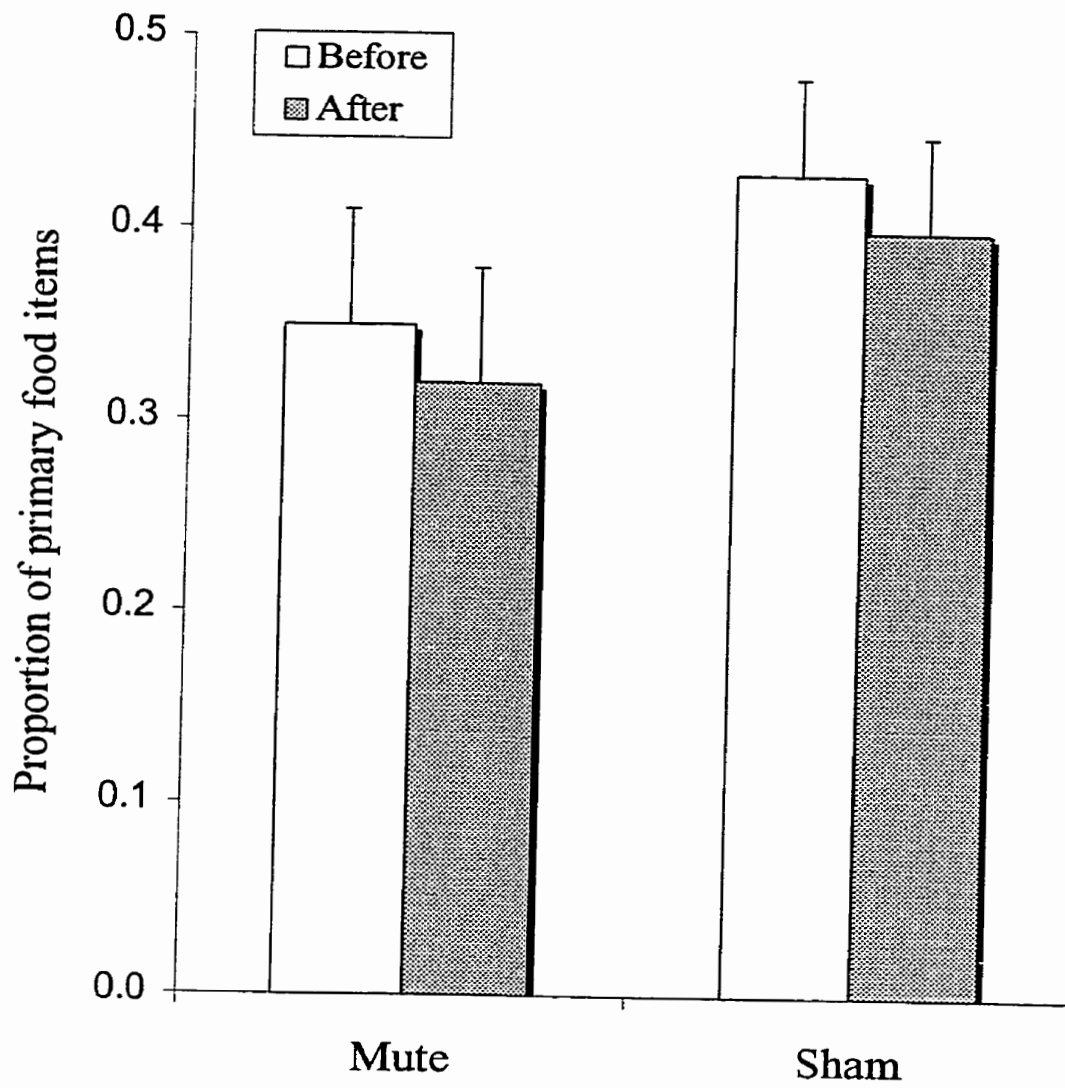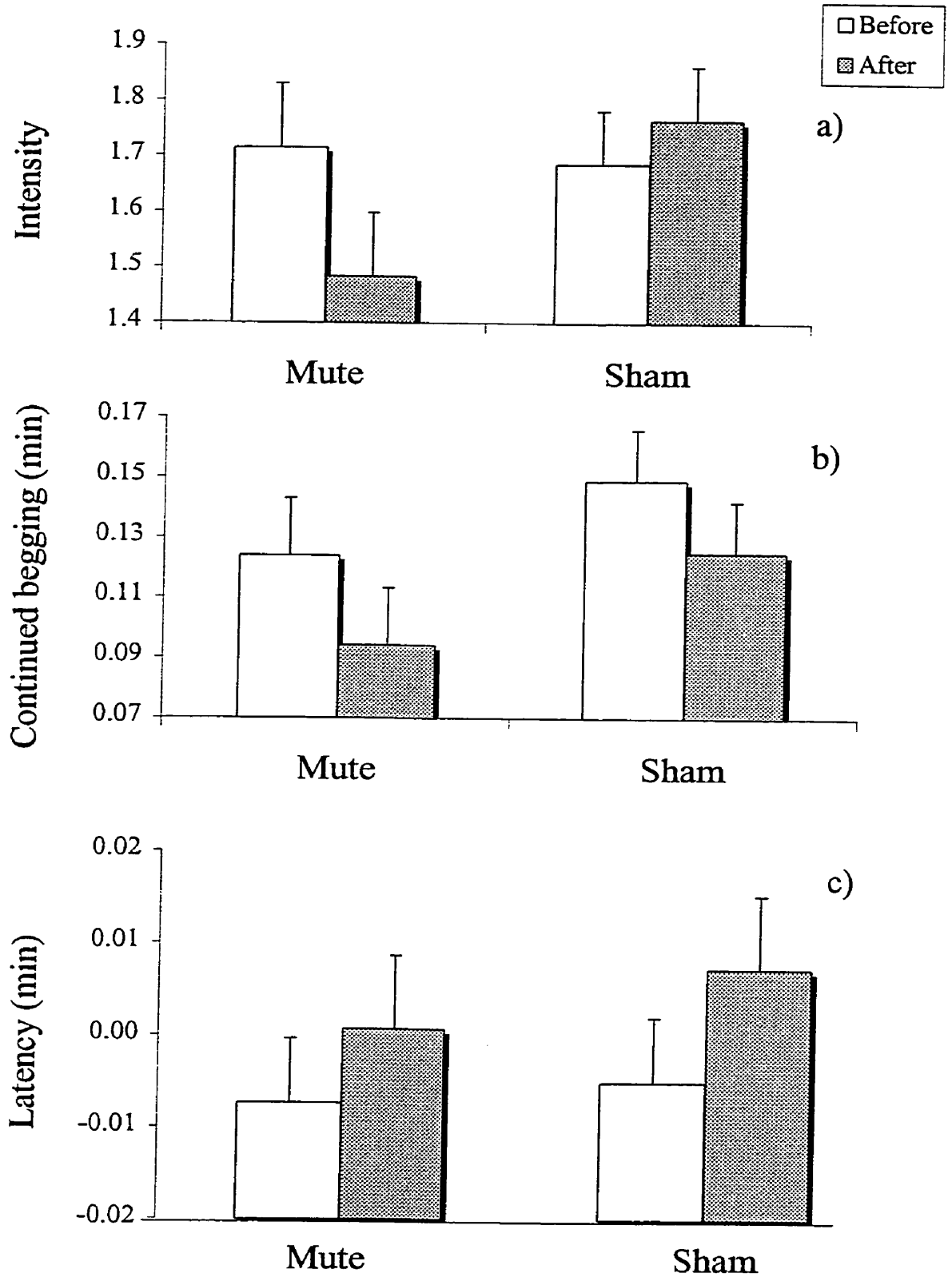sham-treated nestlings, before and after treatment.

Figure 3.3. Muted and sham-muted nestling begging behaviour measured before and after treatement: (a) intensity; (b) duration of continued begging (min); and (c) latency (min).

There was no significant difference in the speed at which muted and sham-muted nestlings responded to the arrival of the parent following treatment (Repeated-measures ANOVA: muted vs. sham-muted $F_{1,18} = 0.336$, P = 0.569, before vs. after $F_{1,18} = 1.869$, P = 0.188, interaction $F_{1,18} = 0.077$, P = 0.784; Fig. 3.3c).

Discussion

Differences in provisioning among nestings within broods

My results suggest that the visual, as opposed to vocal, component of begging is the stronger determinant of within-brood allocation of food. Vocalising was not a prerequisite for food reception by an individual. Food shares to muted nestlings were slightly, but not significantly, smaller which correlated well with substantial (but not significant) decreases in visual begging performance (Fig. 3).

Siblings of treated nestlings modified aspects of their behaviour associated with the non-feeding phase (continued begging), but not the feeding phase (intensity, latency). Untreated nestlings reduced the length of time that they begged slightly, but maintained begging intensity, a competitive behaviour, at control levels.

The results associated with those components of begging which measured during the feeding phase parallel those of earlier studies. Unmanipulated European starling, *Sturnus vulgaris*, nestlings maintained the latency (Cotton *et al.* 1996) and intensity (Kacelnik *et al.* 1995, Cotton *et al.* 1996) of response, in agreement with my study. I was unable to determine whether shortened begging by sham-muted nestling was a direct response to the abbreviated begging displays of their treated nestmates, or due to the procedure itself.

Differences in provisioning among entire broods

As predicted, provisioning to treated broods fell, suggesting that parents adjust their foraging effort in response to the lower cumulative vocalisations of the brood. An immediate reduction in feeding frequency to surgically muted singleton gull chicks was similarly observed by Miller and Conover (1979). Given that in my study the majority of the brood retained its vocal abilities, the magnitude of parental response was surprising. However, the reduction in foraging resulted primarily from increased nest attentiveness, as opposed to longer foraging absences, suggesting that non-vocal behaviour may have contributed to this result.

Earlier work on this system (Chapter 1) has shown that nest attentiveness is governed by the collective effort of the brood: redwing females resume foraging immediately when the majority of the brood continues to beg at high intensity for a lengthy period following food allocation. Conversely, abbreviated, low intensity begging extends the non-feeding phase. Parents increased nest attentiveness following treatment in response to a reduction in the cumulative begging efforts of the brood relative to control levels. By muting a nestling I reduced the vocal output of the brood, and shortened the length of time that nestlings continued to beg following the allocation of food, thereby manipulating both parental foraging rates and visit length through an increase in the length of the non-feeding phase.

Vocalisations appear to function as a collective signal, as Lotem (1998b) has suggested. Because parental foraging effort is not fixed (e.g. Price 1998, Wright 1998), there is the potential for an unfed nestling to influence its *per capita* level of intake by accelerating the next feeding visit through vocal stimulation, as predicted by Cotton *et al.*

(1996). Consequently, my results support the suggestion made by Cotton *et al.* (1996) that, contrary to the assumptions of current theoretical models of parent-offspring conflict (e.g. Godfray 1995), individual feeding visits are not independent events.

My results further suggest that nestlings are concerned not only with the outcome of the current feeding bout (Muller and Smith 1978, Redondo and Castro 1992, Kacelnik *et al.* 1995, Kilner 1995, Cotton *et al.* 1996, Leonard and Horn 1998, Lotem 1998a), but also with manipulating forthcoming levels of parental provisioning. In particular, begging during the non-feeding phase (accompanied by vocalisations) appears to represent not only the selfish attempt of an individual to secure additional food at the expense of nestmates, but also a cooperative, group effort by siblings to induce parents to increase overall levels of provisioning.

References

Bengtsson, H. and O. Ryden. 1981. Development of parent-young interaction in asynchronously hatched broods of altricial birds. Z Tierpsychol. 56: 255-272

Bengtsson, H. and O. Ryden. 1983. Parental feeding rate in relation to begging behavior in asynchronously hatched broods of the great tit *Parus major*. Behav. Ecol. and Sociobiol. 12: 243-251.

Briskie, J.V., C.T. Naugler, and S.M. Leech. 1994. Begging intensity of nestling birds varies with sibling relatedness. Proc. R. Soc. Lond. B. 258: 73-78.

Burford, J. E., T. J. Friedrich, and K Yasukawa. 1998. Response to playback of nestling begging in the red-winged blackbird, *Agelaius phoeniceus*. Anim. Behav. 56: 555-561.

Clark, A.B. and W.-H. Lee. 1998. Red-winged blackbird females fail to increase feeding in response to begging call playbacks. Anim. Behav. 56: 563-570.

Cotton, P. A., A. Kacelink, and J. Wright. 1996. Chick begging as a signal: are nestlings honest? Behav. Ecol. 7: 178-182.

Cotton, P. A., J. Wright and A. Kacelnik. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. Am. Nat. 153: 412-420.

Dufty, A. M. Jr. 1986. Singing and the establishment and maintenance of dominance hierarchies in captive brown-headed cowbirds. Behav. Ecol. Sociobiol. 19: 49-55.

Godfray, H. C. J. 1995. Signalling of need between parents and young: parent-offspring conflict and sibling rivalry. Am. Nat. 146: 1-24.

Gottlander, K. 1987. Parental feeding behaviour and sibling competition in the pied flycatcher *Ficedula hypoleuca*. Ornis. Scand. 18: 269-276.

Gireg-Smith, P. 1985. Weight differences, brood reduction, and sibling competition among nestling stonechats *Saxicola torquata* (Aves: Turdidae). J. Zool. Lond. A 5: 453-465.

Harper, A. B. 1986. The evolution of begging: sibling competition and parent-offspring conflict. Am. Nat. 128: 99-141.

Harris, M. P. 1983. Parent-young communication in the puffin *Fratercula arctica*. Ibis 125: 109-114.

Henderson, B. A. 1975. Role of the chick's begging behaviour in the regulation of parental feeding behaviour of *Larus glaucescens*. Condor 77: 488-492.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Kacelnik, A., Cotton, P. A., Stirling, L. and Wright, J. 1995. Food allocation among nestling starlings: sibling competition and the scope of parental choice. Proc. Royal Soc. Lond. B 259: 259-263.

Kilner, R. 1995. When do canary parents respond to nestling signals of need? Proc. Royal Soc. Lond. B 260: 343-348.

Kolliker, M., H. Richner, I. Werner and P. Hebb. 1998. Begging signals and biparental care: nestling choice between parental feeding locations. Anim. Behav. 55: 215-222.

Leonard, M. L. and A. G. Horn. 1996. Provisioning rules in tree swallows. Behav. Ecol. and Sociobiol. 38: 341-347.

Leonard, M. L. and A.G. Horn. 1998. Need and nestmates affect begging in tree swallow. Behav. Ecol. and Sociobiol. 42: 431-436.

Litovich, E. and Power, H. W. 1982. Parent-offspring conflict and its resolution in the European starling. Ornith. Monogr. No. 47. American Ornithologist's Union, Washington, D.C. 71 pp.

Lotem, A. 1998a. Differences in begging behaviour between barn swallow, *Hirundo rustica*, nestlings. Anim. Behav. 55: 809-818.

Lotem, A. 1998b. Manipulative begging calls by parasitic cuckoo chicks: why whould true offspring not do the same? Trends Ecol. Evol. 13: 342-343.

Macnair, M.R. and G.H. Parker. 1978. Models of parent-offpsring conflict. III. Intra-brood conflict. Anim. Behav. 27: 1202-1209.

McLean, I. G. and J. M. Griffin. 1988. Structure, function and mimicry in begging calls of passerines and cuckoos. Acta XX Congress Int. Ornithol.: 1273-1284.

Miller, D. E. and M. R. Conover. 1979. Differential effects of chick vocalizations and bill-pecking on parental behaviour in Ring-billed Gulls. Auk 96: 284-295.

Mock, D. W. and G. A. Parker. 1997. The Evolution of Sibling Rivalry. Oxford Univ. Press.

Motro, U. 1989. Should a parasite expose itself? (Some theoretical aspects of begging and vigilance behaviour). J. theor. Biol. 140: 279-287.

Muller, R. E. and D.G. Smith. 1978. Parent-offspring interactions in zebra finches. Auk 95: 485-495.

Parker , G. A., D. W. Mock and T. C. Lamey. 1989. How selfish should stronger sibs be? Am. Nat. 133: 846-868.

Parker, G. A. 1985. Models of parent-offspring conflict. V. Effects of the behaviour of the two parents. Anim. Behav. 33: 519-533.

Price, K. 1996. Begging as competition for food in yellow-headed blackbirds. Auk 113: 963-967.

Price, K. 1998. Benefits of begging for yellow-headed blackbird nestlings. Anim.Behav. 56: 57-577.

Price, K. and R.Ydenberg. 1995. Begging and provisioning in broods of asynchronously-hatched yellow-headed blackbird nestlings. Behav. Ecol. Sociobiol. 37: 201-208.

Redondo T. and L. A. de Reyna. 1988. Locatability of begging calls in nestling altricial brids. Anim. Behav. 36: 653-661.

Redondo T. and F.Castro. 1992. Signalling of nutritional need by magpie nestlings. Ethology 92: 192-204.

Ryden, O. and H. Bengtsson. 1980. Differential begging and locomotory behaviour by early and late hatched nestlings affecting the distribution of food in asynchronously hatched broods of altricial birds. Z. Tierpsychol. 53: 209-224.

Smith, D. G. 1977. An experimental analysis of the function of red-winged blackbird song. Behaviour 56: 136-156.

Smith, D. G. 1979. Male singing ability and territory integrity in red-winged blackbirds (*Ageliaus phoeniceus*). Behavior 68: 193-206.

Smith H. G. and R. Montgomerie 1991. Nestling American robins compete with siblings by begging. Behav. Ecol. Sociobiol. 29: 307-312

Stamps, J., A. Clark, P. Arrowood and B. Kus. 1989. Begging behaviour in budgerigars. Ethology 81: 177-192.

Teather, K.L. 1992. An experimental study of competition between male and female nestlings of the red-winged blackbird. Behav. Ecol. Sociobiol. 31: 81-87.

Trivers, R. L. 1972. Parental investment and sexual selection. In: Sexual Selection and the Descent of Man, 1871-1971 (Ed. by B. Campbell), pp. 136-179. Aldine, Atherton, Chicago.

von Haartman, L. 1953. Was reizt den Trauerfliegenschnäpper zu füttern? Die Vogelwarte 16: 157-164.

Whittingham, L. A. and R. J. Robertson 1993. Nestling hunger and parental care in red-winged blackbirds. Auk 110: 240-246.

Wright, J. 1998. Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. Behav. Ecol. and Sociobiol. 42: 423-429.

Chapter 4: The effect of a parasitic brown-headed cowbird nestling on broods of red-winged blackbird nestlings

Abstract

The red-winged blackbird (*Agelaius phoeniceus*) is commonly parasitised by the brown-headed cowbird (*Molothrus ater*). The presence of a brood parasite, unrelated to both host broodmates and parents, has provoked speculation regarding within-brood food allocation, and parental provisioning. I videotaped 28 nests of unparasitised red-winged blackbird broods, and compared them to 25 broods that were parasitised by the cowbird. The presence of the cowbird in the nest modified host nestling begging by stimulating more frequent begging, particularly during the first half of the nestling period. Foraging rates to parasitised broods did not differ from unparasitised broods, although parental attentiveness, particularly thermal care, increased in response to abbreviated begging by the majority host faction. Begging by cowbirds was unique in two ways: (i) the cowbird maintained a consistent begging effort throughout the nestling period (and received a consistent food share); and (ii) cowbirds begged for a lengthy period of time, particularly following the allocation of food.

Introduction

Avian brood parasites lay their eggs in the nests of other birds and leave all further parental care to the host (Rothstein 1975). As brood parasite nestlings are unrelated to their host nestmates, and therefore unconstrained by kin selection (Hamilton 1964), they are considered models for the evolution of selfishness. In particular, the conspicuous and persistent begging displays of nestling brood parasites (Nice 1939, Gochfeld 1979, Eastzer *et al.* 1980, Woodward 1983, Broughton *et al.* 1987, Briskie *et al.* 1994) have been the focal point for this work.

Game theoretical models of begging behaviour predict greater begging intensity by brood parasites, and as a consequence, escalated begging by host nestlings (Harper 1986, Motro 1989). Parents reduce the length of time that they spend at unparasitised red-winged blackbird nests on day five, midway through the nestling period, in response to the escalated demands which are assumed to accompany brood homeothermy (Hill and Beaver 1982, Chapter 1). A shift in parental supply occurs in response to the increased collective demands of the brood (Hussell 1988), so if parents use nestling begging effort to schedule food deliveries, the brood parasite may instigate an early shift in supply, at the expense of brooding.

In this paper I examine the begging behaviour of a brood parasite, the brown-headed cowbird (*Molothrus ater*), and one of its many hosts, the red-winged blackbird (*Agelaius phoeniceus*), over the nestling period. Until very recently, the majority of studies which have assessed cowbird behaviour have focused on older nestlings or fledglings (Nice 1939, Gochfeld 1979, Eastzer *et al.* 1980, Woodward 1983, Broughton *et al.* 1987, Briskie *et al.* 1994, but see Dearborn *et al.* 1998, Lichtenstein and Sealy

1998). Little is known regarding the ontogeny of begging by cowbirds, or how the presence of a cowbird affects the behaviour of host parents and offspring across the nestling period.

In this study I address three basic questions. First, do cowbird nestlings exhibit exaggerated begging displays relative to red-winged blackbird nestlings, and if so, when does this occur? Second, does the presence of the cowbird induce escalated begging by host nestlings, and if so, is the effect consistent across the nestling period? Third, does the presence of the cowbird alter schedules of parental behaviour? Do, for example, parents provision more and brood less at parasitised broods?

Methods

I studied red-winged blackbirds in wetlands near Winnipeg, Manitoba from late April to early August from 1993 to 1999. Five to 15% clutches were parasitised by cowbirds each year. Female cowbirds removed a host egg from about 40% of parasitised blackbird nests. Broods were surveyed daily, and nestling mass was recorded using an electronic balance. The behaviour of nestlings and parent blackbirds was studied by collecting videotape observations from a total of 25 parasitised broods and 28 unparasitised broods aged from 2 - 8 days (hatch = day 0). There was no detectable difference in the total brood size (parasitised: 3.56 ± 0.14, unparasitised: 3.32 ± 0.12, $t = 1.312$, df $= 51$, P $= 0.195$) or collective brood mass (parasitised: 17.10 ± 1.45, unparasitised: 19.74 ± 1.53, $t = -1.243$, df $= 51$, P $= 0.219$) between parasitised and unparasitised broods. Despite the frequent removal of a red-winged blackbird egg by the female cowbird, which resulted in significantly fewer red-winged blackbird nestlings in parasitised broods (parasitised: 2.56

in order for the brood parasite to precipitate an increase in parental supply, it must either elicit the cooperation of host nestlings to achieve a concerted shift in brood begging effort, or project the semblance of an increased group effort through its own begging behaviour (e.g. Davies *et al.* 1998).

Parental behaviour

Parental behaviour was assessed using three measures: i) visit frequency (foraging rate); ii) visit duration; and iii) absence duration. These three measures were related to each other as:

Parental effort/h = (length of visit * no. of visits) + (length of absence * number of absences)

Visits were subdivided into two phases: i) the food distribution phase, which spanned the interval between the parent's arrival and when the last food item was allocated; and ii) the non-feeding phase, which extended from allocation of the last food item until the departure of the parent. Non-feeding activity included behaviours associated with regulating the temperature of the brood (brooding, shading), sanitation (removal of foecal sac and debris), and/or guarding.

Nestling behaviour

For each visit during a one-hour span I measured four indices of "primary begging response" (*sensu* M. L. Leonard and A. Horn, Department of Biology, Dalhousie University, Halifax, Nova Scotia, pers. comm.), defined as begging behaviour initiated in response to the arrival of a food-bearing parent at the nest. First, the latency of begging

was defined as the amount of time between the arrival of the parent on the nest rim and the initiation of begging and. A negative latency indicates that begging commenced before the parent's arrival at the nest, and a positive latency indicates that begging began after the parent arrived at the nest. Secondly, the frequency of begging was defined separately for periods before and after food allocation as the number of visits on which a nestling begged, and the number of visits per hour on which a nestling continued to beg following the allocation of food. Thirdly, the duration of begging was defined as the total length of time that a nestling begged during a visit. Begging duration was subdivided into two measurements: the length of time that nestlings begged while food was being allocated; and the length of time nestlings continued to beg after the last food item was dispensed. Fourthly, the intensity of begging was scored when the parent arrived at the nest, as follows: 0 (not begging), 1 (gaping), or 2 (gaping with neck stretched) (e.g. Cotton *et al.* 1999). The sides of the nest cup often blocked leg and wing activity, precluding the use of a scoring system that included measures of these. To avoid pseudoreplication (Hurlbert 1984), I averaged the values for each behavioural variable for each nestling over the entire one hour observation period. I generated a single, average value per brood for the host nestlings for each behavioural index.

A feeding visit was defined as the arrival of a parent carrying food to the nest. Food loads were usually made up of one large, or primary item, although sometimes smaller prey items or a fragment(s) that had broken off from the primary item were also distributed. I did not attempt to identify prey qualitatively. Individual food reception was measured as the number of primary food items consumed, and as the total number of food items consumed.

Results

Parental behaviour

Parasitised vs. unparasitised broods.

I used a MANOVA to assess whether either parents or host nestlings modified their

behaviour in response to the presence of a cowbird, and to explore the relationship

between development and species within parasitised broods. All tests were two-tailed,

and *post hoc* pairwise comparisons were made using a Bonferonni multiple comparisons

test.

Parents provisioned parasitised and unparasitised broods at essentially the same

hourly rate over the nestling period (brood type: $F_{1,39} = 3.123$, P = 0.085, brood age: $F_{6,39}$

= 2.194, P = 0.064, interaction: $F_{6,39} = 2.301$, P = 0.054; Fig. 4.1a). Two exceptional data

points on day three account for the near-significant interaction effect observed.

Parents spent significantly less time at the nest as broods aged (brood type: $F_{1,39} =$

0.900, P = 0.349, brood age: $F_{6,39} = 2.763$, P = 0.025, interaction: $F_{6,39} = 0.150$, P = 0.088;

Fig. 4.1b), and were absent from parasitised broods for significantly shorter intervals

(brood type: $F_{1,39} = 3.430$, P = 0.044, brood age: $F_{6,39} = 1.165$, P = 0.345, interaction:

$F_{6,39} = 1.766$, P = 0.132; Fig. 4.1c).

An abrupt reduction on day five in the length of the parental visit was apparent at

both parasitised and unparasitised broods (Fig. 4.1b). I divided the data into broods

younger than day five (hereafter "younger broods"), and day five or older (hereafter

"older broods"), in order to assess in more detail which aspects of parental care

Figure 4.1. Mean (± SE) hourly parental behaviour at parasitised (shaded bar) and

unparasitised (white bar) red-winged blackbird broods measured as: a) frequency of

visits/hr; b) length of visits (min); and c) length of foraging absence (min).
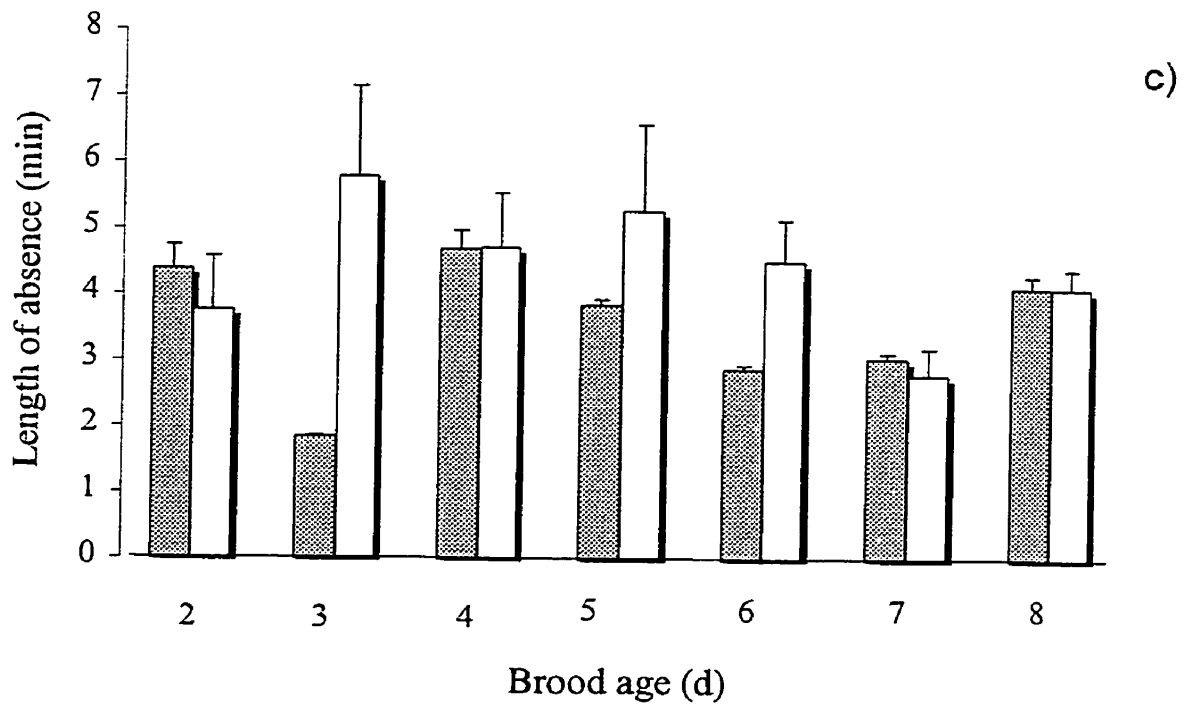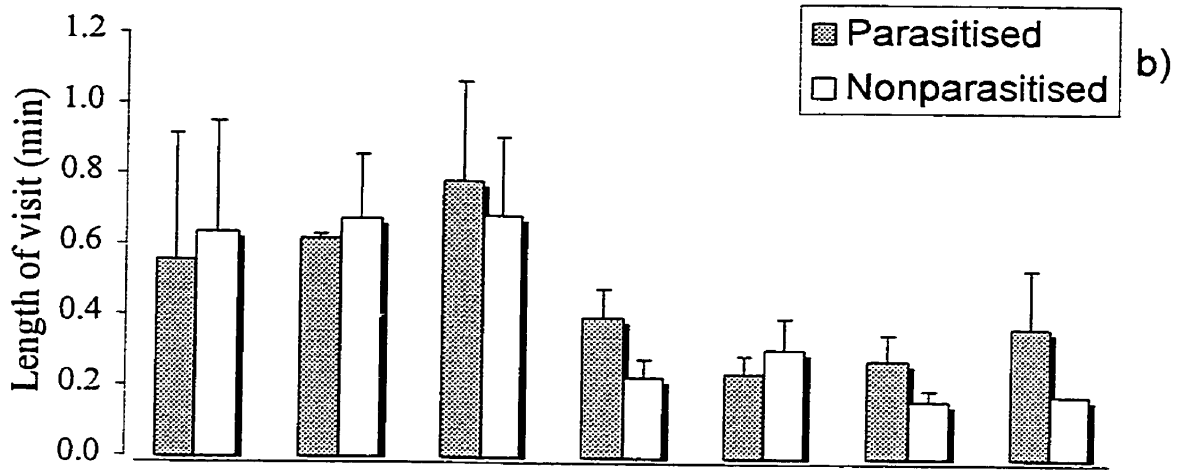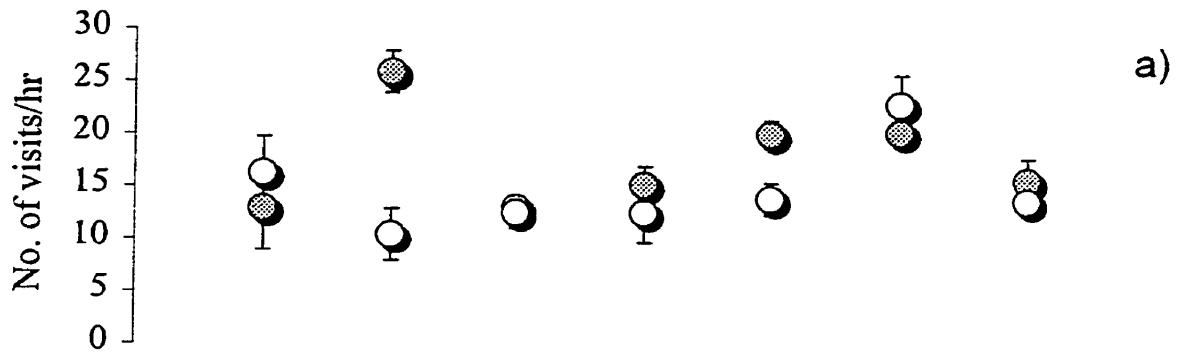
contributed to the longer visit length. Significantly longer visits to younger broods resulted from parents spending more time distributing food (feeding phase) and remaining at the nest for more extended periods following food allocation (non-feeding phase; Table 4.1).

In contrast to unparasitised broods where thermal care was essentially restricted to the first four days, parents both extended thermal care past day five to parasitised broods, and provided more thermal care to younger broods. As a result, parasitised broods received significantly more thermal care over the nestling period as a whole ($t_{51} = 2.431$, $P = 0.019$; Fig. 4.2).

I used exploratory regression analysis to assess the relationship between the length and frequency of feeding visits and brood age, size, and the presence of a cowbird (entered as a dummy variable). The duration of parental visits was principally determined by the age of the brood, with longer visits to younger, larger, parasitised broods (Table 4.2a). Similarily, parents foraged more frequently on behalf of older, often smaller broods, regardless of whether a cowbird was present in the nest (Table 4.2b).

Nestling behaviour

Red-winged blackbird behaviour - parasitised vs. unparasitised broods

The ontogeny of begging behaviour of red-winged blackbird nestlings in unparasitised broods differed from that of host nestlings in parasitised broods. With the exception of the duration of begging during food allocation (prebeg: $F_{1,95} = 2.38$, $P = 0.126$), the data for all behavioural indices associated with nestings from unparasitised broods was best described by a second-order polynomial. Begging reached a local maximum (or

Figure 4.2. The amount of thermal care (mean ± SE length of brooding or shading/hour) provided to parasitised (shaded bar) and unparasitised (shaded bar) red-winged blackbird broods over the nestling period.

Brood age (d)
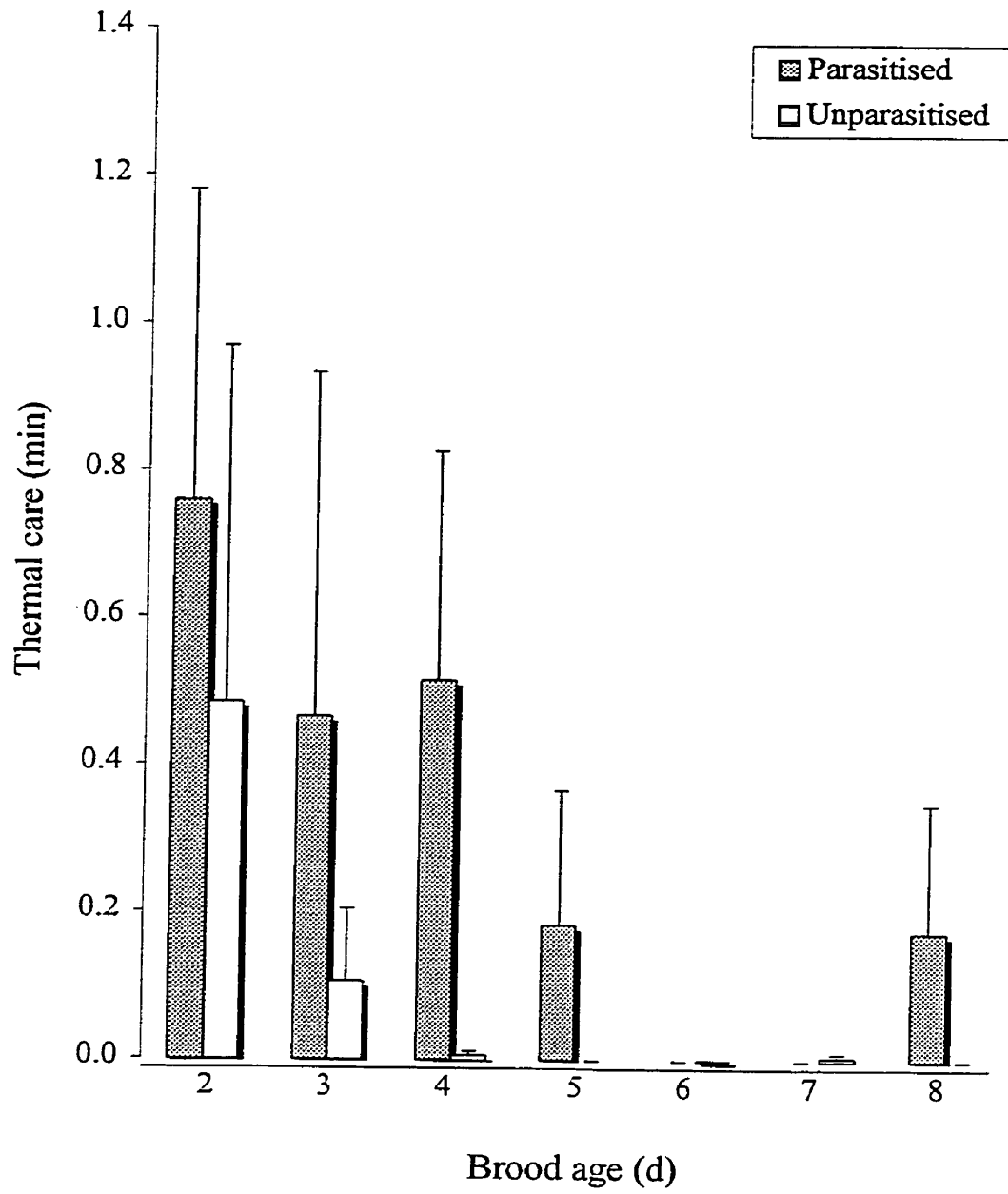
Table 4.1. The duration (mean ± SE) of parental care to younger (hatch to day 4) and older (day 5 to fledge) parasitised and unparasitised broods. Values for the length of the feeding and non-feeding phases are presented separately.

Duration of parental behaviour (min)	Brood type	Younger Broods	Older Broods	t	df	P
Visit length	Parasitised	0.859 ± 0.111	0.284 ± 0.087	3.136	23	0.005
	Unparasitised	0.515 ± 0.117	0.229 ± 0.087	2.667	26	0.013
Feeding phase	Parasitised	0.084 ± 0.014	0.058 ± 0.012	1.664	23	0.110
	Unparasitised	0.100 ± 0.015	0.046 ± 0.011	2.690	26	0.012
Non-feeding phase	Parasitised	0.776 ± 0.109	0.227 ± 0.096	3.036	23	0.006
	Unparasitised	0.415 ± 0.114	0.177 ± 0.085	2.343	26	0.027

Table 4.2. Results of multiple regression analysis to determine which brood characteristics (brood age, presence of cowbird, or total brood size) contributed to: a) visit length (overall and best fit adjusted $R^2 = 0.253$, P = 0.001), and b) visit frequency (overall adjusted $R^2 = 0.081$, P = 0.069; best fit adjusted $R^2 = 0.092$, P = 0.033).

a)

Brood Parameter	B (slope)	SE	t	P
Brood age	-0.135	0.032	-4.196	0.000
Presence of cowbird	0.142	0.104	1.373	0.176
Brood size	-0.157	0.093	-1.679	0.099

b)

Brood parameter	B	SE	t	P
Brood age	1.338	0.496	2.696	0.010
Presence of cowbird	0.979	1.595	0.614	0.542
Brood size	1.998	1.434	1.393	0.170

minimum in the case of latency) at about day five (latency: $F_{1,94} = 7.46$, P = 0.001,

intensity: $F_{1,94} = 29.34$, P < 0.001, proportion of visits nestling begged: $F_{94} = 20.92$, P <

0.001, proportion of visits nestling continued to beg: $F_{1,94} = 22.85$, p < 0.001, duration of

continued begging: $F_{1,94} = 3.77$, P = 0.027). This means that the begging efforts of

hatchlings were initially low, increased over the first four days and then remained

consistently high over the rest of the nestling period (day 5-8). In contrast, the

relationship between begging and the age of host nestlings in parasitised broods either

increased in a linear fashion (intensity: $F_{1,61} = 7.51$, P = 0.008; proportion of visits

nestling begged: $F_{1,61} = 4.56$, P = 0.037; proportion of visits nestling continued to beg:

$F_{1,61} = 6.65$, P = 0.012), or did not change with age (prebeg: $F_{1,61} = 2.39$, P = 0.127,

latency: $F_{1,61} = 1.39$, P = 0.242, total continued: $F_{1,61} = 1.42$, P = 0.237).

I assessed whether host nestlings modified their behaviour in response to the

presence of a cowbird by comparing the begging behaviour of unparasitised and

parasitised red-winged blackbird nestlings using a MANOVA with brood age (younger

vs. older) and brood type (parasitised vs. unparasitised) as fixed factors.

Behaviour measured during the feeding phase was not affected by the presence of

a cowbird, although there was an effect of brood age. Red-winged blackbird nestlings in

younger broods initiated begging later (parasitised vs. unparasitised: $F_{1,152} = 0.004$, P =

0.952, younger vs. older: $F_{1,152} = 9.671$, P = 0.002, interaction: $F_{1,152} = 1.406$, P = 0.238,

Table 3) and at a lower intensity as compared to nestlings in older broods (parasitised vs.

unparasitised: $F_{1,152} = 1.392$, P = 0.240, younger vs. older: $F_{1,152} = 31.312$, P < 0.001,

interaction: $F_{1,152} = 2.928$, P = 0.089, Table 4.3).

Begging behaviour during the non-feeding phase differed significantly between red-

winged blackbirds in parasitised and unparasitised broods. Unparasitised nestlings continued to beg less frequently (parasitised vs. unparasitised: $F_{1,152} = 6.678$, P = 0.011, younger vs. older: $F_{1,152} = 36.924$, P <0.001, interaction: $F_{1,152} = 1.409$, P = 0.237; Table 4.3), but for a longer duration (parasitised vs. unparasitised: $F_{1,152} = 4.613$, P = 0.033, younger vs. older: $F_{1,152} = 0.661$, P = 0.417, interaction: $F_{1,152} = 0.006$, P = 0.941; Table 4.3), following the allocation of food than those sharing a nest with a cowbird.

Red-winged blackbird vs. cowbird behaviour - parasitised broods

The frequency at which nestlings responded to the arrival of the parent was consistent between species and over the nestling period, with begging occurring on the majority of visits (age $F_{8,72} = 1.754$, P = 0.103, species: $F_{1,72} = 0.180$, P = 0.673, interaction: $F_{7,72} = 0.511$, P = 0.824). Nestlings generally began begging when the parent arrived on the nest rim (age: $F_{8,72} = 1.962$, P = 0.064, species: $F_{1,72} = 0.137$, P = 0.712, interaction: $F_{7,72} = 1.031$, P = 0.417). Begging intensity increased significantly with age, as older nestlings of both species stretched their necks while gaping (age: $F_{8,72} = 2.115$, P = 0.045, species: $F_{1,72} = 1.394$, P = 0.242, interaction: $F_{7,72} = 0.425$, P = 0.884). Older nestlings begged for less time while food was being allocated (age: $F_{8,72} = 3.090$, P = 0.005, species: $F_{1,72} = 0.605$, P = 0.439, interaction: $F_{7,72} = 0.561$, P = 0.785), most likely because parents distributed food more quickly.

During the non-feeding phase, the length of time that nestlings continued to beg following the allocation of food did not change with age, although there was a significant species effect. Continued begging by the cowbird consistently exceeded begging by host nestlings (age: $F_{8,72} = 0.599$, P = 0.775, species: $F_{1,72} = 5.937$, P = 0. 017, interaction:

Table 4.3. The mean (± SE) begging behaviour of red-winged blackbird nestlings in parasitised and unparasitised nests at younger (hatch to day 4) and older (day 5 to fledge) broods.

Begging behaviour	Brood type	Younger broods	Older broods
Intensity	Unparasitised	1.273 ± 0.066	1.758 ± 0.054
	Parasitised	1.465 ± 0.072	1.722 ± 0.071
Latency (min)	Unparasitised	0.010 ± 0.004	-0.006 ± 0.003
	Parasitised	0.006 ± 0.004	-0.001 ± 0.004
Duration of begging following the allocation of food (min)	Unparasitised	0.155 ± 0.014	0.166 ± 0.012
	Parasitised	0.123 ± 0.016	0.136 ± 0.015
Duration of begging while food is being allocated(min)	Unparasitised	0.083 ± 0.008	0.0471 ± 0.007
	Parasitised	0.076 ● 0.009	0.066 ± 0.008
Proportion of visits on which begging was initiated	Unparasitised	0.774 ± 0.026	0.947 ± 0.022
	Parasitised	0.829 ± 0.029	0.913 ± 0.028
Proportion of visits on which begging continued after food distribution	Unparasitised	0.672 ± 0.031	0.894 ± 0.025
	Parasitised	0.803 ± 0.034	0.936 ± 0.033

$F_{7,72} = 1.529$, P $= 0.171$) and cowbirds more frequently continued begging after food was allocated (age: $F_{8,72} = 1.669$, P $= 0.121$, species: $F_{1,72} = 6.264$, P $= 0.015$, interaction: $F_{7,72} = 0.666$, P $= 0.700$).

The behaviour of the cowbird was remarkable for its consistency. There was no detectable change in any of the begging indices with age (intensity: $F_{1,23} = 3.10$, P $= 0.092$, total continued: $F_{1,23} = 0.23$, P $= 0.634$, pretotal: $F_{1,23} = 2.31$, P $= 0.142$, latency: $F_{1,23} = 0.46$, P $= 0.505$, proportion of visits on which nestling begs: $F_{1,23} = 1.03$, P $= 0.320$, proportion of visits on which nestling continues to beg: $F_{1,23} = 0.60$, P $= 0.447$).

Red-winged blackbird vs. cowbird food reception - parasitised broods

Host nestlings received more primary food items than a brood parasite of the same age (age: $F_{8,72} = 1.087$, P $= 0.382$, species: $F_{1,72} = 11.271$, P $= 0.001$, interaction: $F_{7,72} = 0.827$, P $= 0.569$; Fig. 3a). In contrast to cowbird nestlings that received the same amount of primary food items regardless of age or size (age: $F_{1,23} = 0.15$, P $= 0.704$, size: $F_{1,23} = 0.31$, P $= 0.580$; Figs. 3a,b), the number of primary food items received by red-winged blackbird nestlings increased significantly as they grew and aged (age: $F_{1,62} = 15.97$, P < 0.001, size: $F_{1,62} = 22.34$, P < 0.001; Figs. 3a,b).

The overall pattern of food reception paralleled that of primary prey consumption. Host nestlings received more total food items than a cowbird nestling (age: $F_{8,72} = 0.815$, P $= 0.592$, species: $F_{1,72} = 6.038$, P $= 0.016$, interaction: $F_{7,72} = 0.142$, P $= 0.211$), indicating that cowbirds were unable to make up the deficit in primary items by accessing food that was dispensed later in the visit.

In order to determine whether nestlings were offered more food than they

Figure 4.3. Food reception by cowbird (grey circle) and red-winged blackbird (white circle) nestlings from parasitised broods, measured as consumption of primary food items/hr by a nestling for a given a) age and b) mass (g).

a)

b)
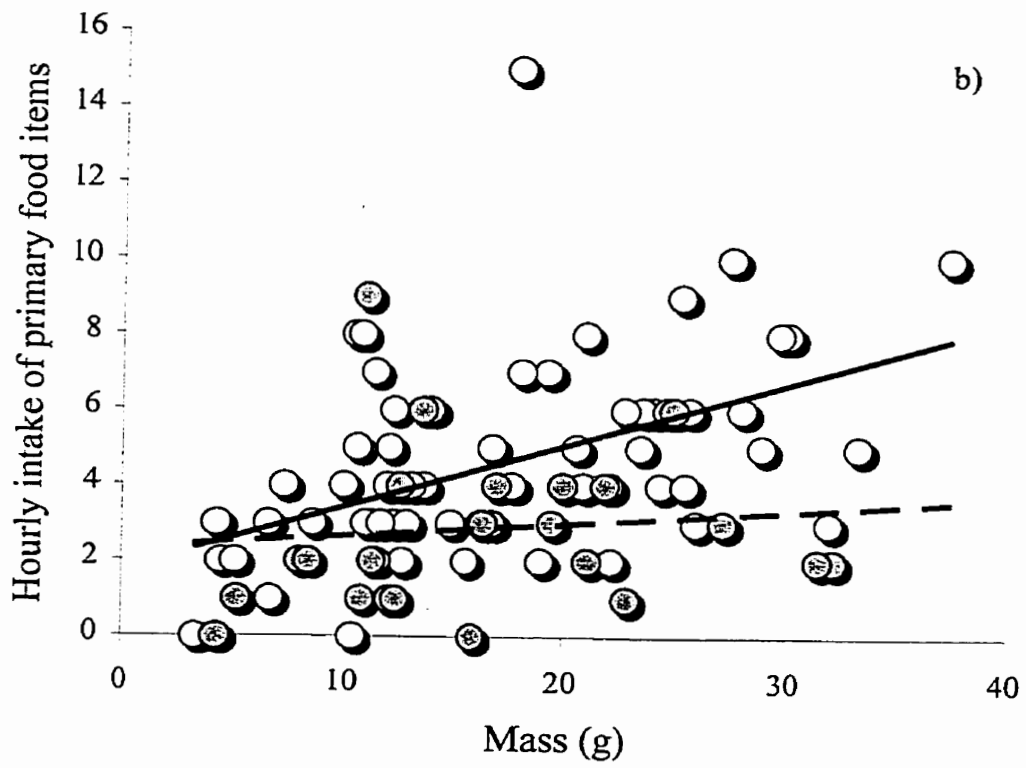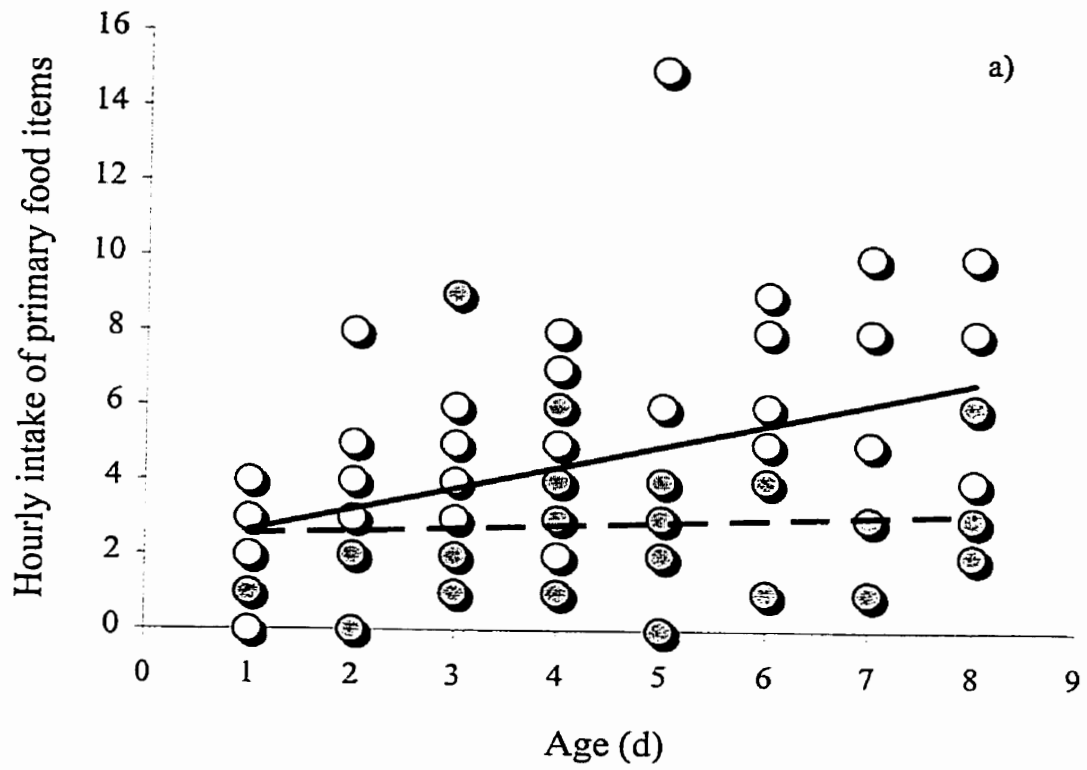
received, I differentiated between food items that were placed in a nestling's gaping mouth, but subsequently removed and fed to another nestling (offered first), and food items that were placed in a nestling's mouth, and swallowed (fed first). Both red-winged blackbird nestlings (offered first: $\bar{x}$ = 4.94 ± 0.35, fed first: $\bar{x}$ = 4.50 ± 0.35, paired t = 4.200, df = 63, P < 0.001) and cowbird nestlings (offered first: $\bar{x}$ = 3.08 ± 0.44, fed first: $\bar{x}$ = 2.88 ± 0.43, paired t = 4.200, df = 24, P = 0.057) were offered more food items per hour than they consumed, and in the former case the difference was significant. The magnitude of difference between the two species was equivelant to less than half of a prey item (t = 1.332, df = 87, P = 0.186), indicating that parents were slightly, albeit non-significantly, less likely to remove food from a brood parasite as from one of their own offspring.

Discussion

Begging by cowbirds was unique in two ways: i) the cowbird maintained a consistent begging effort throughout the nestling period; and ii) cowbirds begged for a lengthy period of time, particularly following the allocation of food. Aside from a slightly more extended neck, a nine-day old cowbird nestling begged in the same manner as a two-day old nestling, and received a consistent amount of food.

My results indicate that the cowbird did not receive a greater food share than that of the host nestlings, suggesting that the loud and persistent vocalizations of the cowbird documented elsewere (Nice 1939, Gochfeld 1979, Eastzer *et al.* 1980, Woodward 1983, Broughton *et al.* 1987, Briskie *et al.* 1994) do not render it a competitive advantage. Despite begging longer, cowbirds were fed less frequently than host nestlings, contrary to

the predictions of begging models (Harper 1986, Redondo and de Reyna 1988, Motro 1989, Briskie *et al.* 1994). A potential cost associated with continued begging is the removal and redistribution of the prey item by the parent (e.g., Lichtenstein 1997). However, I found no evidence that parents actively discriminate against the cowbird by selectively removing food from its gape.

Although hatchling cowbirds and red-winged blackbirds received a roughly equivalent food share, cowbirds fell steadily behind, as broods grew older. In fact, the *per capita* food intake of cowbirds did not change with nestling age, whereas that of blackbird nestlings almost trebled over the first week of life (Fig. 3). Evidently young cowbirds did more with less. Differences between cowbird and red-winged blackbird physiology may provide clues as to how this was achieved.

Red-winged blackbird growth rates are high during the first three days of the nestling period, and slow when physiological endothermy is initiated (Fiala and Congdon 1983, Olson 1992). Beginning on day four, nestlings must increase their energetic intake in order to subsidize the additional metabolic requirements that thermoregulation imposes, as well as costs associated with maintenance and digestion (Holcomb and Twiest 1971, Fiala and Congdon 1983, Olson 1992). Begging by unparasitised red-winged blackbirds nestlings follows the same pattern. After increasing over the first four days, begging efforts generally remain high for the remainder of the nestling period.

In contrast, Neal (1973) observed that cowbirds begin to defend against ambient temperature on day two (hatch = day 0), but found no evidence that nestlings attained endothermy earlier than that of other passerines described in the literature, suggesting that the energy budget of cowbirds may differ from host nestlings. Since growth varies

inversely with metabolism, delaying thermal independence could minimize metabolic costs without requiring a longer period of development (Ricklefs and Webb 1985). This scenario would be consistent with the conclusions of Lustick (1970), who noted that adult cowbirds have a low metabolic rate relative to other passerine species. Given that rapid growth by young altricial nestlings is facilitated by accelerated development of the digestive system (Dunn 1975), my results also hint at potential anatomical differences in the digestive system of young cowbirds that may allow them to process and/or assimilate food energy more efficiently.

The behaviour of host nestlings was modified by the presence of a cowbird in the nest. Frequent begging by the cowbird appears to have stimulated host nestlings to beg more often, particularly during the first half of the nestling period. Given that parents brooded young parasitised broods more, and provided an extra day of thermal care, my results suggest that the presence of the by the cowbird may have changed the thermal environment of the nest.

Red-winged blackbird nestlings are dependent on the parent as a primary heat source during the inertial stage of brood development (day $0 - 4$), and on thermal inertia for the maintenance of body temperature and metabolic rate when the parent is off the nest (Hill and Beaver 1982, Olson 1992, Webb and King 1983). Although parasitised broods contained fewer redwing nestlings, the presence of the cowbird maintained the total brood size and the brood mass at the level of unparasitised broods. However thermal inertia is primarily achieved by huddling, particularly in open cup nests which store negligible amounts of heat after being warmed by a brooding parent (Webb and King 1983). Huddling slows the rate of convective heat loss by increasing insulation and

reducing the exposed surface area (Dunn 1976, Webb 1993). Given that cowbird nestlings are very active, both during visits and when the parent is absent (see Dearborn 1998), and that host nestlings respond to this activity by begging, I suspect that the increased activity in parasitised broods may have compromised the huddle. Less time spent huddling may have resulted in a faster rate of heat loss, requiring more parental brooding.

Earlier work on this system (Chapter 1) has shown that pararental attentiveness at unparasitised nests is governed by the collective effort of the brood: redwing females resume foraging immediately when the majority of the brood continues to beg at high intensity for a lengthy period following food allocation. Conversely, abbreviated, low intensity begging extends the non-feeding phase. Although cowbird nestlings begged for a long time at nearly every meal, they often found themselves in the minority. Nestling blackbirds may have declined to participate because they were physiologically unable to sustain the effort, particularly when young (Choi and Bakken 1990), or because they were satiated. Prolonged begging by cowbird nestlings failed to induce the parent to deliver more food to the brood, presumably because the cowbird was unable to effect a shift in brood demand by its own efforts. Rather, host nestlings increased parental nest attendance through abbreviated begging. By responding to the begging efforts of the majority, parents appear to have been safeguarded against capitulating to the demands of the brood parasite over those of their own offspring.

This system of communication ("respond to the majority") appears to work in favour of the brood parasite when the cowbird is larger and more successful than host offspring (e.g. Lichtenstein and Sealy 1998, Dearborn *et al.* 1998). Prolonged begging by the

brown-headed cowbird has been observed in parasitised broods of indigo buntings (*Passerina cyanea*, Dearborn *et al.* 1998). In contrast to my system, the smaller, less successful and presumably hungrier host nestlings also prolonged their begging efforts, which resulted in an increase in parental provisioning to the brood (Dearborn 1998, Dearborn *et al.* 1998).

My results indicate that foraging rates were correlated with the age and size of the brood, as opposed to the presence of a parasite *per se* (see also Soler *et al.* 1995). Host nestlings stopped begging sooner than the cowbird, which reduced the amount of time that the host faction augmented the calls of the brood parasite, particularly during the non-feeding phase. Brown-headed cowbirds are generalist brood parasites, and show no evidence of host mimicry (Broughton *et al.* 1987, Redondo 1993). In particular, there is no evidence of vocal mimicry - the vocalizations of cowbird nestlings, when audible, are easily discernible from those of blackbird vocalizations by the human ear. My results indicate that continued vocalizations by the cowbird alone did not provide sufficient stimulus for the parent to increase food deliveries to the brood, suggesting that provisioning by host parents may be governed by the vocalizations of their own offspring.

Prolonged begging by hungry passerine nestlings often occurs as a result of size differences within asynchronously hatched broods (Smith and Montgomerie 1991, Mondloch 1995, Cotton *et al.* 1999, Smiseth 1999). In contrast, the brown-headed cowbird consistently continues to beg following the distribution of food, regardless of its age or status. My results suggest that cowbird begging targets the non-feeding phase in order to increase the foraging rate of the foster parent. Because parental foraging effort is

not fixed (e.g. Price 1998; Wright 1998), the cowbird nestling may be attempting to influence its *per capita* level of intake by accelerating the next feeding visit, creating a trickle-down effect. However, since the cowbird is in the minority, the success of this strategy is dependent on the behaviour, and ultimately the size, of host nestlings.

References

Briskie, J.V., C.T. Naugler, and S.M. Leech. 1994. Begging intensity of nestling birds varies with sibling relatedness. Proc. R. Soc. Lond. B. 258: 73-78.

Broughton, K.E., A.L. Middleton and E.D. Bailey. 1987. Early vocalizations of the Brown-headed Cowbird and three host species. Bird Behaviour 7: 27-30.

Choi, I.-H. and G.S. Bakken. 1990. Begging response in nestling red-winged blackbirds (*Agelaius phoeniceus*): effect of body temperature. Physiol. Zool. 63: 965-986

Cotton, P.A., J. Wright and A. Kacelnik. 1999. Chick begging strategies in relation to brood hierarchies and hatching asynchrony. Am. Nat. 153: 412-420.

Davies, N.B., R.M. Kilner and D.G. Noble. 1998. Nestling cuckoos *Cuculus canorus* exploit hosts with begging calls that mimic a brood. Proc. R. Soc. London. B: 265: 673-678.

Dearborn, D.C. 1998. Begging behaviour and food acquisition by brown-headed cowbird nestlings. Behav. Ecol. Sociobiol. 43: 247-257.

Dearborn, D.C., A.D. Anders, F.R. Thompson III and J. Faaborg. 1998. Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. Condor 100: 325-334.

Dunn, E.H. 1975. Growth, body components and energy content of nestling double-crested cormorants. Condor 77: 431-438.

Dunn, E.H. 1976. The relationship between brood size and age of effective homeothemy in nestling House Wrens. Wilson Bull. 88: 478-482.

Eastzer, D., P.R. Chu and A.P. King. 1980. The young cowbird: average or optimal nestling? Condor 82: 417-425.

Fiala, K.L. and J.D. Congdon. 1983. Energetic consequences of sexual size dimorphism in nestling red-winged blackbirds. Ecology 64: 642-647.

Gochfeld, M. 1979. Begging by nestling shiny cowbirds: adaptive or maladaptive. Living Bird 17: 41-50.

Hamilton, W.J. 1964. The genetical evolution of social behaviour. I. J. theoret. Biol. 7: 1-16.

Harper, A.B. 1986. The evolution of begging: sibling competition and parent-offspring conflict. Am. Nat. 128: 99-114.

Hill, R.W. and D.L. Beaver. 1982. Inertial thermostability and thermoregulation in broods of red-winged blackbirds. Physiol. Zool. 55: 250-266.

Holcomb, L. C. and G.Twiest. 1971. Growth and calculation of age for red-winged blackbird nestlings. Bird-Banding 42: 1-78.

Hussell, D.J.T. 1988. Supply and demand in tree swallow broods: a model of parent-offspring food-provisioning interactions in birds. Am. Nat. 131: 175-202.

Hurlbert, S. H. 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187-211.

Lichtenstein, G. and S.G. Sealy. 1998. Nestling competition, rather than supernormal stimulus, explains the success of parasitic brown-headed cowbird chicks in yellow warbler nests. Proc. R. Soc. Lond. B: 249-254.

Lichtenstein, G. 1997. Begging behaviour and host manipulation by three species of parasitic cowbirds. PhD thesis, University of Cambridge, UK.

Lustick, S. 1970. Energetics and water regulation in the cowbird (*Molothrus ater obscurus*). Physiol. Zool. 43: 270-287.

Mondloch, C.J. 1995. Chick begging affects parental allocation of feedings in pigeons. Anim. Behav. 49: 601-613.

Motro, U. 1989. Should a parasite expose itself? (Some theoretical aspects of begging and vigilance behaviour). J. theor. Biol. 140: 279-287.

Neal, C.M. 1973. Cooling rates and development of homeothermy in the brown-headed cowbird (*Molothrus ater ater*). Condor 75: 351-352.

Nice, M.M. 1939. Observations on the behaviour of a young cowbird. Wilson Bull. 51: 233-239.

Olson J. M. 1992. Growth, the development of endothermy, and the allocation of energy in red-winged blackbirds (*Agelaius phoeniceus*) during the nestling period. Physiol. Zool. 65: 124-152

Price, K. 1998. Benefits of begging for yellow-headed blackbird nestlings. Anim. Behav. 56: 571- 577.

Redondo, T. 1993. Expoitation of host mechanisms for parental care by avian brood parasites. Etologia 3: 235-297.

Redondo, T. and L. A. de Reyna. 1988. Locatability of begging calls in nestling altricial birds. Anim. Behav. 36: 653-661.

Rothstein, S. 1975. Evolutionary rates and host defenses against avian brood parasitism. Am. Nat. 109: 161-176.

Røskaft, E., G.H. Orians, L.D. Beletsky. 1990. Why do red-winged blackbirds accept eggs of brown-headed cowbirds? Evol. Ecol. 4: 35-42.

Smith H. G., and R. Montgomerie. 1991. Nestling American robins compete with siblings by begging. Behav. Ecol. Sociobiol. 29: 307-312

Smiseth, P.T. 1999. Social evolution in monogomous families: mate choice and conflicts over parental care in the Bluethroat (*Luscinia s. svecica*). PhD thesis. Norwegian University of Science and Technology.

Soler, M., J.G. Martinez, J.J. Soler and A.P. Møller. 1995. Preferential allocation of food by magpies *Pica pica* to great spotted cuckoo *Clamator glandarius* chicks. Behav. Ecol. Sociobiol. 37: 7-13.

Weatherhead, P.J. 1989. Sex ratios, host-specific reproductive success, and impact of Brown-headed Cowbirds. Auk 106:358-366.

Webb, D.R. 1993. Maternal-nestling contact geometry and heat transfer in an altricial bird. J. Therm. Biol. 18: 117-124.

Webb, D.R. and J. R. King 1983. Heat-transfer relations of avian nestlings. J. Therm. Biol. 8: 301-310.

Woodward, P.W. 1983. Behavioural ecology of fledgling brown-headed cowbirds and their hosts. Condor 85: 151-163.

Wright, J. 1998. Helpers-at-the-nest have the same provisioning rule as parents: experimental evidence from play-backs of chick begging. Behav. Ecol. Sociobiol. 42: 423-429.

Concluding Remarks

Red-winged blackbird nestlings undergo large-scale morphological and physiological changes in the ten days between hatching and fledging. Nestlings begin life as ectotherms, a period during which they are reliant on brooding by the female parent for heat, and on their nestmates for insulation. The transition to endothermy, initiated midway through the nesting period, rapidly conveys thermal independence. However, as thermoregulation demands a greater energetic expenditure, food requirements escalate.

It is well established that begging behaviour is used to communicate hunger and nutritional needs to parents, but little is known about how passerine offspring communicate their thermal needs. This question is of particular interest given that heat is a form of "unshared parental investment " (Lazarus and Inglis 1986), meaning that the benefits of thermal care are experienced collectively. The direct benefits of food, in contrast, are restricted to the individual that receives it ("shared parental investment", Lazarus and Inglis 1986).

The results presented in Chapter 1 indicate that the ontogeny of begging by nestling red-winged blackbirds follows the same pattern as has been shown for energy allocation. I show that the collective begging effort of the brood determines whether the parent female broods or forages. My results indicate that a weak collective effort, characteristic of young broods, stimulates nest attentiveness. The female parent responds to an abrupt increase in brood demand midway through the nestling period by spending less time at the nest. Parents appear to derive information regarding both the nutritional and thermal requirements of the brood by assessing the strength of the collective begging

effort, and in doing so respond to the needs of the majority.

Blackbird nestlings hatch asynchronously, resulting in broods of mixed ages. Consequently first-hatched "core" (*sensu* Mock and Forbes 1995) offspring reach key developmental landmarks, like the initiation of endothermy, and sensory maturation, ahead of their later-hatched "marginal" siblings. The results presented in Chapter 2 show that, marginal offspring are able to compete effectively during the inertial stage, when the size difference between broodmates is the smallest, there are fewer competitors at a given visit, and behavioural begging contributes to the outcome of competitions for food. Additional energetic requirements associated with thermoregulation are first imposed on core nestlings midway through the nestling period (Hill and Beaver 1982, Olson 1992), which their size advantage allows them to meet. Mortality of marginal offspring increased during this stage, which I attributed to reduced intake.

The results of Chapter 3 indicate that the functions of vocal and visual signals differ. Whereas the collective vocalizations of the brood serve primarily to regulate parental foraging, visual signals are used in begging competitions between siblings. Single chicks that were muted temporarily (1h) continued to be fed at essentially the same rate as either the same individual prior to muting or sham muted nestlings in the same brood.

A secondary effect of the muting procedure was to reduce the length of time that treated nestlings were able to sustain their begging efforts. Abbreviated visual and vocal begging by the brood, following the allocation of food, stimulated an increase in parental nest attentiveness. These results are particularly interesting given that all of the broods used for the experiment were in the regulatory stage of development, and are consistent

with data presented in Chapter 1, which indicated that thermal care was provided to older broods (day 6 and 7) when the collective effort was weak.

The results presented in Chapter 4 indicate that the presence of the brown-headed cowbird modifies the begging behaviour of red-winged blackbird nestlings, particularly during the inertial stage of development. The results indicate, not only that cowbird nestlings beg for a long time (see also Dearborn 1998, Dearborn et al. 1998), but that the majority of begging occurs after food has been allocated. Consequently, in view of the results presented in Chapter 1, I suggest that the cowbird is targeting the non-feeding phase of the parental visit, in order to stimulate foraging. Given that nest attentiveness, particularly thermal care, was increased to parasitised broods, parents appear to have responded to the abbreviated begging efforts of the host majority, as opposed to the cowbird. Cowbirds were consistently more active than redwing nestlings, which may have changed the thermal environment of the brood, requiring that parents supply more thermal care.

References

Dearborn, D.C. 1998. Begging behaviour and food acquisition by brown-headed cowbird nestlings. Behav. Ecol. and Sociobiol. 43: 247-257.

Dearborn, D.C., A.D. Anders, F.R. Thompson III and J. Faaborg. 1998. Effects of cowbird parasitism on parental provisioning and nestling food acquisition and growth. Condor 100: 325-334.

Hill, R.W. and D.L. Beaver. 1982. Inertial thermostability and thermoregulation in broods of Redwing Blackbirds. Physiol. Zool. 55: 250-266.

Lazarus, J. and I.R. Inglis. 1986. Shared and unshared parental investment, parent-offspring conflict and brood size. Anim. Behav. 34: 1791-1804.

Mock, D.W. and L.S. Forbes. 1995. The evolution of parental optimism. Trends Ecol Evol 10: 130-134.

Olson, J. M. 1992. Growth, the development of endothermy, and the allocation of energy in red-winged blackbirds (*Agelaius phoeniceus*) during the nestling period. Physiol. Zool. 65: 124-152.