

# THE BEHAVIOURAL ECOLOGY OF BEGGING BY YELLOW-HEADED BLACKBIRD NESTLINGS

by

Karen Price

B.Sc. University of British Columbia 1985

M.Sc. Simon Fraser University 1990

THESIS SUBMITTED IN PARTIAL FULFILLMENT OF THE  
REQUIREMENTS FOR THE DEGREE OF  
DOCTOR OF PHILOSOPHY  
in the Department  
of  
Biological Sciences

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August 1994

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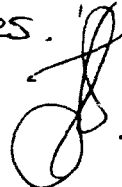
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TITLE OF THESIS:

THE BEHAVIOURAL ECOLOGY OF BEGGING BY YELLOW-HEADED  
BLACKBIRDS

Examining Committee:

Chair: Dr. F. Cooke Professor

~~Dr. R. C. Ydenberg, Associate Professor, Senior Supervisor,  
Department of Biological Sciences, S.F.U.~~

~~Dr. L. Dill, Professor  
Department of Biology, S.F.U.~~

~~Dr. C. Crawford, Professor  
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~~Dr. J. Smith, Professor  
Department of Zoology, U.B.C.~~

~~Dr. B. Roitberg, Professor  
Department of Biological Sciences, S.F.U.  
Public Examiner~~

~~Dr. B.J. Crespi, Assistant Professor  
Department of Biological Sciences, S.F.U.  
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Department of Biology, Beloit College  
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## Abstract

Many young birds vocalize loudly during parental visits to the nest. Such "begging" brings potential benefits in the form of increased provisioning, but likely carries energetic and predation costs. I investigated whether begging can signal nestling need, particularly long-term need, in yellow-headed blackbirds (*Xanthocephalus xanthocephalus*), an asynchronously-hatching species with nestlings of asymmetric ability, need and quality.

Nestlings benefitted from begging. Parents increased provisioning to broods with enhanced overall begging due to playback and, within broods, increased their feeding of deprived, noisy chicks. Nestlings competed by begging, both in the field and under laboratory conditions. They begged more when paired with a noisy (hungry) nestmate than with a silent (satiated) nestmate, and in response to brood enlargement. Given that parents respond to begging, and that chicks compete by begging, begging may not be a reliable signal of need. High quality nestlings may outcompete their needier siblings. Experiments, however, demonstrated that chicks begged according to need. When I controlled hunger, chicks begged more when paired with a large than with a small nestmate, and males and chicks in poor condition begged more than females and chicks in good condition, respectively. In yellow-headed blackbirds, smaller nestlings, males, and chicks in poor condition should value food especially highly. I found no evidence that begging transmitted signals of quality.

A genetic algorithm model examining the evolution of begging and provisioning 1) showed that parental responses to escalated begging can evolve, 2) confirmed the importance of competition between siblings, and 3) suggested that bigger chicks should be more sensitive to hunger, begging less

than smaller chicks at low hunger levels. Such leniency by big chicks could evolve under two conditions: under low starvation risk, big siblings increase their inclusive fitness benefits by reducing the risk of their sibling's death; and under high starvation and predation risks, big siblings decrease the probability of predation by reducing overall begging levels. Depending upon environmental conditions, loud begging by small chicks may be an "honest" signal of their need, or may act to "manipulate" their siblings' behaviour.

For Mom and Dad who've invested far more in me than demanded by  
 $r=0.5$ —and who didn't make me beg for it!



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## Acknowledgements

Many people assisted in the growth and development of this thesis. Ron Ydenberg invested much in me through the years and gave me the freedom to do things my way with minimal POC. Larry Dill was a tremendous help in honestly signalling things I hadn't thought about and should have, and especially in editing the thesis with his usual insight and care. At committee meetings, Jamie Smith played his role as a brood parasite well, asking "non-SFU" questions, and Charles Crawford expanded my focus beyond begging. I thank my external examiner, Ken Yasukawa, and my public examiners Bernie Roitberg and Bernie Crespi for reading the thesis carefully, asking interesting questions, making the defence fun and not letting me drown at the fledging boundary!

At SFU, many people responded to my begging to help me understand my thesis and may recognize their ideas (perhaps mutated). I thank Rob Z (who thought he didn't understand and then drew what is now Figure 1.1), Don for having good ideas about game issues, Drew and Ian for working out an interesting graphical model which I never did test, but which formed the basis for Figure 1.2, Bernie Roitberg for making me step back and really think about begging, and David Green, H el ene, Bernie Crespi, Tamara, Robin Gutsell, Felix Breden and Dave Moore for discussing various aspects of begging. Ex-Ydenbergers and my nestmates in the Association of Serious Scientists for Holistic and Organismal Landmark Ecological Studies helped me get started and supported me along the way. I thank Clive and Scott for their encouragement and Lourdes for showing us all how to enjoy life. Discussions with other beggars clarified many issues. I especially enjoyed the perspectives of Arnon Lotem, Anne Clark, Judy Stamps and David Haskell.

In Creston, I was lucky to have some wonderful assistance in the field. Yolanda Morbey assisted efficiently and capably in 1991, Jessica Roberts rose at dawn cheerfully and enjoyed (!) watching endless videos of nestlings begging in 1992, and H el ene Harvey and I had fun designing lab experiments and enjoying the marsh in 1993. I thank H el ene for her considerable input into Chapter 6. Steven Roller, Cobey Oliemans and Audrey Roburn volunteered field assistance. I thank them for their diligent work, chocolate chip cookies, and most of all for helping me keep my perspectives in order. In Creston, I also thank Brian Stushnoff, Don Grayson, Bob Houston, Anne de Jaeger and the Schallas for their help and logistical support, and Joanne, Barb, Steve, Brent, Doug, Pete, Wally and Gary for sharing feeding visits (and wine) and field talk to anchor each day.

I received financial support from an NSERC 1967 Science and Engineering Scholarship and from SFU. Ron Ydenberg's NSERC supported all field work and equipment. I thank the SFU electronics and machine shops for designing and creating my playback equipment.

I thank my parents for always encouraging my desire to learn about animals. Dad even let me take up his disk space and use his printer to produce this thesis (true PI). Finally, I thank Dave for his constant love and support. More concretely, Chapter 2 of this thesis represents our first cooperative effort. Dave coded the "blackbird model from hell", discussed all aspects of begging theory with me and helped interpret the results. I couldn't ask for a better mate.

# Introduction

In many bird species, nestlings "beg" during and between parental food deliveries. Begging consists of a range of behaviours including vocalizing, bill gaping, head rearing and wing fluttering (O'Connor 1984). Begging can benefit nestlings by increasing the amount of food parents deliver (Muller and Smith 1978, Khayutin and Dmitrieva 1979, Harris 1983, Bengtsson and Ryden 1983, Drummond and Chavelas 1989, Smith and Montgomerie 1991, Litovich and Power 1992), but it likely carries costs. All components of begging may incur an energetic cost (although recent evidence suggests that this cost is low; John McCarty, Cornell University, personal communication) and vocalizations may attract predators (Skutch 1949, Perrins 1965, Dunn 1977, Gochfeld 1978, Redondo and Castro 1992, David Haskell, Cornell University, personal communication). Given that altricial nestlings are defenceless, tasty (Orians and Janzen 1974), come in bite-sized morsels and cannot escape, predators should be selected to recognize signals of nest location. Predation costs generally fall on the entire brood (Lockie 1955, Ricklefs 1969) whereas the benefits of begging may accrue only to the begging chick. Loud vocalizations are especially paradoxical because nests are usually carefully hidden, suggesting that predation costs are important. The evolution of loud begging is thus an interesting problem in itself, and because it involves allocation decisions by parents and often rivalry between nestmates, it is also relevant in the context of parent-offspring conflict and of sibling competition.

This thesis investigates several aspects of begging. I ask 1) whether chicks benefit from begging, 2) whether they compete for food through begging, and 3) whether begging can signal long-term need in families of competing chicks of unequal ability, need and quality. Chapter 1 discusses the existing theory of begging. Begging has proven a fertile area for development of general behavioural theory, but because many models were developed to



evaluate general theory rather than to examine begging specifically, they form a confusing picture as a whole. The theory has produced few testable predictions, and has stimulated a limited number of empirical studies. Chapter 1 provides a framework for organizing the various ideas, discussing models of begging as evidence of parent-offspring conflict and models of begging as communication of information about a nestling's quality or need. Most models do not consider that chicks vary in their ability, need and quality, and cannot look at the stability of begging as a signal of need in broods of unequal chicks. Chapter 2 develops a model to address this limitation, modelling the evolution of begging and provisioning strategies in families of three (a parent and two potentially unequal offspring). I use the model to look at the effects of asymmetries in chick ability and need on begging. Because confusion about the costs of begging exists in theoretical discussions (see Chapter 1), and because there is little empirical evidence for either energetic or predation costs of begging, I also use the model to examine the effects of both types of cost on evolved begging strategy.

The remainder of the thesis uses yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) as a study system to look at the effects of chick asymmetries on begging. Yellow-headed blackbirds hatch asynchronously (Richter 1984). Hatching asynchrony (occurring when incubation begins before the final egg is laid) creates a hierarchy of chick ages or ranks and results in chicks of varying body condition (Lack 1966, O'Connor 1978, Howe 1978). Among passerines, yellow-headed blackbirds have one of the highest levels of hatching asynchrony, and seem a likely candidate with which to investigate differences in chick ability and need. Yellow-headed blackbirds nest in large colonies in marshes. Their nests are easily accessible

and amenable to field and laboratory studies. Their nestlings beg loudly and can be heard up to 1 km away (personal observation).

First, I ask if begging benefits chicks. If begging acts as communication, parents must respond under some circumstances. Several studies have shown that parents increase their visits in response to increased begging (see Chapter 1), but these studies have not explicitly related increased provisioning visits with increased food. Chapter 3 evaluates the whole-brood benefits of begging in two playback experiments. I look at changes in provisioning and in chick growth, measuring mass over the short- and long-term to see if chicks gain mass following playback, i.e., if they really benefit from increased visits. Chapter 4 evaluates the benefits of begging to individual nestlings within broods of unequal chicks by manipulating nestling hunger level. In one experiment, I satiate and deprive chicks and observe their subsequent begging and feeding, and in a second experiment, I deprive three unequal chicks in turn to look at the effect of short-term need on the begging and provisioning of chicks with differing ability, quality and long-term need. Other studies have demonstrated that parents increase their feeding to hungry chicks who beg more (see Chapter 1), but have not looked at the effect of nestling asymmetries.

Second, I ask whether nestlings compete for food by begging. Chapter 5 investigates the effects of brood size on begging in the field and under laboratory conditions, to see whether increased competition for food leads to increased begging. By bringing nestlings into a laboratory, I can control their hunger level. No other studies have looked at competition for food by begging while controlling hunger level. I also look for evidence of competition in other chapters. Parts of Chapters 4 and 6 examine whether

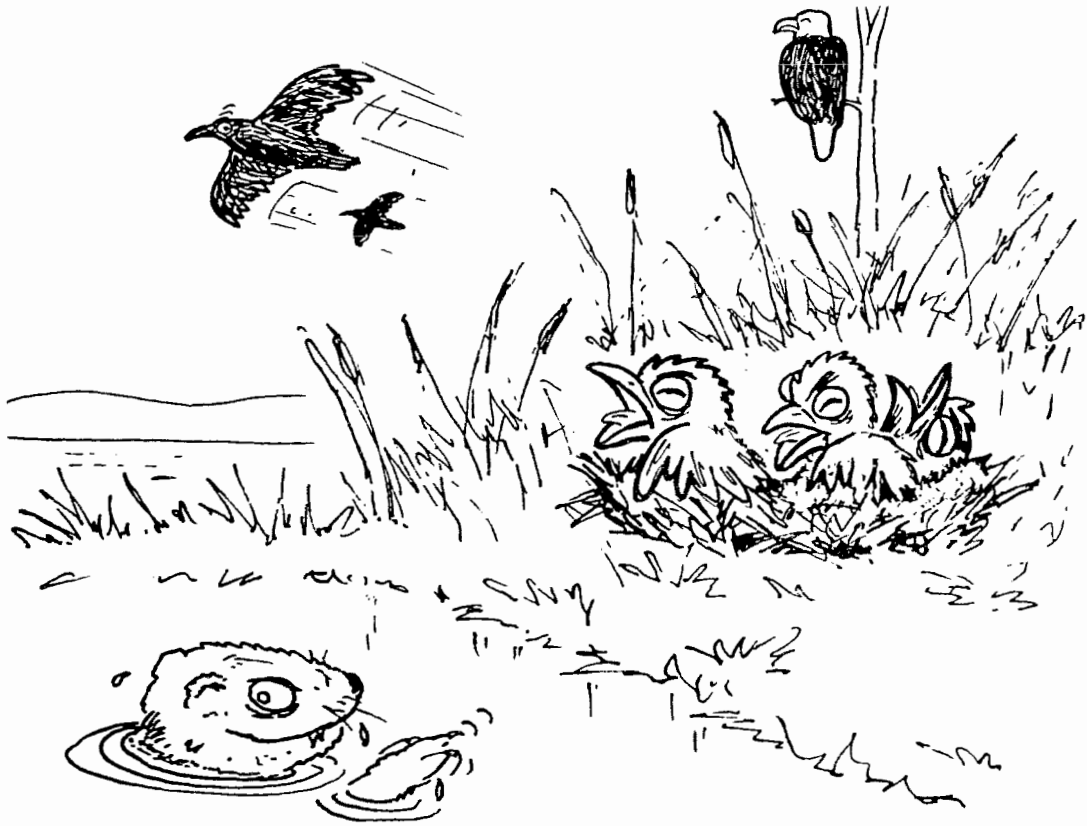
chicks change their begging level in response to changes in their nestmates' begging levels.

Finally, given that yellow-headed blackbird chicks benefit from begging and that they compete by begging, Chapter 6 asks whether begging can signal long-term need. Most models of chick need consider hunger level (short-term need) rather than long-term need. To discriminate between begging as a signal of need versus begging as a signal of quality, studies must look at long-term need (see Chapter 1). No one has yet examined this issue. Chapter 6 asks how much chicks of different long-term need beg. I use field and laboratory experiments to examine the begging behaviour of chicks of different relative size, gender and body condition to see if needy chicks beg more.

Chapter 7 summarizes my findings and points out some important questions they raise. Two appendices document my attempts to find a predation cost to begging, and evidence for a pressure to fledge quickly in yellow-headed blackbirds.

# Chapter 1

## Behavioural theories of begging



## Introduction

From roots in observational studies of nests full of squawking chicks, the study of begging has branched into three areas. People interested in parent-offspring conflict (Trivers 1974) have investigated begging as a possible manifestation of genetic conflict (chicks beg to "persuade" their parents to invest more than they "want" to); those interested in communication and signalling have debated the information content of begging (as an "honest" signal of nestling state); and those interested in sibling interactions have discussed competition and cooperation between begging nestmates. The varied approaches form a broad base for research, but the extensive literature is confusing because each group approaches the problem from a different perspective, each with associated biases and jargon. Value-laden words often obscure relationships between the different perspectives and lead to fruitless semantic disagreement. This chapter presents a framework for examining the existing theoretical and empirical literature, compares modelling efforts and describes a unified approach for examining the evolution of loud begging.

I use several terms to represent a chick's state: quality, need (short- and long-term) and competitive ability. These four terms form a minimum set for my conceptual model of the evolution of loud begging as a signal of need or value in a competitive system. I define "quality" as some measure of expected reproductive success. For nestlings, I assume that the probability of surviving until fledging is the critical component of offspring quality. While reproductive value has other components (e.g., size at fledging), survival to fledging is measurable, and is obviously important. I discuss two types of need. I define "short-term need" as nestling hunger, an aspect of state that changes rapidly. Operationally, I define hunger level as the number of pieces of food a nestling will accept (Chapter 6). I define "long-term need" as

nestling condition, an aspect of state that changes slowly, and is influenced by unchanging factors including gender and rank within a brood. Specifically, I define condition as the deviation from a gender-specific regression of mass against age (Chapter 6). Males have steeper growth trajectories than females, and have more mass to gain before fledging. For the same mass, at the same age, males have a greater long-term need for food. In species with simultaneous fledging, smaller, late-hatched nestlings also have more mass to gain before fledging, and hence have a greater long-term need. Finally, I define "competitive ability" as the relative ability to beg. This ability depends on two components: the energetic cost of begging and the total energy a chick has available to beg. A given level of begging may be less costly to a large chick (because it is bigger), and chicks in good condition may be able to bear higher costs of begging. I assume that nestling quality and competitive ability are positively correlated. The next section steps back to define begging itself, and to set begging by nestlings in a broader context.

### **What is begging?**

The term "begging" carries its own implications, and several authors have shunned its use, preferring the more general "solicitation" (Parker and Macnair 1978, Macnair and Parker 1978, Godfray 1991) or "hunger signalling" (Hussell 1988). "Begging" implies communication: a behaviour designed to ask for something from another party ("to ask for earnestly"; Funk and Wagnalls Dictionary); it is thus synonymous with "solicitation" in general usage. "Hunger signalling" implies that hunger is the sole basis for begging--an implication I do not accept. "Begging" furthermore implies an asymmetry in ability or power because it cannot be followed by action (as opposed to "territorial advertisement", which can be followed by chasing, e.g., Lair (1990),

or signalling to predators, which can be followed by flight, e.g., FitzGibbon and Fanshawe (1988)). I accept the presence of an asymmetry.

For begging to remain part of a behavioural repertoire, it must, under at least some circumstances, influence another individual's behaviour. A response requires that a witness to begging has a perceived interest in acting. Begging can transmit two messages of interest to potential responders: the beggar's quality or the beggar's need. Need and quality may be inversely correlated (i.e., individuals with low quality have high need) or related in some more complex fashion. Non-reciprocating, non-relatives may be interested only in signals of quality (for a general example, consider solicitation for mating, where potential mates are interested primarily in knowing the quality of their prospective partner). Relatives may find both types of signal useful in deciding how to allocate investment to maximize inclusive fitness (see Clutton-Brock 1991).

Parents have a particularly strong genetic interest in adjusting their provisioning to the need or quality of their offspring. Provisioning decisions would be more effective with a knowledge of offspring state, and, assuming that offspring know their current state and that parents do not, this information must be communicated explicitly. Begging as communication of state to parents, and subsequent provisioning allocation by parents, could explain why offspring signal, but this idea seems less able to explain why they should do so in such a potentially costly manner (i.e., by loud vocalizations).

Sound travels farther through complex environments faster than other modes of communication, and juveniles of many species use auditory signals in dangerous situations (e.g., Rohwer et al. 1976, Stefanski and Falls 1972, Chaiken 1992) and as locating beacons (e.g., Beecher et al. 1981, McArthur 1982). Not all species with postnatal parental care have noisy

juveniles, however. Many juvenile mammals are silent, excepting alarm calls (e.g., hares, deer). Some birds utter very quiet calls (e.g., some doves (Columbidae), Skutch 1956, 1964; single-chick Cotingidae, Harper 1986; eastern kingbirds, *Tyrannus tyrannus*, Siderius 1994; thick-billed murre, *Uria lomvia*, Grant Gilchrist, University of British Columbia, personal communication). Loud begging is thus not necessary to communicate with parents for the purpose of garnering parental care.

The observation that chicks beg and that parents respond to begging (Stamps et al. 1989, Smith and Montgomerie 1991, Litovich and Power 1992), has led many to assume (not necessarily explicitly) that begging originally evolved as a reliable signal to parents of need or quality. There is, however, considerable discussion about whether begging can remain an "honest" signal. Genetic disagreement between parents and offspring (see below), as well as sibling competition, suggests that chicks may exaggerate their needs (Stamps et al. 1978, Parker and Macnair 1979, Macnair and Parker 1979, Parker 1985). I will examine the theory of begging in two sections: models dealing with the possibility of exaggerated signals (termed parent-offspring compromise models) and models dealing with begging as honest communication of information (information models). I subdivide the latter category to deal with signals of quality and signals of need. My categories are not mutually exclusive, and I conclude by examining links between the three bodies of theory.

### **Parent-offspring compromise models**

If begging simply expressed a nestling's need for parental care, parents should respond by altering their allocation of care. However, parents and offspring are differentially related: while parents are equally related to their



offspring, offspring are related more to themselves than to their siblings (Trivers 1974). Thus, parents are selected to invest in all offspring equally (given equal quality), but each chick is selected to demand a bigger share for itself than for its siblings. This genetic conflict, and its attendant potential for phenotypic conflict, suggests that loud begging may have evolved from signal exaggeration.

Trivers' (1974) initial insight into genetic disagreement, and his graphical model, based on Hamilton's (1964) concept of inclusive fitness, generated considerable theoretical interest. Alexander (1974) challenged the notion of parent-offspring conflict, suggesting that offspring would rarely win the battle, given the size asymmetry inherent in parent-offspring interactions. A heated debate over the logic of parent-offspring conflict followed (Dawkins 1976, Alexander 1979). Once the lines were drawn, much of the discussion focussed on who wins behavioural conflicts, or more specifically on whether offspring can ever win. (For reviews of the parent-offspring conflict battle, see Litovich and Power 1992, Mock and Forbes 1992). The emphasis on finding a winner reduces a rich and complex problem to two states and obscures evolutionary interplay. While as a metaphor for parent-offspring interactions it has encouraged numerous studies, the "who wins" controversy has taken on a value of its own and has swamped discussion of the stable policies adopted by each player. Charnov (1982) pointed out that whenever offspring can influence the resources they get from parents, the genetic disagreement will be important. As an evolutionary game (Maynard Smith 1982), the decisions made by one player may alter the best policy adopted by the other. Such a scenario has no clear winner.

A plethora of models has investigated the logic of Trivers' parent-offspring conflict theory (Blick 1977, Parker and Macnair 1978, 1979, Macnair

and Parker 1978, 1979, Parker 1985, Stamps et al. 1978, Metcalf et al. 1979, Stamps and Metcalf 1980, Feldman and Eshel 1982, Harper 1986). Many of these models specifically examined begging and provisioning, using population genetic and evolutionarily stable strategy techniques to find stable combinations of begging level and parental provisioning level. One of the important findings of these mathematical models is that begging must be costly to stabilize at an absolute level (Parker and Macnair 1979, Macnair and Parker 1979, Parker et al. 1989, Metcalf et al. 1979). With costly begging, the stable begging and provisioning levels most frequently represent a compromise between the ideal interests of parents and offspring, in which parents feed at more than their optimal level in order to reduce further expensive begging by chicks (Parker 1985). This result demonstrates that offspring can, theoretically, affect the care allocation decisions of their parents (i.e., parents do not have complete control and are not always "winners"). Parker and Macnair (1978, 1979, Macnair and Parker 1978, 1979, Parker 1985) investigate variations on this theme, examining begging and provisioning within and between broods, with different mating systems and parental care systems, with different degrees of relatedness, and with parental "retaliation".

Theoretical considerations of begging behaviour incorporate costs in several ways. Some models include only energetic costs, borne solely by the noisy chick (Hussell 1988, Parker et al. 1989). Other models deal with mortality costs due to predation, that are paid by the entire brood (Macnair and Parker 1979, Harper 1986). Macnair and Parker (1979) compare energetic and mortality costs, viewing mortality costs as being shared among siblings. They calculate costs based on the mean level of begging per nest (with an infinite brood size) and conclude that shared costs reduce the relative cost increment of begging to a chick, resulting in a higher stable level of begging.

Macnair and Parker's (1979) prediction that conflict will be most intense (and that begging level will be higher) when costs fall on all members of the brood rather than on the solicitor alone has been counted as among the robust predictions of parent-offspring conflict (Clutton-Brock 1991). However, predators usually take all siblings, at least in passerines (Lockie 1955, Ricklefs 1969). Rather than spreading the risk around and hence tending to increase the level of begging, the whole-nest-risk effect may tend to reduce the level of begging via kin selection: the deaths of siblings (or of non-siblings) do not decrease the cost of the death of the beggar. If predators removed only one chick, selected at random from the brood, begging costs would be shared. A more realistic formulation would sum rather than share mortality costs (Godfray and Parker 1992), and might result in an opposite prediction (see Harper 1986).

Two general assumptions limit the generality of Parker and Macnair's series of models. First, they fix the relationship between begging and provisioning, assuming that provisioning increases with begging level. They do not examine the initial evolution of a parental response to begging and do not ask how much a nestling of a given short-term need should beg relative to its siblings. Second, their intra-brood conflict models (Parker and Macnair 1979, Macnair and Parker 1979) consider only conflict between siblings of equal competitive ability. With broods of equal chicks, Parker and Macnair's models cannot look at the effects of variation in a chick's quality, long-term need or competitive ability on begging.

A later model by Harper (1986) extends the Parker and Macnair series by allowing the begging/provisioning relationship to evolve freely, and by using a finite brood size. Harper (1986) concludes first that parents are selected to respond to begging in order to minimize the differences in investment

among their offspring (as long as offspring beg more when they need investment), and second, given the selection for parental response, that scramble competition between siblings drives up the mean begging level. His model predicts that with increasing brood size, predation costs should limit overall brood begging levels, and that energetic costs should limit individual begging levels. Importantly, Harper's model shows that, while begging may escalate, the variation around a brood's mean begging level will still contain information (i.e., will reflect the need of individual chicks). His model can be used to ask how much a nestling with a certain short-term need should beg relative to its nestmates, but, since it does not consider asymmetries in chick competitive ability or quality, it cannot be used to compare the effects of quality on begging.

Zahavi (1977) follows a rather different line of reasoning and proposes a "threat by self-destruction" hypothesis, whereby competitively subordinate chicks manipulate their parents into bringing more food by begging and thus attracting predators to the nest. Zahavi has not developed his threat hypothesis, and the models of Harper (1986) and Parker and Macnair (1979) do not support the idea that parental response to begging level is affected by predation risk (Harper 1986). Neither model, however, allows for the asymmetry in chick ability that forms the basis for Zahavi's idea. Parker and Macnair's (1979) model does demonstrate that parents may increase their investment beyond that selected for without begging, because such a response lowers the begging intensities and associated costs to the chicks.

Aside from being cited as an interesting if unlikely view, Zahavi's hypothesis has not been explicitly considered in existing models. Any evidence that a change in predation level has the potential to change chick begging behaviour would support his idea that chicks can alter the costs and

benefits under which parents make their decisions, and thereby influence parental behaviour.

Much discussion in the parent-offspring compromise literature asks if chicks can manipulate their parents, and Zahavi's (1977) blackmail hypothesis obviously implies manipulation. Manipulation can be interpreted simply as the alteration of another's actions: a definition which covers any response to communication (Krebs and Dawkins 1984, Litovich and Power 1992). Alternatively, signals can be thought of as benefitting both signaller and receiver on average, and manipulation (or non-cooperative signalling) as benefitting only one participant (Grafen 1990b, Harper 1991). Begging obviously counts as manipulation by the first definition, and may fall somewhere between a signal and manipulation by the second definition since parents and chicks may both benefit on average, yet chicks may persuade parents to respond at a higher level than is optimal for them (an evolutionary compromise). Rather than discussing whether chicks can or do manipulate their parents, a less ambiguous and more neutral approach is to discuss the decisions chicks and parents make under varying circumstances.

### **Information models**

The models discussed so far use the conflict between parents and offspring as a starting point. The remaining models in my begging framework begin with a different perspective: that begging communicates nestling quality or need to parents (i.e., it is an "honest" signal). While these models do not explicitly assume parent-offspring conflict, genotypic conflict is often embedded in their structure.

### Signals of quality

Zahavi (1975, 1977) proposes that stable signals are both costly and honest (i.e., convey accurate information). Zahavi's second hypothesis for the evolution of begging suggests that begging must be costly to convey reliable information to parents, and agrees with the findings of the parent-offspring compromise models that begging without cost is not stable. Zahavi's handicap theory (1975) can be applied to begging by chicks and suggests that signal costs should be correlated with signaller quality in some form. Grafen (1990 a, b), using population genetics and ESS approaches, modelled Zahavi's verbal models and confirmed that signals of quality are stable if they are costly and if the costs correlate with quality (i.e., costs are lower for better individuals).

Models of begging as a signal of quality (Zahavi 1975, 1977, Grafen 1990 a, b) can accommodate the existence of energetic costs of begging (because better chicks, with a higher competitive ability, are able to put more energy into begging), but cannot explain potential mortality costs, since these costs are not correlated with nestling quality. Without incorporating predation risk, models cannot account for some of the interspecific differences in begging level, for example, that cavity nesters, with lower predation rates, beg more loudly and give more locatable calls than open nesters (Kilham 1977, Fraga 1980, Redondo and Arias de Reyna 1988). Although such models do not account for all aspects of the evolution of begging, they have important implications. Any discussion of the begging levels of chicks with asymmetrical abilities must consider that when signal costs correlate with ability, begging will likely carry information about ability. The "signal of quality" hypothesis is particularly important to remember when investigating

begging as a signal of need among asymmetrical chicks, since asymmetries in ability (quality) could counteract selection towards begging as a signal of need.

### Signals of need

The final category in my review looks at begging as a signal of chick need. These models aim to determine if begging can be stable as communication of a need for parental care, and as such return to early perceptions of begging as communication between offspring and parents. Signal-of-need models fit a narrower range of circumstances than signal-of-quality models, generally requiring relatedness between the signaller and responder.

Hussell (1988) uses a supply-and-demand approach to suggest that parents respond to changes in the needs of their broods. His mechanistic model does not include relatedness between parent and offspring. From initial assumptions that parents increase feeding in response to increased begging (the supply function) and that chicks decrease begging in response to increased feeding (the demand function), Hussell models how parents might use brood begging levels as a proximate measure of food availability at a given place or time. He models broods of equal, non-competitive chicks and hence cannot examine intra-brood competitive effects.

Maynard Smith (1991) and Johnstone and Grafen (1993) model systems in which altruistic behaviour is stable under certain conditions. Godfray (1991) uses a similar model to examine the stability of begging as a signal of need in chicks. Godfray's single-chick begging scenario elegantly shows that begging can be a stable signal of chick need provided that it is costly, that the benefits of being fed increase with need, and that the parent and chick are related. Nestlings in Godfray's model decide to pay the costs (which could be

energetic or mortality: single chicks cannot spread predation costs) only if they need the benefits of parental care.

Godfray (1991) suggests an alternative explanation for the apparent increase in behavioural conflict at weaning or fledging, often cited as an example of parent-offspring conflict (see Clutton-Brock 1991). If offspring condition varies more towards independence, he reasons that solicitation should intensify, not as manipulation, but as intense communication between parents and offspring. Godfray's model is not completely isolated from parent-offspring conflict, however, since its requirement for costly begging arises directly from a tendency for signal escalation, which in turn arises from sibling competition between years (a manifestation of parent-offspring conflict). The incorporation of genetic conflict does not detract from Godfray's model, but simply illustrates that fundamental links exist between many of the approaches to begging.

Godfray's (1991) model deals with single chicks and does not obviously extend to larger broods of asymmetric nestlings. Multi-chick broods pose problems at two levels. First, large siblings may be able to monopolize food, removing the decision from the parent's arena. Second, from a parent's perspective, contemporary chicks likely vary in quality. Faced with a nest full of chicks varying in both quality and need, it is unclear how a parent should allocate food. Godfray discusses the stability of signals of nestling quality, referring to Grafen's (1990b) model, but does not suggest how his signals of need and Grafen's signals of quality might be simultaneously stable. This problem is not trivial, given that the two signals may be negatively correlated. The difficulty of the problem depends upon whether "need" represents a short-term deficit in provisioning (i.e., hunger) or a long-term need (i.e., poor condition, low size rank, or larger gender in dimorphic species). Short-term



need is less problematical: all nestlings will be hungry at times, and begging could represent a product of quality and need (i.e., a large hungry nestling could beg more than a small hungry nestling, but a large full nestling might not). Dealing with long-term need is more difficult: long-term "needy" chicks are those in poor condition and likely qualify as poor quality chicks in a model of value. Grafen's model predicts that high quality chicks should beg more, but Godfray's model predicts that needy chicks should beg more. Figure 1.1 illustrates these opposing predictions, and shows the difficulties associated with accepting begging as both a signal of long-term need and a signal of quality.

### Unifying the approaches

Existing models of begging fall into two broad groups. Parent-offspring compromise models suggest that loud begging has arisen due to escalation between competing siblings (within or between broods), and that parents respond to reduce subsequent costly begging. Information models suggest that vigorous begging can communicate offspring quality (if quality is related positively to competitive ability) and also that costly begging to relatives can signal chick need. While these two perspectives seem very different (manipulation of a parent's optimal allocation versus honest signalling of state), they can be reconciled. The escalated begging of the parent-offspring compromise models must still contain information in the variation around the mean (i.e., be *relatively* "honest", though *absolutely* "dishonest"), or else parents would no longer respond; and the honest signals of the information models must be costly, or else they would escalate infinitely due to sibling competition (arising from genotypic conflict).

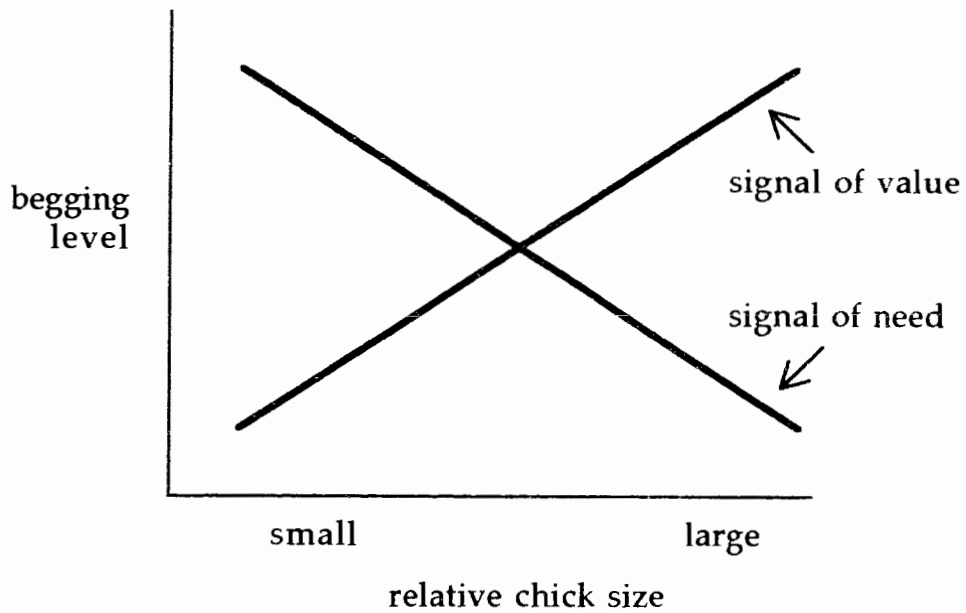


Figure 1.1. If begging signals chick quality (as suggested by Grafen 1990b), larger chicks should beg more; if begging signals chick need (as suggested by Godfray 1991), smaller chicks should beg more. It is unlikely that both signals are stable simultaneously, and is not obvious how they should be related.

It is more difficult to reconcile models of the two types of information potentially carried by begging. In deciding how to allocate food, parents should consider both offspring quality and offspring need. By feeding high quality offspring, parents are assured that their investment goes to a nestling with a good probability of surviving; by feeding offspring with high need, parents increase the probability that these chicks survive as well. The decision about whom to feed is not obvious, and may change as the nestlings grow. A unit of food may increment the probability of surviving by different amounts depending on chick age and condition, and on the environmental situation (Figure 1.2).

Begging may not be equally informative about need and quality in broods of unequal chicks. While vigorous begging may be an unfakeable signal of competitive ability (likely related to quality), it cannot be an unfakeable signal of need. In some species, stronger chicks can monopolize resources at the nest. Even in less hierarchical scramble competition, stronger chicks might beg more loudly than their needier smaller siblings. None of the above models offer insight into whether signals of need can remain stable when contemporary siblings compete. For a complete understanding of begging, models must examine signals of quality and of need together, looking at contemporary siblings varying in quality, need and competitive ability.

A set of models by Parker et al. (1989) comes closest to investigating these relationships. Parker et al. (1989) model two situations of asymmetric broods: a hierarchical case, where the largest sibling controls food allocation, and a scramble competition case, where begging level determines food allocation. In the begging model, they assume that parents feed the loudest

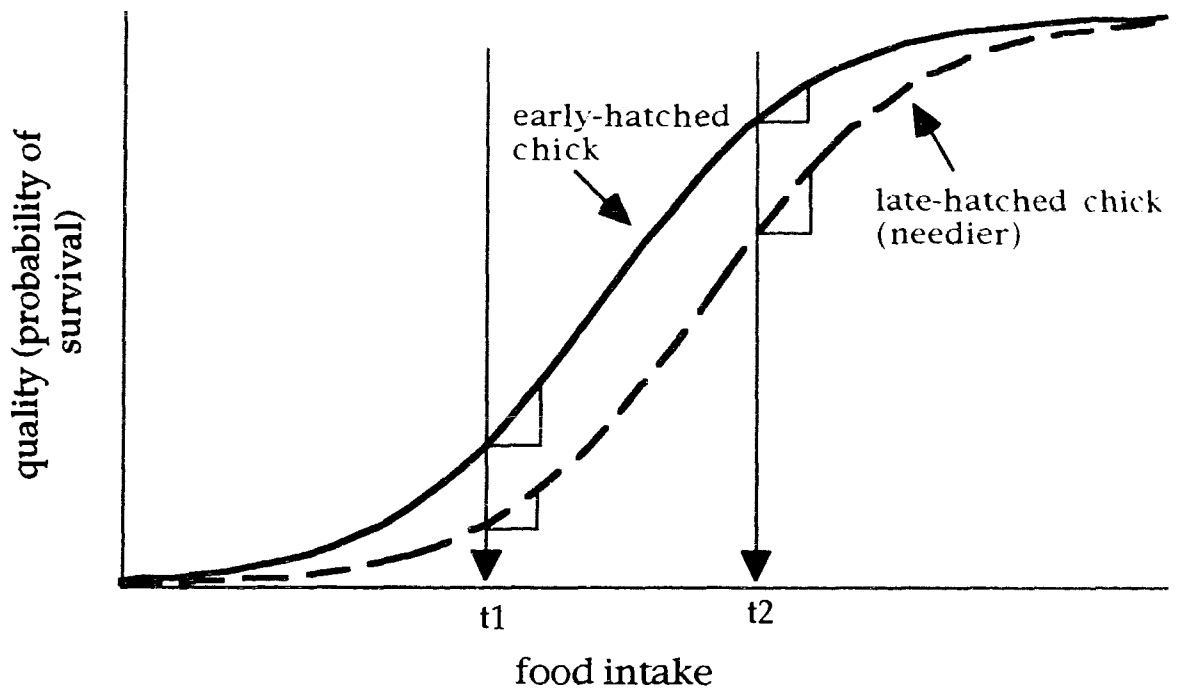


Figure 1.2. One possible trajectory of the probability of survival over time for two chicks in different conditions, given that each receives food each period. Optimal provisioning patterns for parents (maximizing their increment in potential reproductive success) change with chick age and condition. At time  $t_1$ , a parent should feed the high quality chick; at time  $t_2$ , a parent should feed the needier chick.

beggar, and that gains are proportional to the relative level of begging. Chicks differ in competitive ability, reflected in their begging effectiveness (i.e., large chicks get more for a given begging effort). The models show that the large (competitively superior) chick begs less than its smaller sibling, and that as the asymmetry increases, the difference in begging level widens. The large chick, however, always gains a higher net benefit for begging than the small chick (because with a higher competitive ability, it pays lower costs for a given level of begging). This model provides important evidence that large chicks should sometimes reduce their begging (show "lenience"), and opens a path for small chicks to signal their need.

The Parker et al. (1989) model is essentially a two person game between large and small chicks, analogous to Godfray's (1991) game between a parent and its chick. No one has yet combined these models to look at a situation with a parent and two unequal siblings to examine parental and nestling decisions simultaneously. Parents, large siblings (with high competitive ability and high quality) and small siblings each have different ideal food allocations (O'Connor 1978). Given accurate information about nestling quality, the ideal portion of food for a large nestling will be less from its parents' than from its own perspective (though the parent may still favour this valuable chick), and even less from its smaller sibling's perspective.

In summary, begging theory suggests that chicks beg to alter food allocation, either by providing information to parents about their quality or need, or by changing the context of decisions about provisioning (made by parents) or about begging (made by siblings). Information about each offspring's quality and need will certainly aid parents in allocating food in their ideal manner. Because this allocation pattern will not necessarily be the ideal pattern for chicks, offspring may change the context of decisions in at

least two ways. First, large chicks may monopolize resources (e.g., "hole-blocking" in cavity-nesting species; Litovich and Power 1992). Second, small chicks (who cannot monopolize resources) may be able to change the decision environment of their parents (or larger siblings) by increasing the perceived probability of predation (Zahavi 1977). An increase in predation risk may decrease the relative value of food to the large sibling, thus increasing its leniency to its junior. Figure 1.3 summarizes four means of increasing allocation by begging.

### **The empirical evidence**

Theoretical discussions of begging behaviour moved forward without waiting for confirmation of some of their basic assumptions (Stamps et al. 1989). This single-minded development resulted in models that ignored important biological details, such as the observation that siblings are rarely equal in value or ability, and that predators generally take entire broods. In this section, I outline some of the empirical findings about begging and provisioning in birds, and point out where evidence is lacking.

### **Tests of the models**

Little empirical effort has been spent in looking at begging as parent-offspring conflict, although much theoretical effort was applied to this idea. Parent-offspring conflict, while widely believed theoretically, has rarely been tested (see discussions in Mock and Forbes 1992, Clutton-Brock 1991), in part because of difficulties in calculating optimal investment levels from a parent's and offspring's perspective and in measuring the costs to offspring of increased soliciting and the costs to parents of retaliating (e.g., Stamps et al. 1985).

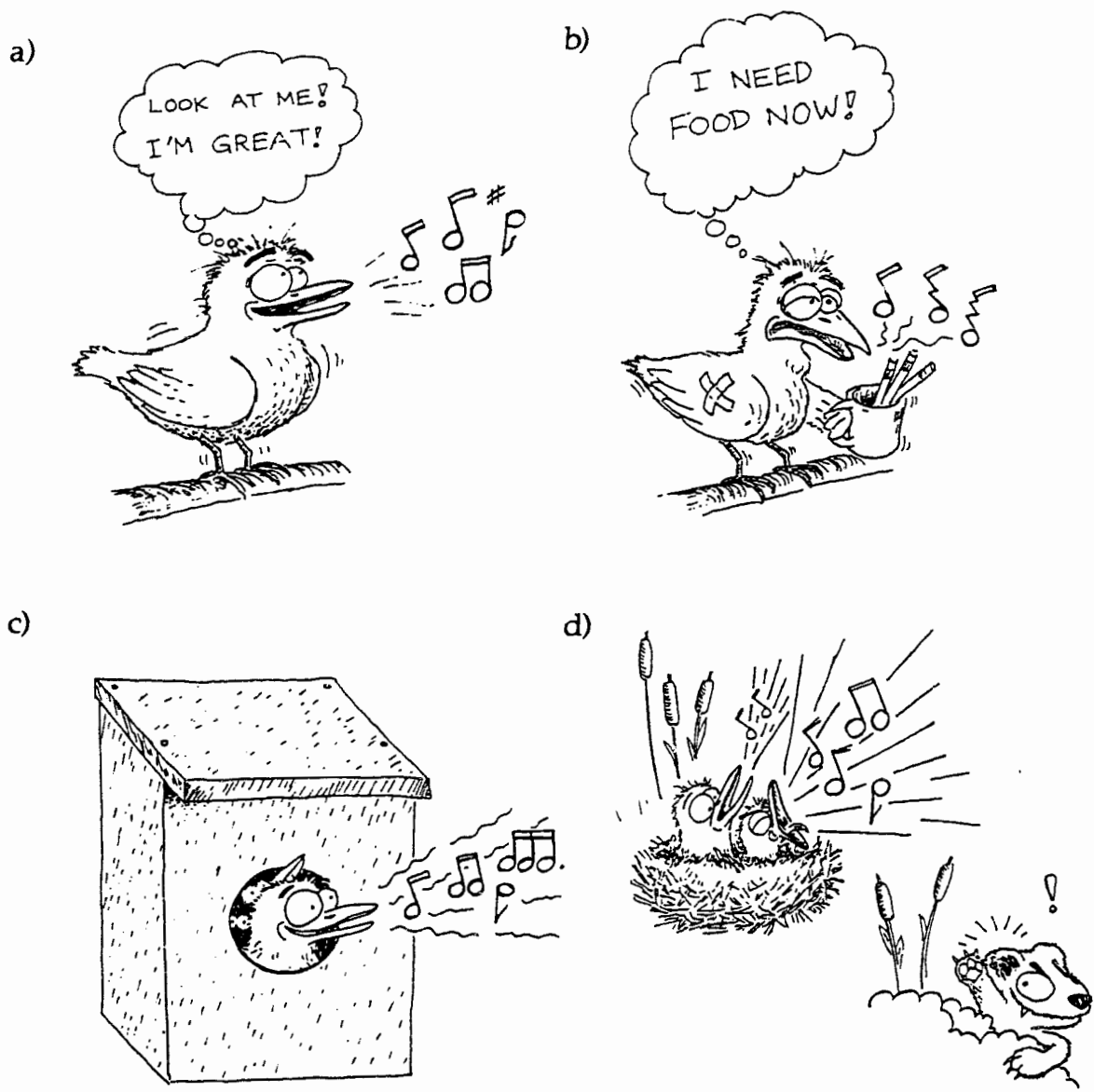


Figure 1.3. Representation of four means of increasing provisioning. a) Begging as a signal of quality. b) Begging as a signal of need. c) Hole-blocking by chicks with high ability. d) Begging by needy chicks increasing the risk of predation.

Litovich and Power (1992) aimed to test explicitly whether parent-offspring conflict is expressed by begging in starlings (*Sturnus vulgaris*). They concluded that chicks cannot manipulate the allocation of food, and that parents always win the conflict by feeding the "best-beggar" or "hole-blocker". They did not consider that large chicks, as well as small chicks, may have a different optimal investment pattern from their parents. Using their definition, parent starlings may not be "winning": large chicks may have manipulated the context of their parent's decision to their own advantage. Parents do not necessarily do best by feeding the chick with the highest competitive ability, but may prefer to also allocate food to less competitive, needier offspring (e.g., Figure 1.2). Litovich and Power's (1992) conclusions are not as unambiguous as they claim.

Another experimental study (Smith and Montgomerie 1991) explicitly tested the prediction from Harper's (1986) model that scramble competition should drive up begging levels. Smith and Montgomerie (1991) deprived individual robin (*Turdus migratorius*) chicks of food, and returned them to their nests. Their undeprived nestmates increased their begging, apparently in response to the increased begging of the deprived chick. This experiment shows that begging may signal short-term chick need, and that nestmates compete by begging.

### Benefits of begging

Studies covering several orders show that whole-brood begging levels can affect the provisioning of a nest (Table 1.1). These experiments examined the effects of begging over short time periods (from 2 min to a day), and did not look at either the parental costs of increased visit rate, or at chick benefits from the increased feeding (although the muting and deafening experiments



Table 1.1.  
Experimental studies of provisioning in relation to whole-brood  
begging levels.

change to perceived brood begging	manipulation	provisioning response	species	source
increased	begging playback	increased visits*	<i>Poephila guttata</i>	Muller and Smith 1978
increased	begging playback	increased visits	<i>Parus major</i>	Khayutin and Dmetrieva 1979
increased	playback/deprivation	increased visits	<i>Parus major</i>	Bengtsson and Ryden 1983
increased	playback	increased visits	<i>Fratercula arctica</i>	Harris 1983
increased	deprivation	increased visits	<i>Agelaius phoeniceus</i>	Whittingham and Robertson 1993
decreased	muting	males fed **		
decreased	sating/intoxicating	decreased visits	<i>Larus delawarensis</i>	Miller and Conover 1979
decreased	deafening parents	decreased visits	<i>Sturnus vulgaris</i>	Litovich and Power 1992
		decreased visits	<i>Streptopelia risoria</i>	Nottebohm and Nottebohm 1971

\* directly following 2 min playback

\*\* at secondary broods

showed costs of decreased feeding via starvation). Parents visiting frequently may bring less or lower quality food (e.g. pied flycatchers *Ficedula hypoleuca*, Lifjeld 1988; starlings *Sturnus vulgaris*, Tinbergen 1981), and chicks may not benefit. Stamps et al. (1989) looked at the relationship between long-term begging and feeding rates in budgerigars (*Melopsittacus undulatus*) and found that, although broods that begged more received more food over 12 days, this correlation stemmed primarily from an effect of brood sex ratio (where female-biased broods both begged more and were fed more).

Parents also respond to within-brood begging levels. Several observational and experimental studies have found a positive correlation between individual begging level and provisioning (Table 1.2). The experimental studies indicate that changes in a chick's begging level can lead to changes in its allocation of food, but do not look at the effects of chick ability or value on begging.

To assess the benefits of begging to individual chicks, it is necessary to see how asymmetries in quality or ability affect begging and provisioning patterns. Studies of asynchronously-hatching species have found that late-hatched chicks generally beg more than their large siblings, either absolutely, or for the same amount of food (Khayutin and Dmitrieva 1977, Ryden and Bengtsson 1980, Bengtsson and Ryden 1981, Fujioka 1985, Greig-Smith 1985, Drummond et al. 1986, McGillivray and Levenson 1986, Stamps et al. 1989), but that they may be fed less (Lockie 1955, Royama 1966, Ryden and Bengtsson 1980, Bengtsson and Ryden 1981, Richter 1984, Fujioka 1985, Greig-Smith 1985, Drummond et al. 1986, Litovich and Power 1992; although smaller budgerigars were fed more by their mothers, and received more food following the fledging of their larger siblings, Stamps et al. 1985, Stamps et al. 1989). These results pose a paradox: how can small chicks beg more and

Table 1.2.  
Studies of provisioning in relation to within-brood begging levels.

type of study	relationship between feeding and begging	species	source
observation	positive	<i>Ficedula hypoleuca</i>	Gottlander 1987
observation	positive	<i>Melopsittacus undulatus</i>	Stamps et al. 1989
observation/ deprivation	positive	<i>Sula neboxii</i>	Drummond and Chavelas 1989
observation*	positive	<i>Agelaius phoeniceus</i>	Teather 1992
observation	positive**	<i>Pica pica</i>	Redondo and Castro 1993
deprivation	positive	<i>Turdus migratorius</i>	Smith and Montgomerie 1991
intoxication	positive	<i>Sturnus vulgaris</i>	Litovich and Power 1992

\* created broods of two males and two females

\*\* mass gain and begging

receive less food when food increases with increased begging? The relationship between begging and provisioning is obviously not as straightforward as assumed by various begging models. Empirical work will have to discriminate between provisioning as affected by begging and as affected by chick quality. Perhaps parents use other aspects of begging along with vocalizations in deciding how to allocate food. Chick position in the nest seems an important predictor of allocation in some species (e.g., Ryden and Bengtsson 1980, Reed 1981, Greig-Smith 1985, Gottlander 1987). While small chicks can vocalize, they likely cannot remove their large siblings from good positions.

#### Costs of begging

Evidence for energetic or predation costs to begging is sparse. John McCarty (Cornell University, personal communication) found that begging chicks use very little energy in vocalizing. While anecdotal support for a predation costs exists for several species (Skutch 1949, Perrins 1965, Kilham 1977, Gochfeld 1978), it has proven a difficult cost to demonstrate convincingly. Redondo and Castro (1992) found that larger broods of magpies were depredated more frequently, but did not manipulate brood size, and were unable to discount effects of parental quality or other complicating factors. David Haskell (Cornell University, personal communication) has recently shown that predators find more mock nests with associated played-back begging calls than without, provided that the nests are on the ground. He found no effect of playback for nests in trees. Haskell used only one study area, focussing on one type of predator (corvids). Other areas with different predators may show an effect in other types of nest. Yasukawa (1989) provided evidence that marsh predators (mink, *Mustela vison*) can and do

cue to sound by playing back a nest-associated call given by female red-winged blackbirds at mock nests. Mink found nests with played-back calls faster than nests without.

Chicks are fed frequently throughout the nesting period, but are not often depredated (never more than once). Investigations of begging costs are therefore more difficult logistically than those of begging benefits. More effort must be spent on trying to determine the importance of predation costs to begging.

### Who should beg?

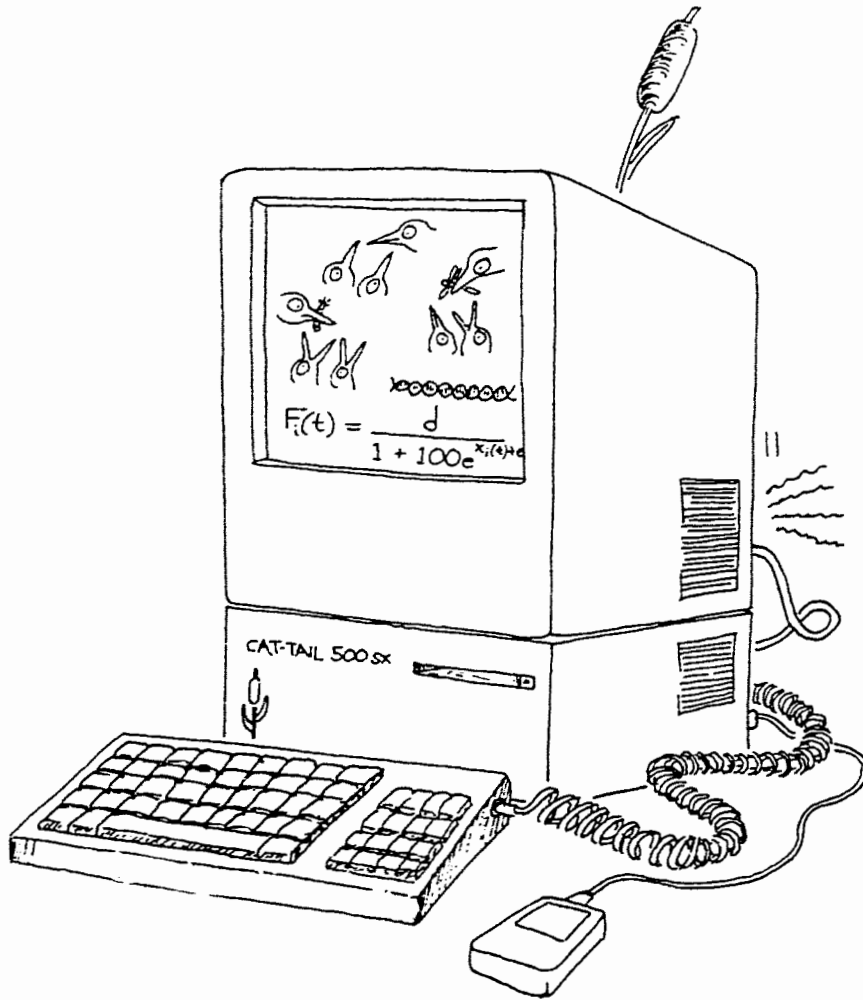
Assuming that begging has associated benefits (for which there is reasonable evidence) and costs (for which there is little evidence), it is interesting to ask how these costs and benefits should affect the begging levels of chicks of differing needs and values. Hungry chicks beg more (Henderson 1975, Bengtsson and Ryden 1983, Drummond and Chavelas 1989, Smith and Montgomerie 1991, Redondo and Castro 1993), hence begging can signal short-term need. Parents should respond to increases in the hunger level of their offspring, and, indeed they seem to (Smith and Montgomerie 1991).

A more interesting question asks how begging varies with long-term need. Hunger level changes between parental visits, while aspects of long-term need change slowly or remain static. Chicks in poor body condition and near starvation need more food to survive and fledge than their healthy siblings (e.g. Richter 1984, Litovich and Power 1992). In dimorphic species, the faster-growing sex, with higher energy demands, needs more food (Fiala and Congdon 1983, Teather 1987, Teather and Weatherhead 1988). In species with a pressure to fledge quickly, later-hatched nestlings benefit more from food. Food is more valuable to these various classes of needy chicks, therefore, they

should weigh the costs and benefits of begging differently, and should beg more than their less needy siblings. While several studies show that smaller chicks beg more (discussed above), these studies do not control for hunger level, and small chicks may just be hungrier. Controlled experiments are necessary to tease apart begging as a signal of long-term versus short-term need.

## Chapter 2

### The evolution of state-dependent begging



A version of this chapter will be submitted for publication co-authored with  
Dave Daust

## Introduction

The begging behaviour of nestlings has long been a favourite topic for modelling exercises, but has led to little in the way of testable predictions. Most investigations have used begging to probe general theory and have not focussed on begging itself (e.g., Parker and Macnair 1979, Macnair and Parker 1979, Stamps et al. 1978, Godfray 1991, Grafen 1990b). Rather than exploring the behavioural complexities of begging, research has been polarized into searches for honest vs. dishonest communication, and into discussions of winners vs. losers in parent-offspring conflicts (Chapter 1). A focus on the dynamics of begging leads away from false dichotomies and leads to testable questions about the function of begging.

Most models of begging do not explicitly examine competition between siblings, assuming either an infinite brood size (e.g., Macnair and Parker 1979, Parker and Macnair 1979, Parker 1985; cf. Chapter 1) or broods of one (e.g., Godfray 1991, Hussell 1988). Even fewer consider the importance of competition between nestmates of differing size and competitive ability (but see Parker et al. 1989). Interactions between siblings are undoubtedly important: if a large sibling can out-compete its smaller nestmate, food allocation may reflect nestmate competition rather than parental choice. Investigations of begging as conveying information about chick need must therefore also consider sibling interactions. If siblings compete for food by begging, and if begging ability correlates with some aspect of chick quality (e.g., size), begging as an "honest" signal of need may be unstable, and may change into begging as an "honest" signal of quality (and hence a "dishonest" signal of need). While signals about both need and quality are potentially useful to a parent deciding to whom to allocate food, both may not be available.



Investigations into the evolution of begging as an honest signal of need should thus consider at least three individuals: a parent and two unequal nestmates. Published models, however, consist either of a parent and brood of equal chicks, or of nestmates competing without a parent.

Many begging models start with assumptions that begging increases with hunger level and that parents feed chicks who beg most (e.g., Parker and Macnair 1979, Macnair and Parker 1979, Hussell 1988, Parker et al. 1989). These models do not allow free evolution of chick or parent strategies, and represent chick state solely by hunger level. Harper (1986) develops a model in which begging evolves (given a parental response) and in which parental response evolves (given that begging carries a message), but does not examine the evolution of the signal and response in tandem. To examine the origin of begging, both strategies must be able to evolve freely. Begging may represent aspects of chick state other than hunger level (Chapter 6); without looking beyond effects of hunger, it is not possible to examine the evolution of begging as a signal of long-term need.

Models of begging usually contain costs (either energetic or, more rarely, predation), and several authors conclude that cost-free begging is evolutionarily unstable (Parker et al. 1989, Macnair and Parker 1979, Stamps et al. 1978). Few models compare begging patterns over a range of costs and none look at the effects of different types of cost on broods of competitively unequal nestlings. Macnair and Parker (1979) and Harper (1986) compare the effects of predation and of energetic costs, but Macnair and Parker conclude that individual begging levels should be higher with predation costs, while Harper (1986) concludes that they should be higher with energetic costs. The differences are due to their different assumptions about "shared" costs (see Chapter 1).

This chapter describes a model in which the state-dependent begging strategies of chicks and the food allocation strategy of their parent can both evolve. I compare the effects of energetic and predation costs on begging, and compare begging by equal and unequal nestmates. I use the model to ask several questions. First, can begging carry information in an evolutionarily stable manner without costs? Second, how do asymmetries in nestmate abilities affect stable begging effort? Third, how do different types and levels of costs affect begging? I also use the model to propose some testable predictions about how much chicks should beg under different conditions.

### **The model**

I embed simulations of begging and provisioning within the framework of a genetic algorithm (Goldberg 1989) in a two-tiered model. The genetic algorithm creates begging and provisioning strategies in families with two chicks and one parent by combining "chromosomes" composed of "genes" (representing particular strategic options). I test the performance of these strategies in a simulation, where chicks beg according to their state, parents allocate food, and chicks either grow to fledging, starve or are eaten by predators. Successful strategies from the simulation re-enter the genetic algorithm and the process is repeated.

I examine two types of models: in "parent-fixed" models, I fix the parental strategy, assuming that parents feed the noisiest beggar, and look for successful chick strategies; and in "parent-evolves" models, I allow provisioning strategies to evolve in tandem with begging strategies. Where appropriate, I choose model parameters to represent begging by yellow-headed blackbird nestlings. For simplicity, I refer to "chicks" and "parents" rather than to sets of strategies.

### The genetic algorithm

Genetic algorithms were developed as a procedure to help optimize engineering design (Goldberg 1989) and have only recently been adopted by behavioural ecologists in the search for successful strategy sets (Sumida et al. 1990). Genetic algorithms are based on biological selection principles, and include analogues of mating, cross-over and mutation on "chromosomes" (see Goldberg 1989 for a readable introduction). As well as having an intuitive appeal for biologists, they are amenable to behavioural questions, including investigations of begging.

Begging chicks are related to their nestmates and to their provisioning parent. Incorporating inclusive fitness into models of sibling behaviour can create difficulties due to possible non-additivity of costs and benefits (Queller 1985). Within a genetic algorithm, individuals are related explicitly and there is no need to calculate inclusive fitness.

Begging level depends on chick state (e.g., hunger, body condition, age etc.; see Chapter 6), and hence models need to allow for state-dependence. Begging should also be modelled as a game between parents and their offspring and between siblings, since the strategy adopted by one will affect those adopted by other family members. State-dependent games are notoriously difficult to solve (Mangel and Clark 1988), particularly when they include more than two players. The minimum set required to examine the evolution of begging includes three players: one parent and two nestmates. Within a genetic algorithm, chick strategies can play against one another—the game aspect is implicit. The explicit relatedness and implicit game aspect allowed in a genetic algorithm considerably simplify the modelling of begging behaviour.

## The chromosome

I model begging behaviour as a state-dependent strategy coded on a "chromosome". Each chromosome contains five "genes", each of which consists of five binary subunits (in the form of a 0/1 bit-string), and codes for a "phenotype-limited" strategy (Parker 1982). Two of the genes determine begging behaviour if an individual becomes the a chick; two determine its begging if it becomes the b chick (status randomly assigned); and the final gene describes a bird's provisioning behaviour if it survives to become a parent (Figure 2.1).

The begging genes determine how much a chick will beg when in a set maximum state ( $X_{\max}$ ), and how much it will beg at a set minimum ( $X_{\min}$ ). Both begging levels are standardized to vary between zero and one in 32 intervals (i.e.,  $2^5$ ). I extrapolate linearly between these points to calculate a chick's begging effort for any given state (Figure 2.2). In the "parent-evolves" models, the parental gene determines the probability that a parent feeds the noisiest chick, and is also standardized between zero and one in 32 increments. A zero gene causes parents to always feed the quietest chick, one causes feeding of the loudest chick, and 0.5 causes random feeding in relation to relative begging. For simplicity, I refer only to begging loudness in the model, but the encoded behaviour could as easily refer to any other aspect of begging.

## Reproduction

To begin the model, all 25 subunits (20 in "parent-fixed" models) are set randomly on each of an initial population of 80 chromosomes. Each chromosome can be considered equivalent to a haploid parent. These produce offspring chromosomes by pairing up (randomly) and crossing over

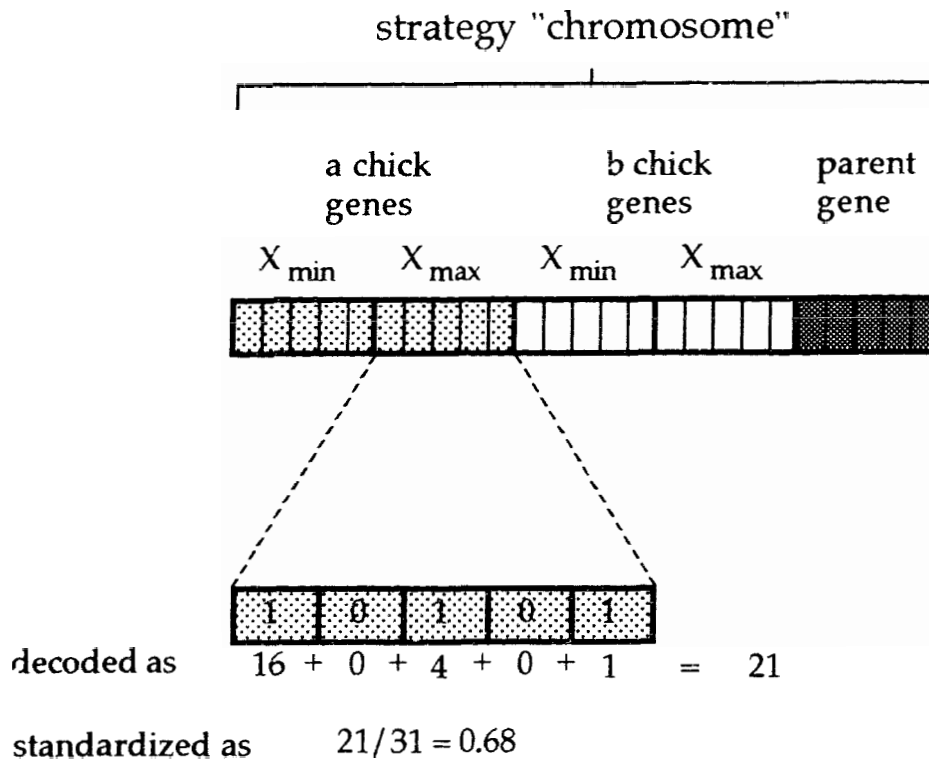


Figure 2.1. Representation of a chromosome with five genes which code for a chick's begging strategy (when hungry or satiated as either an a or b chick), and its provisioning strategy if it survives to reproduce. Each gene consists of a string of five binary subunits which is decoded and standardized to give strategies.

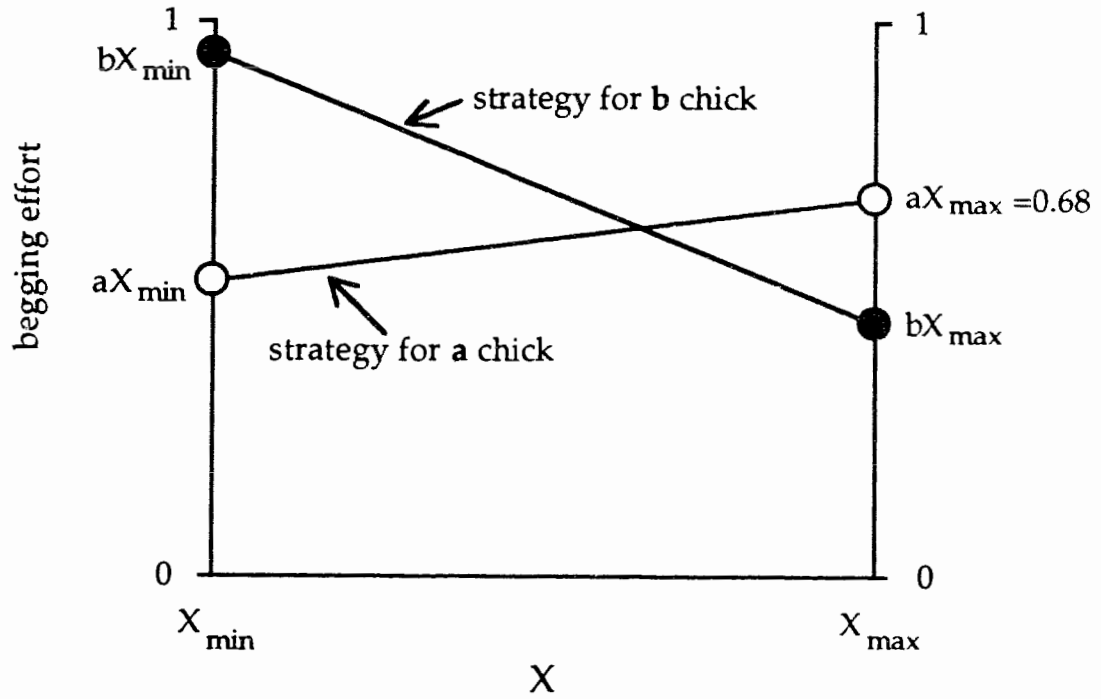


Figure 2.2. An example of begging strategy as a function of chick state. Begging effort is interpolated between the extreme strategies encoded on genes. The value for  $aX_{\max}$  is taken from the chromosome in Figure 2.1.

at a single random location to recombine the genes of each parent. The model randomly selects one of the two chromosomes produced by this technique and discards the other. The parental chromosomes cross over randomly once more and produce another pair of offspring, again retaining only one for use in the model (Figure 2.3). By mating parents twice and choosing one offspring from each cross-over, I guarantee that the two nestmates selected are related, on average, by  $r = 0.5$  (i.e., full siblings). Retaining both chromosomes produced by one cross-over produces chicks who are related to their parent by an average of 0.5, but unrelated to each other ( $r = 0$ ). I create identical ( $r = 1$ ) chicks by duplicating one chromosome from a single cross-over. The model creates two new chicks from each of 40 randomly chosen pairs of parents so that 40 nests each have two chicks. One randomly selected parent provisions the chicks in its nest. Parents are selected for mating with replacement (i.e., each parent can produce more than one family, and some may not reproduce).

During crossing over and recombination, each subunit mutates (changes from a 0 to 1, or 1 to 0, with a low probability ( $p = 0.01$  or  $0.02$ )). Mutation adds variation to each generation. I determined an appropriate mutation rate first by trial and error in a simple version of the begging model. With mutation rate set too high, strategies do not converge; set too low, they easily become trapped on local optima. I used a lower mutation rate in "parent-evolves" models, since these models have 25 rather than 20 subunits. With a mutation rate of 0.01, the probability that any chromosome will be changed in "parent-fixed" models (i.e., with 20 subunits) is  $1 - (0.99)^{20} = 0.18$ .

The 40 families (each with two nestmates and a provisioning parent) enter the simulation stage of the model. Each nestling begs and is fed at the level given by the appropriate genes, and either lives or dies. I consider

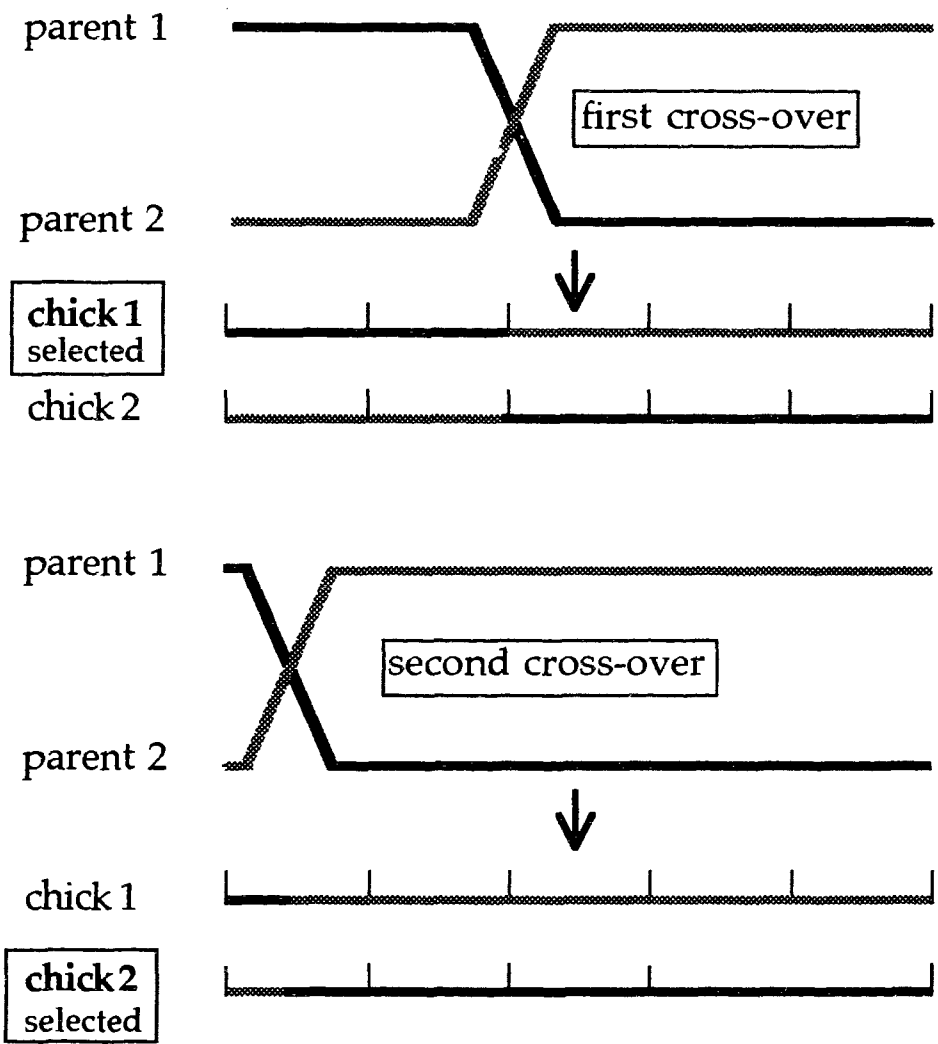


Figure 2.3. Representation of crossing over and recombination of two parental chromosomes to produce two chick chromosomes. Only one chick is used from the two produced by each cross-over. Parents are chosen randomly to be the first and second parent.



chicks alive at the end of a simulation to have fledged. Their chromosomes enter the next generation as parents. Hence, the fitness function is binary (one or zero at the completion of a simulation). As chicks die within the simulation, randomly selected parents pair again to produce replacements (to keep a constant population size). Simulations run until there is a full complement of 80 survivors to act as parents in the next generation. For simplicity, I assume no relationship between state at fledging and future reproductive success (an unknown factor in yellow-headed blackbirds). The genetic algorithm runs for 500 generations of chicks.

### Begging Simulation

In each of 500 generations, at least 80 chicks (40 pairs of nestmates) experience a nestling period composed of 100 periods ( $t=1,2,3,\dots,100$ ) of begging and feeding. Chicks beg (i.e., make noise) as a function of their state according to the strategy set by their genes. I define the state of the  $i^{\text{th}}$  chick in each period  $t$  as the difference between its mass,  $m_i(t)$ , and the expected mass,  $\bar{m}(t)$ , where

$$\bar{m}(t) = G(t),$$

and represents the average growth in the population (Figure 2.4). I assume linear growth for simplicity. State is therefore calculated as

$$X_i(t) = m_i(t) - \bar{m}(t) \quad \{1\}$$

where

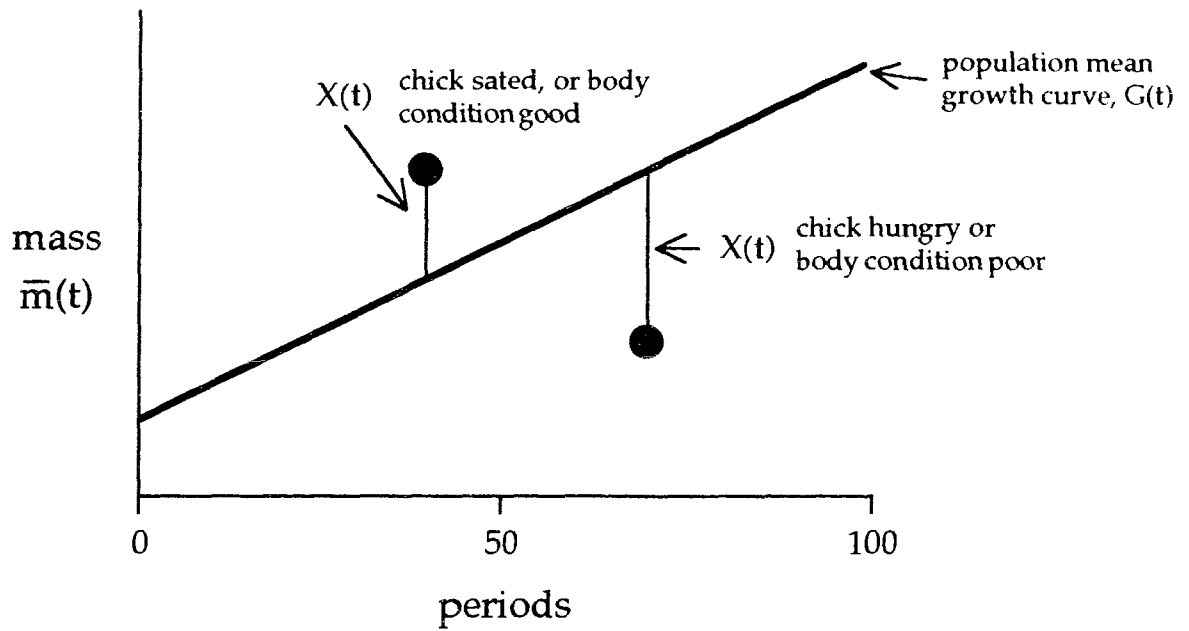


Figure 2.4. Chick mass against time within the simulation model, illustrating the calculation of chick state  $X(t)$  as the deviation of a chick's mass from the expected population mean mass.

$$X_{\min} \leq X_i(t) \leq X_{\max}, \text{ and } X_{\min} = -X_{\max}.$$

At  $X_i(t) = X_{\min}$  chicks starve; at  $X_i(t) = X_{\max}$  chicks satiate. Each chick's chromosome (i.e., strategy) dictates its begging level at  $X_{\min}$  and  $X_{\max}$  (Figure 2.2). For intermediate states, I interpolate linearly between the extremes. In newly-hatched nestlings,  $X_i(0) = 0$  (i.e., no deviation from the set growth curve).

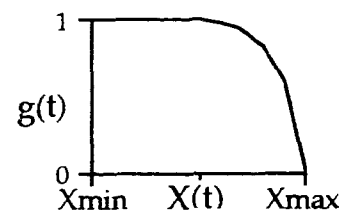
Following begging by each chick (an a and a b chick), the parent decides where to allocate the single unit of food it delivers in that period. The parent feeds the loudest beggar with probability  $p = 1$  in "parent-fixed" models, and  $0 \leq p \leq 1$  in "parent-evolves" models. Hence, each nestling may or may not be fed the single unit of food during each time period.

I assume that the total food quantity delivered does not vary over the nestling period, and that it provides a constant level barely sufficient to raise two chicks to fledging (i.e., I examine intra-brood rather than inter-brood conflict; Parker 1985). Total food quantity can be varied as a model parameter to examine the effects of harsher or easier environments, but these cases seem less interesting for the questions I address here.

Chick mass increases with food provisioned and decreases by a constant maintenance cost ( $c$ ) each period. Unfed chicks therefore lose mass. As chicks approach satiation, the value of food decreases so that the mass increment,  $g_i(t)$  of a chick fed the unit of food depends on  $X_i(t)$ :

$$g_i(t) = 1 - d / (1 + 100 \exp(-X_i(t) + e)),$$

{2}



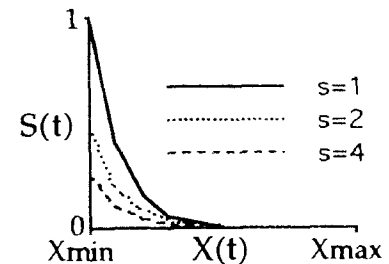
where  $d$  and  $e$  are shape parameters. I assume that chicks have a limited capacity for food and use equation {2} to set this maximum capacity. A chick's mass in the next period ( $t + 1$ ) is

$$m_i(t + 1) = m_i(t) + g_i(t) - c.$$

I calculate chick state (which can be interpreted as either body condition or hunger level) by using equation {1}.

Chicks starve in each period with a state-dependent probability,  $S_i(t)$  that increases to 1 at  $X_i(t) = X_{\min}$ :

$$S_i(t) = [d / (1 + 100 \exp^{(X_i(t) + e)})] / s, \quad \{3\}$$



subject to  $X_i(t) < 0$ , where  $d$  and  $e$  are shape parameters, and  $s$  serves as a parameter to decrease starvation risk to chicks with  $X_i(t) > X_{\min}$ . I chose the exponential form of this curve by comparing the probability of starvation and chick condition (deviation from a regression of mass on tarsus for the whole population) in 168 yellow-headed blackbird nestlings. I use  $s = 1$  to simulate high starvation; most model trials use moderate ( $s = 2$ ) or low starvation levels ( $s = 4$ ).

The surviving chick does not starve following the death of its nestmate. I used two different assumptions to look at single chick survival until fledging. In the first, I assume that single chicks always fledge without having to beg, and end the simulation following the death of one nestmate (the "home-free" assumption). In the second, I assume that the single chick continues to beg at the loudness given by its encoded strategy until it fledges after 100 periods. Singletons are therefore only susceptible to predation under

the second assumption. In general, starvation kills only one chick from any nest (rarely, both chicks starve simultaneously). This assumption seems reasonable for most brood-reducing species, including yellow-headed blackbirds (personal observation), although whole broods sometimes starve.

### Sibling asymmetry

I incorporate sibling asymmetries in ability into the model by assuming that **a** chicks are more effective beggars than **b** chicks (following Parker et al. 1989). For a given begging effort (the value coded on each chick's chromosome), **a** chicks beg more loudly than their nestmate (**a** level = 1.5 × **a** effort, whereas **b** level = **b** effort). This assumption seems reasonable if begging ability increases with chick size or age, which is the basic asymmetry observed in natural yellow-headed blackbird nests (see Chapter 6, Appendix 2)

I manipulate chick long-term need by giving **b** chicks a relatively higher risk of starvation (by shifting the starvation risk curve). For a given state, **b** chicks, with a higher risk of starvation, should be prepared to beg at a higher level because the benefits of food are relatively greater for them. From a parent's perspective, an increase in **b**'s starvation risk can be interpreted as an increase in **a**'s relative value. I create asymmetric broods of two types by manipulating need and ability simultaneously: a large nestling has a higher ability and a lower need than its small sibling; and a male nestling has a higher ability and a higher need than its female sibling.

### Costs of begging

The simulation includes both energetic and predation costs. I assume that energetic costs are a simple linear function of begging effort: as well as paying the fixed cost of maintenance in each time period, chicks lose mass

due to begging. I increase the quantity of food available in runs with energetic costs since chicks must pay this added cost. Energetic costs reflect begging strategy, and hence change with chick state, removing the possibility of setting a food quantity just sufficient for both chicks to survive. The model provides sufficient food for both to survive if both chicks beg at the mean effort (0.5), and hence pay mean energetic costs.

I incorporate the probability of predation,  $P_i(t)$ , as a function of the total begging level by both chicks. In most cases, I use a linear function:

$$P_i(t) = k (a \text{ level} + b \text{ level}), \quad \{4\}$$

where  $k$  is the strength of predation risk ( $k \geq 0$ ). Predation kills both chicks. Surviving families keep begging and provisioning until the chicks fledge after 100 begging episodes. The genes of survivors pass on to the next generation of simulations via the genetic algorithm portion of the model. Simulations within a generation run until 80 chicks have fledged. When starvation or predation risks are high, many more than 40 families undergo the simulation.

### **Model output**

Table 2.1 lists the various parameters and variables of the model and the ranges of values used in the model. The raw model output shows the evolution of begging strategies over 500 generations. Although it is not possible to determine the success of any particular mutant strategy in a population, and hence to search explicitly for evolutionarily stable strategies (Maynard Smith 1982), strategy sets compete and evolve in the model. Variation arises randomly via mutation and recombination throughout the

Table 2.1.

Parameters and variables used in the simulation and genetic algorithm and their range of values.

parameter or variable	description	range of values
t	period in simulation	1,2,3,...,100
$X_i(t)$	chick state	$X_{\min} \dots 0 \dots X_{\max}$
$\bar{m}(t)$	mean mass at t	0.5 x t
$m_i(t)$	chick mass	0...55
$g_i(t)$	chick growth	equation 2
$S_i(t)$	risk of starvation	equation 3
$P_i(t)$	risk of predation	equation 4
c	maintenance cost	0.5
d	steepness parameter	5.9
e	shift parameter	2
k	predation risk parameter	0, 0.005, 0.01, 0.02, 0.04
r	relatedness	0, 0.5, 1
s	starvation risk parameter	1, 2, 4, 10
	energetic cost of begging	0, 0.3
	food abundance	2, 2.3, 2.5
	begging effectiveness	1, 1.5
	mutation rate	0.01, 0.02

model process. With an appropriate mutation rate, examination of strategies over generations reveals stability. Figure 2.5 shows a typical result in a simple "parent-fixed" model with identical nestmates ( $r = 1$ ), where begging strategies start randomly at generation 0, and evolve rapidly towards stable levels. The graph shows the mean begging strategy of the 40 a and b chicks in every fifth generation when each is satiated ( $X(t) = X_{\max}$ ), and starving ( $X(t) = X_{\min}$ ). Note that the stable strategy is for both chicks to beg at a lower level at  $X_{\max}$ .

Stable strategies do not always evolve so quickly, particularly in more complex versions of the model. Figure 2.6 shows the results from a "parent-evolves" simulation in which no stable pattern evolves for 150 generations. Some combinations of parameters never lead to stability. Non-convergence cannot be interpreted as evidence against any possible stable strategy since it may be an artifact of parameter values and have no biological implication. Only analytical models are well-suited to documenting non-convergence. Figure 2.7 illustrates the effect of varying mutation rate on strategy convergence: with high mutation rates, strategies oscillate each generation; with low mutation rates, they oscillate less, but can become trapped on local optima more easily.

To identify stable strategies for each set of parameter values, I replicated each run of the model ten times. I used the last 50 generations (i.e., generations 451-500) of each simulation and calculated the mean begging and provisioning strategies. I also calculated the standard deviation around the mean for each population of 80 chicks in each generation, and looked for small and constant deviations between years to discriminate between random and selected strategies. Obviously, with a mutation rate greater than zero, there will always be some variation within each generation, even with complete convergence.



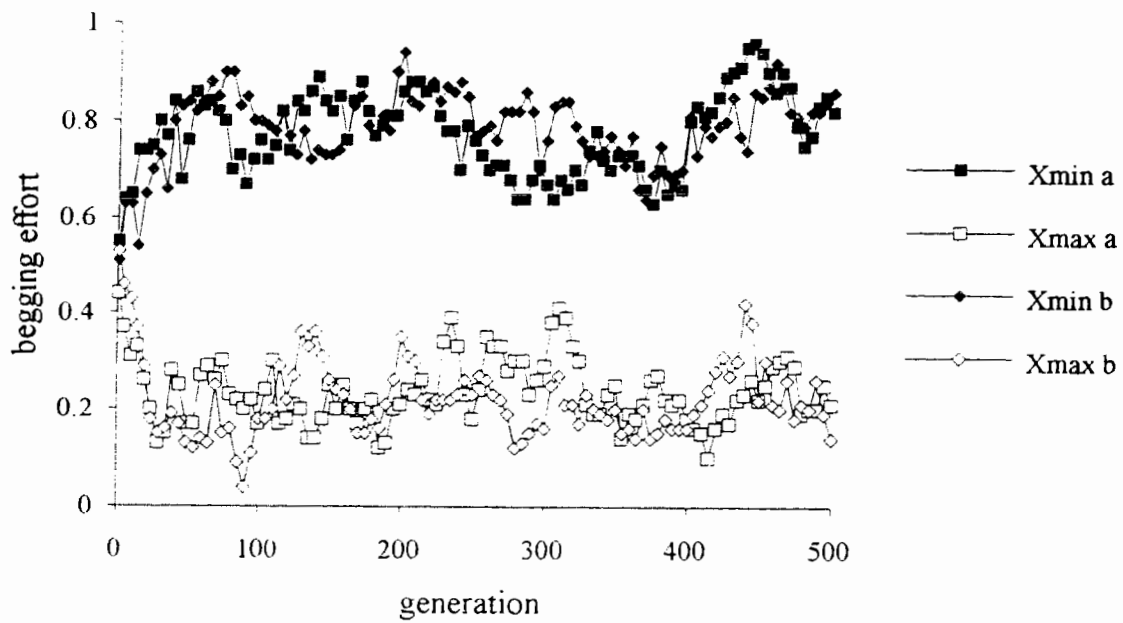


Figure 2.5. Evolution of begging strategies (begging effort) for hungry and full chicks over 500 generations of the model. In this trial, **a** and **b** chicks have equal competitive ability and are identical ( $r = 1$ ).

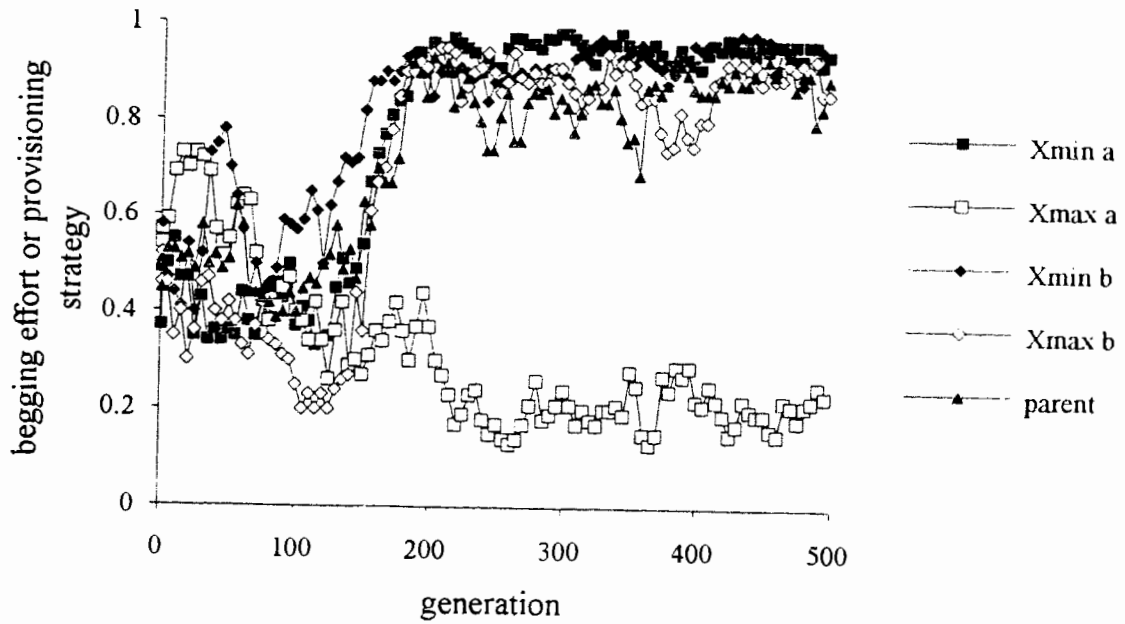


Figure 2.6. Evolution of begging and provisioning strategies over 500 generations. A stable pattern emerges after 150 generations. In this trial, a chicks have a competitive advantage of 1.5.

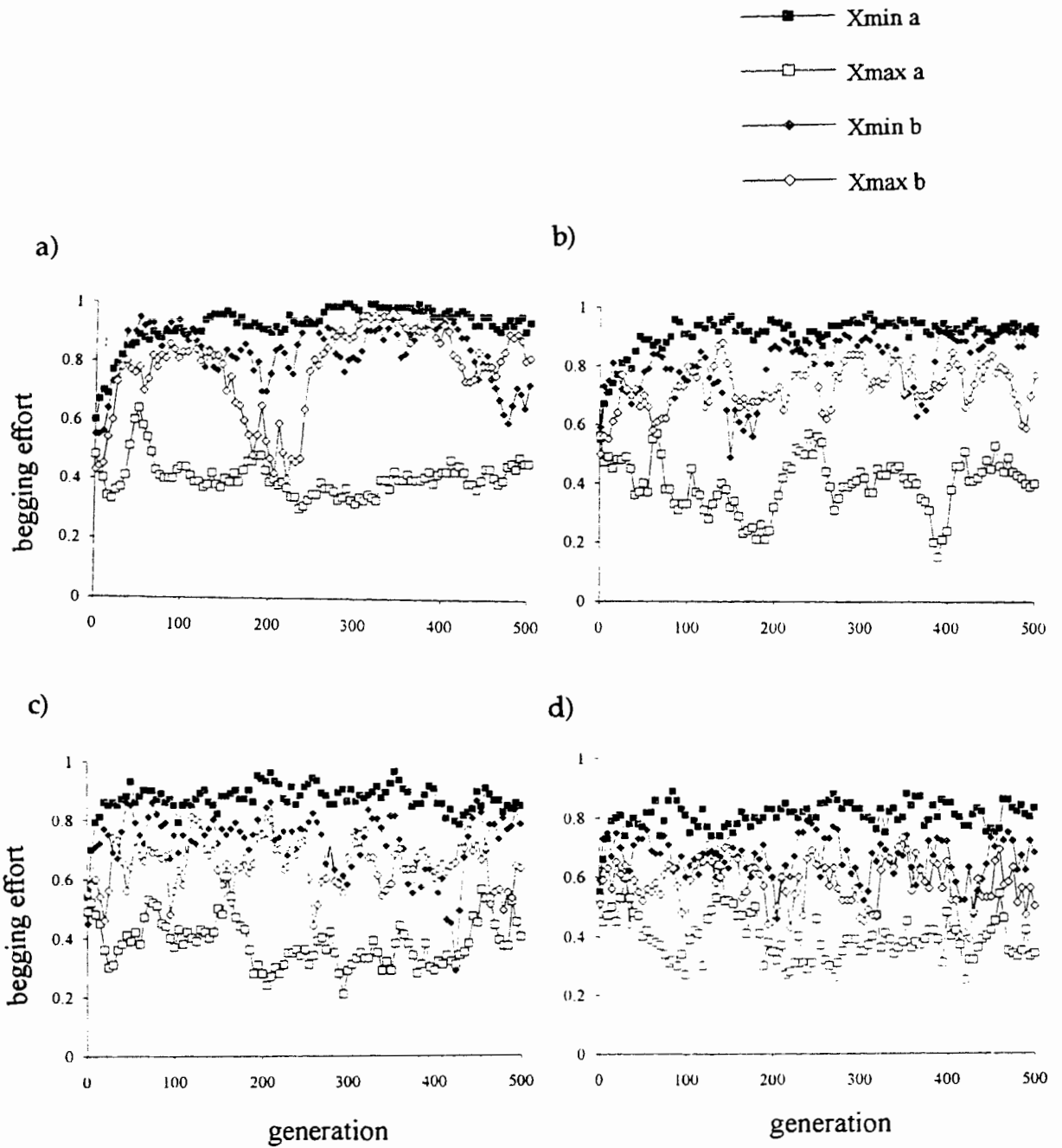


Figure 2.7. The effect of mutation rate on strategy convergence. a) mutation = 0.005, b) mutation = 0.01, c) mutation = 0.02, d) mutation = 0.04.

The genetic algorithm results illustrate which begging strategies evolve, but do not show the states in which chicks find themselves, and hence do not reveal manifested begging behaviour. For example, although a big chick's strategy may be to be lenient at low hunger levels, it may be constantly hungry, and hence beg loudly. I calculated actual chick states by running the mean evolved strategy through the simulation portion of the model separated from the genetic algorithm. In most cases, chick states stabilized at levels where each was fed in turn.

I now use this model to examine the effects of relatedness, chick asymmetries and costs on begging behaviour, and to examine the evolution of parental provisioning behaviour.

## Results

### Effects of relatedness (fixed parent)

Unrelated chicks ( $r = 0$ ) always evolve escalation, and show no sensitivity to their state (Figure 2.8). Both chicks beg loudly whether hungry or full, and whether equal or asymmetrical in effectiveness or need. This pattern is robust although many chicks die: in most families, only one chick survives (on average,  $74.1 \pm 0.4$  deaths to 80 survivors per generation).

Variation in begging costs does not change the escalation pattern.

Full siblings ( $r = 0.5$ ) escalate when hungry, but show some sensitivity to their state by reducing their begging effort when full (Figure 2.9). Both nestlings exhibit the same behaviour. More families fledge two chicks when the chicks show hunger sensitivity ( $58.5 \pm 1.7$  deaths per generation). Begging strategies of related chicks are sensitive to other parameter values including the asymmetries and costs discussed below.

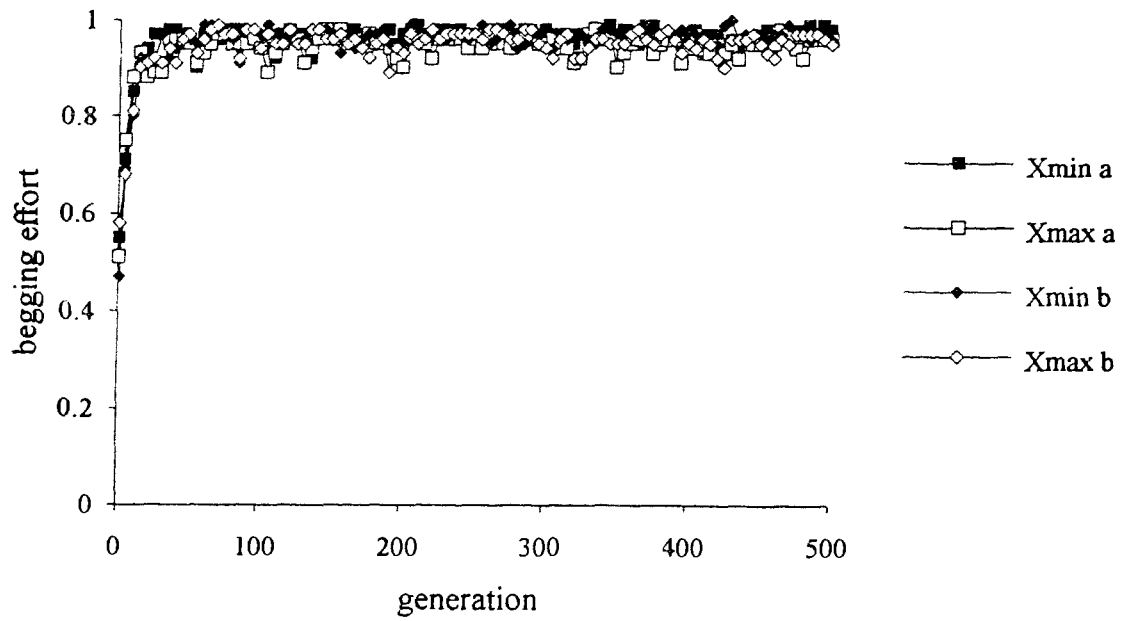


Figure 2.8. Evolved begging strategies when nestmates are unrelated ( $r = 0$ ) and of equal ability.

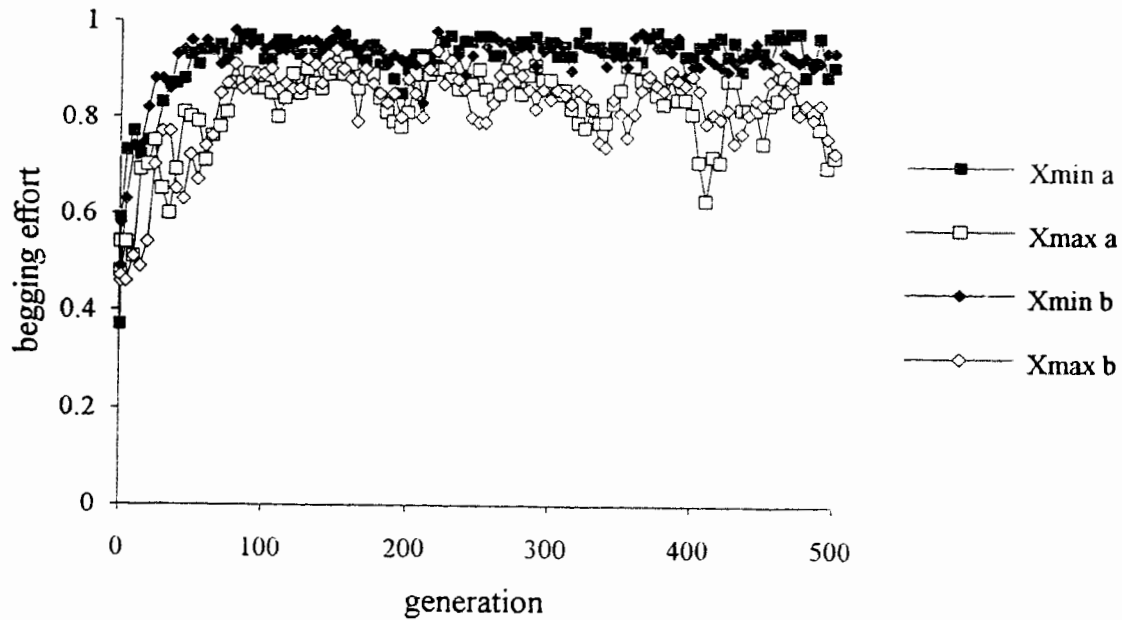


Figure 2.9. Evolved begging strategies of full siblings ( $r = 0.5$ ) of equal ability.

Changes in resource abundance also affect these results. Reducing the amount of food so that one chick always dies leads to full escalation; abundant resources increase the state-sensitivity. Identical chicks ( $r = 1$ ) show increased state-sensitivity, as well as decreased overall levels of begging (Figure 2.5). Identical siblings show the highest mean fitness ( $26.2 \pm 0.8$  deaths per generation). Figure 2.10 compares mean begging strategies for unrelated, full sibling and identical chicks ( $r = 0, 0.5$  and  $1$ , respectively) for a given starvation risk and food abundance. Begging has no cost in any of these simulations. In all subsequent runs, nestlings are full siblings.

#### Effect of asymmetries (fixed parent)

When a chicks beg more effectively than their siblings, their evolved begging strategy changes (compare Figure 2.9 with Figure 2.11). The a chicks become more sensitive to their state while b chicks retain low sensitivity. The a chicks can always out-compete their juniors, but do so only when hungry. Their begging effort is more sensitive to state, due to the inclusive fitness increment garnered from their juniors. The decrease in begging effort by a chicks translates into a decrease in actual begging loudness (or begging "level") relative to the loudness of their nestmates. Whether a chicks on average beg more or less loudly than their nestmate depends on their mean state, since they beg more when hungry but less when full. The a chicks were generally less hungry than their small siblings (Figure 2.12). The b chicks, risking starvation constantly, cannot afford to decrease begging and, given no costs to begging, lose nothing by begging hard. The b chicks die almost three times as frequently as their larger siblings (a chicks:  $6.5 \pm 0.4$  dead per generation; b chicks:  $19.1 \pm 1.2$  dead per generation).

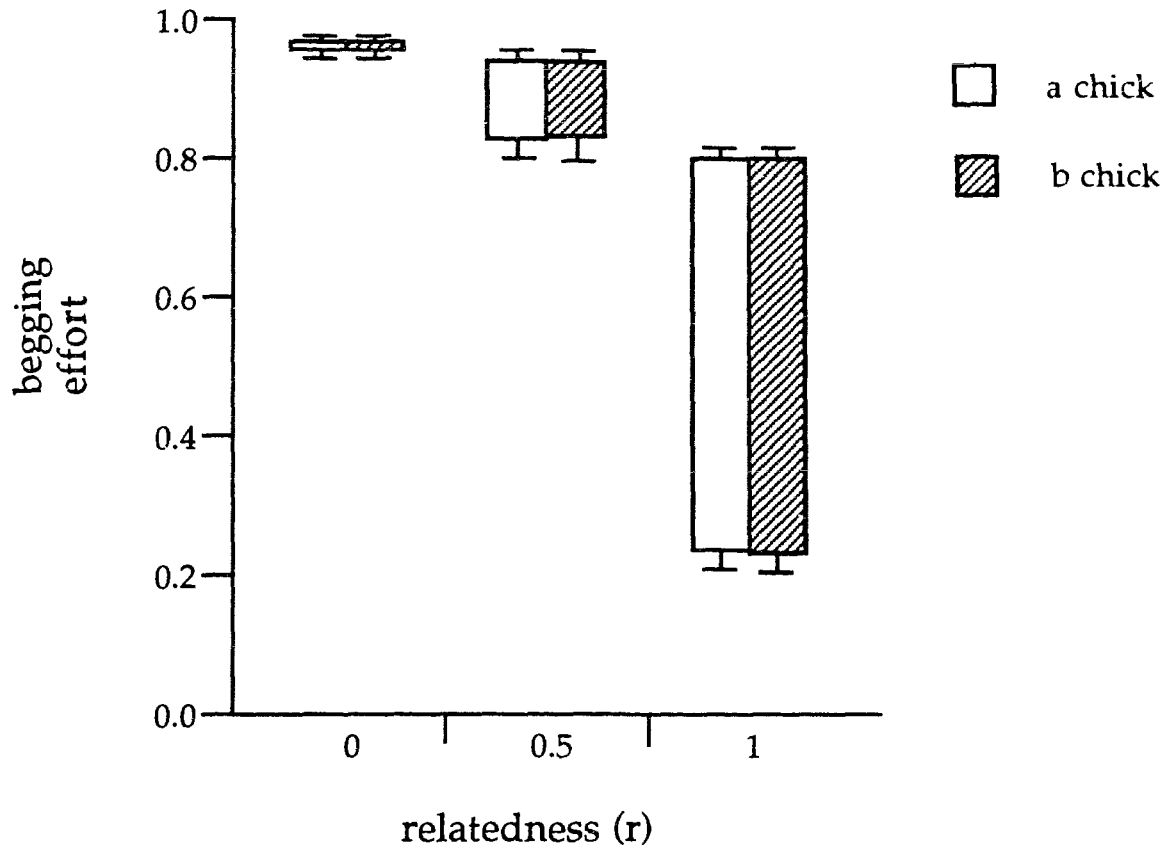


Figure 2.10. Begging strategies of unrelated, full sibling and identical pairs of chicks. Boxes represent the range of begging effort, with the upper border showing the mean begging effort at  $X_{\min}$ , the lower border showing the mean effort at  $X_{\max}$ , and the error bars representing the standard error around each. Food abundance parameter = 2; starvation risk parameter  $s = 4$ .



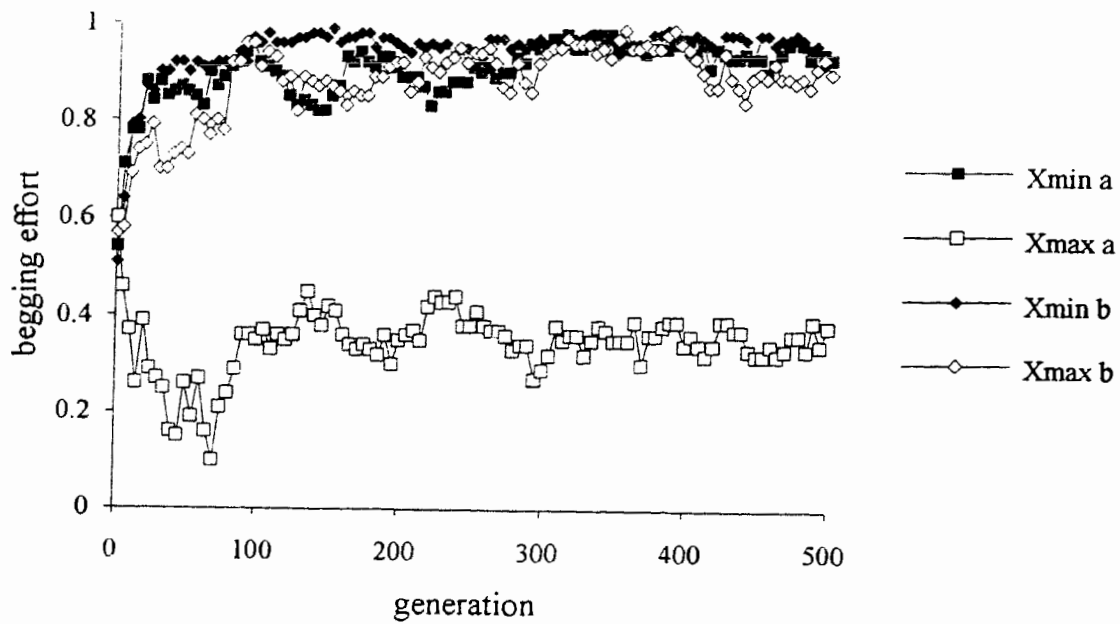


Figure 2.11. Evolved begging strategies when one chick has a competitive advantage (a beg level = 1.5 x beg effort; b beg level = 1.0 x beg effort). Note that the graph shows begging effort.

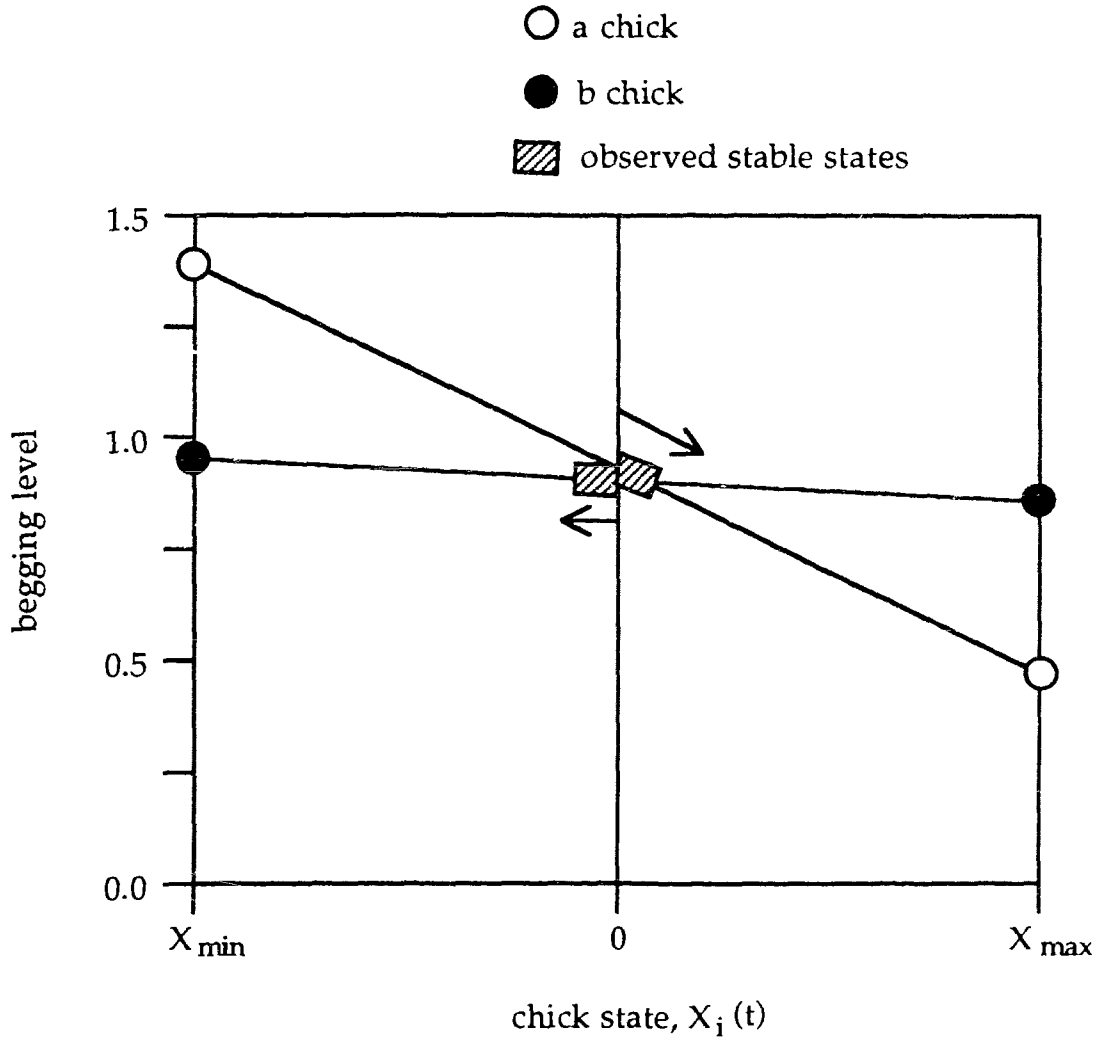


Figure 2.12. Mean evolved begging strategies and resultant states for asymmetric chicks, plotted against chick state. Chicks begin at  $X(0) = 0$ . The parent feeds the loudest beggar (here, the a chick), who then moves along its begging/state trajectory. In the next time period, the b chick begs more, and is fed. Begging levels and chick states oscillate within the shaded boxes which represent the value of a single food item.

Asymmetries in chick need (via an increased risk of starvation to **b** chicks for the same state) affect begging strategies differently depending on whether the chicks have associated asymmetries in ability (Figure 2.13). With equal ability, asymmetries in need change begging strategies only slightly relative to those evolved in equal chicks (ability  $a = b$  in Figure 2.13). Cases where chicks differ in both need and competitive ability are both more interesting as well as more biologically plausible. If a chicks have a begging advantage over their needy siblings (i.e., **a** chicks represent larger or older nestlings who are less needy and can beg louder, Chapter 6), they decrease their begging effort and loudness to a level below that of **b** chicks when full (i.e., they show lenience at low hunger levels; ability  $a > b$  in Figure 2.13). Conversely, if needy chicks can beg louder (i.e., **b** chicks represent male chicks who are larger and can beg more, but are also needier than females; Teather 1992, Chapter 6), these chicks put less effort than their less needy, less able, siblings into begging at low hunger levels, but always beg more loudly (ability  $a < b$  in Figure 2.13).

#### Costs of begging (fixed parent)

Incorporating an energetic cost into the model requires an associated increase in food quantity, since chicks now use more energy. Energetic costs of begging in models with insufficient food lead to full escalation. With sufficient food for the costs associated with a mean begging level, energetic costs frequently produce escalation, but sometimes (2/10 trials) increase sensitivity to state (Figure 2.14). Mean fitness varies considerably between the two results, with a chick dying from every brood in the escalated trials (80 deaths to 80 survivors per generation) and a chick dying from 53% of the nests (26 deaths/53 broods and 30 deaths/55 broods per generation) in the

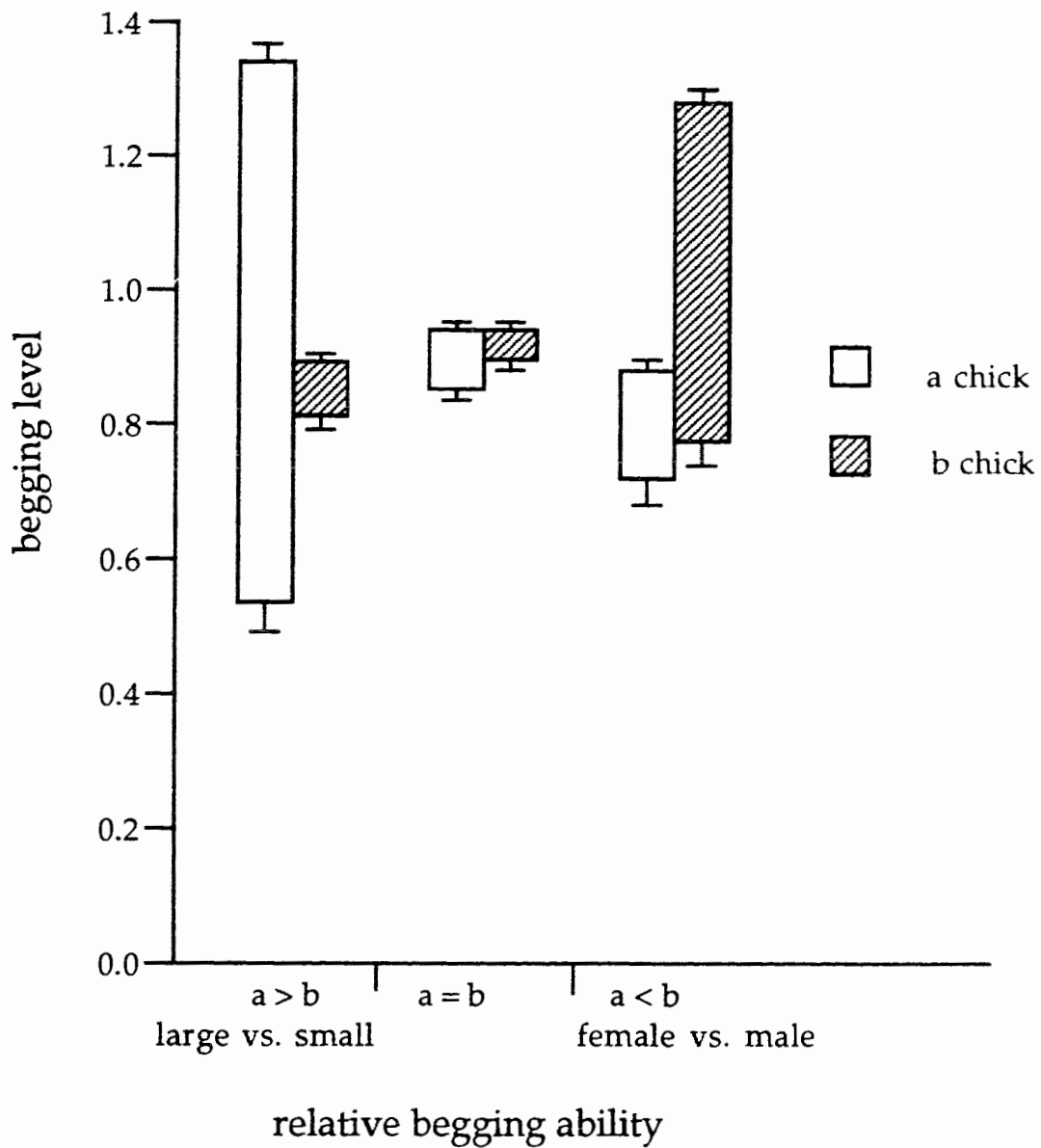


Figure 2.13. Begging level of pairs of chicks with asymmetries in need and ability. Boxes as in Figure 2.10. The *b* chick always has a higher long-term need than the *a* chick in this figure, and the three evolved strategy pairs represent different asymmetries in ability.

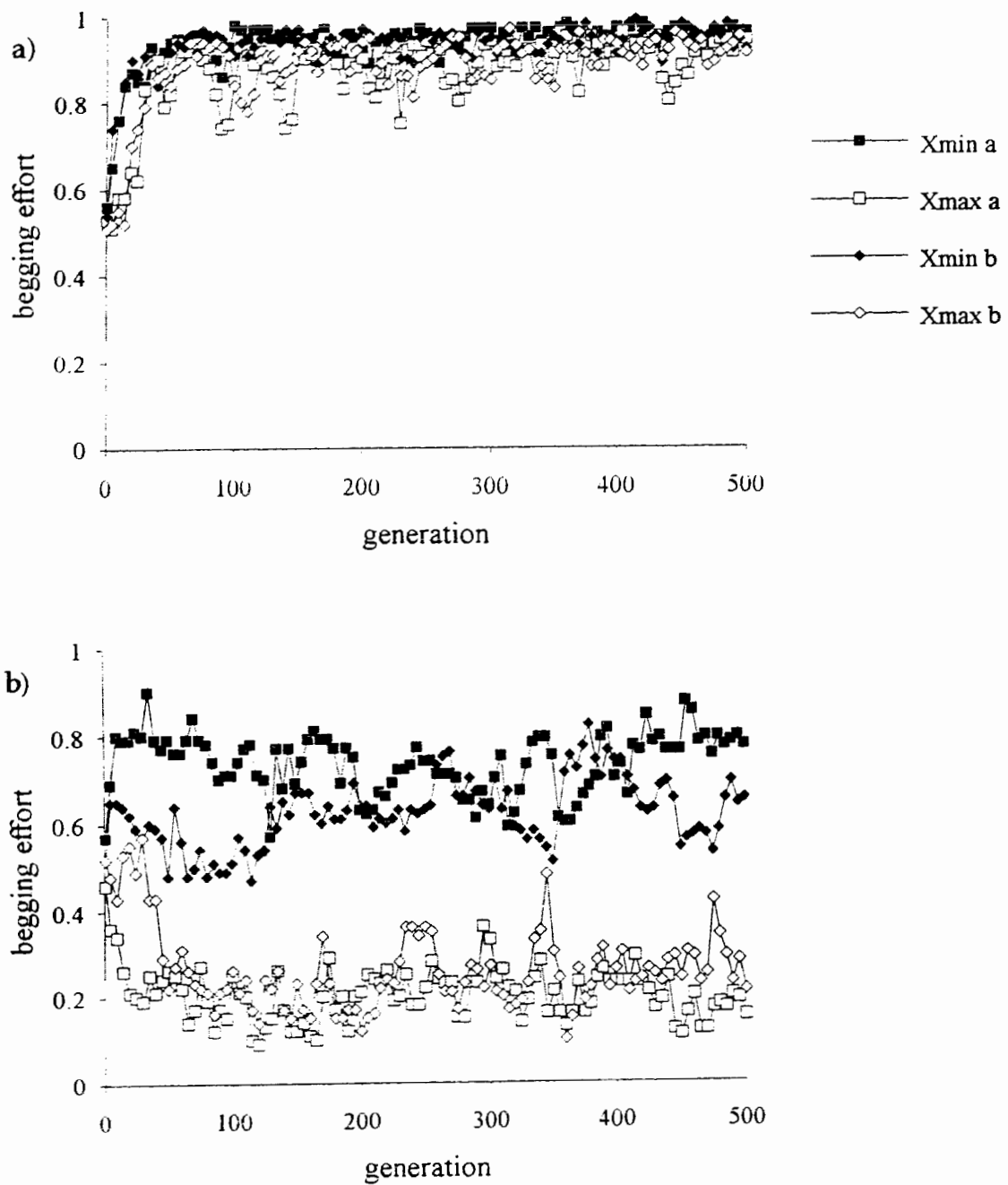


Figure 2.14. Evolved begging strategies when begging carries an associated energetic cost. a) Escalation evolves and chicks always beg loudly. b) Evolved strategies show state-sensitivity. Both trials used the same model parameters.

state-sensitive trials. Energetic costs reduce the difference in behaviour between asymmetric siblings, because **b** chicks lower their begging effort at low hunger levels (Figure 2.15).

Predation costs (which affect both nestmates) interact with starvation level to produce different patterns of begging. With moderate starvation levels and asymmetric pairs of chicks, **a** chicks do not change their begging levels in response to the added predation risk, and always show high sensitivity to state. Under the same conditions, **b** chicks change their strategy from relatively state-insensitive, continuous high begging levels to state-sensitive, somewhat lower levels. Overall, adding predation to simulations with moderate starvation risk has relatively little effect on **a** or **b** begging strategies (i.e., **a** is more sensitive than **b** with or without predation; Figure 2.16).

Adding predation to simulations with a harsher starvation regime ( $s = 1$ ), changes the relative strategies. With high starvation, but without predation, both chicks beg at high levels in a state-insensitive manner. Many chicks, particularly **b** chicks, die (Figure 2.17) and must compete intensely to survive. With the addition of predation, **b** chicks keep begging in a state-insensitive manner, but **a** chicks vary their begging with state (Figure 2.16). This change in begging strategy with the addition of predation cost under conditions of high starvation contrasts with the slight change in behaviour attributed to predation risk in the moderate starvation scenario.

Increasing the risk of predation leads to a decrease in begging level by both chicks, and in extreme cases ( $k = 0.04$ ), leads to a counter-intuitive switch in stable **b**-chick behaviour, where **b** chicks beg more when full than when hungry (Figure 2.18). As long as hungry **b** chicks beg more than full **a** chicks, **b** chicks have the potential to survive using this strategy, although many

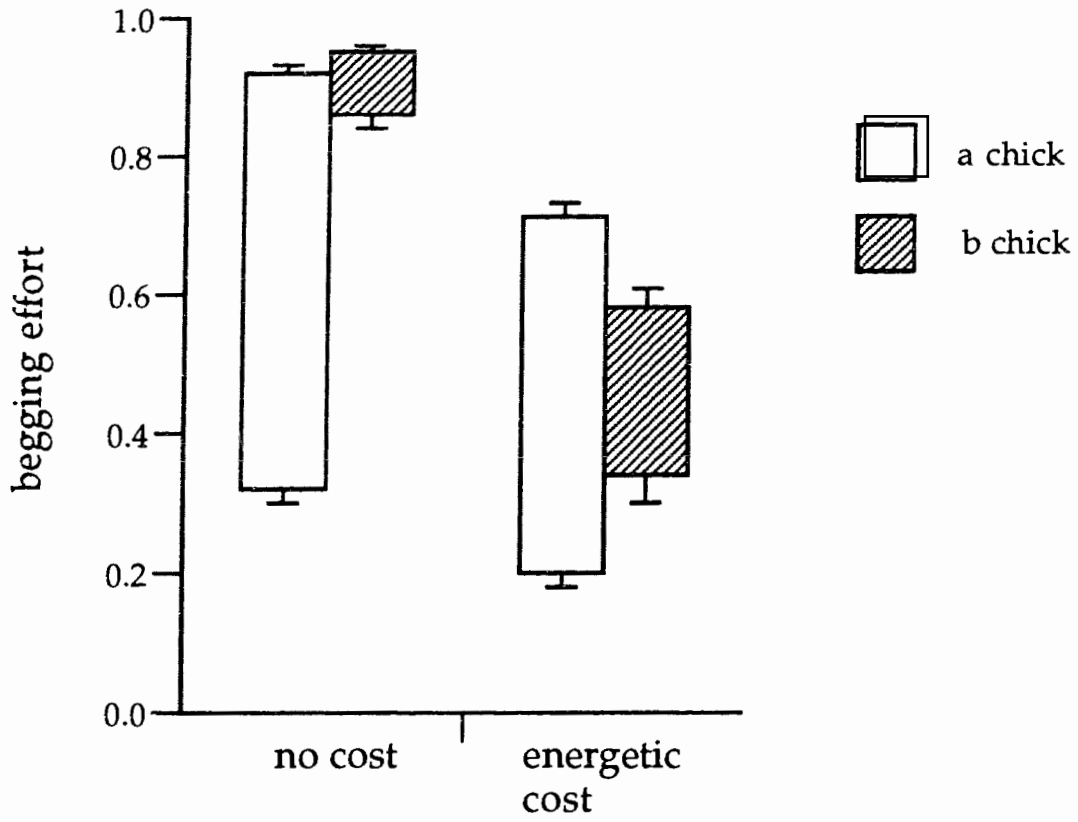


Figure 2.15. Begging strategies of asymmetric chicks (a has a higher ability) with and without energetic costs to begging. Boxes as in Figure 2.10.

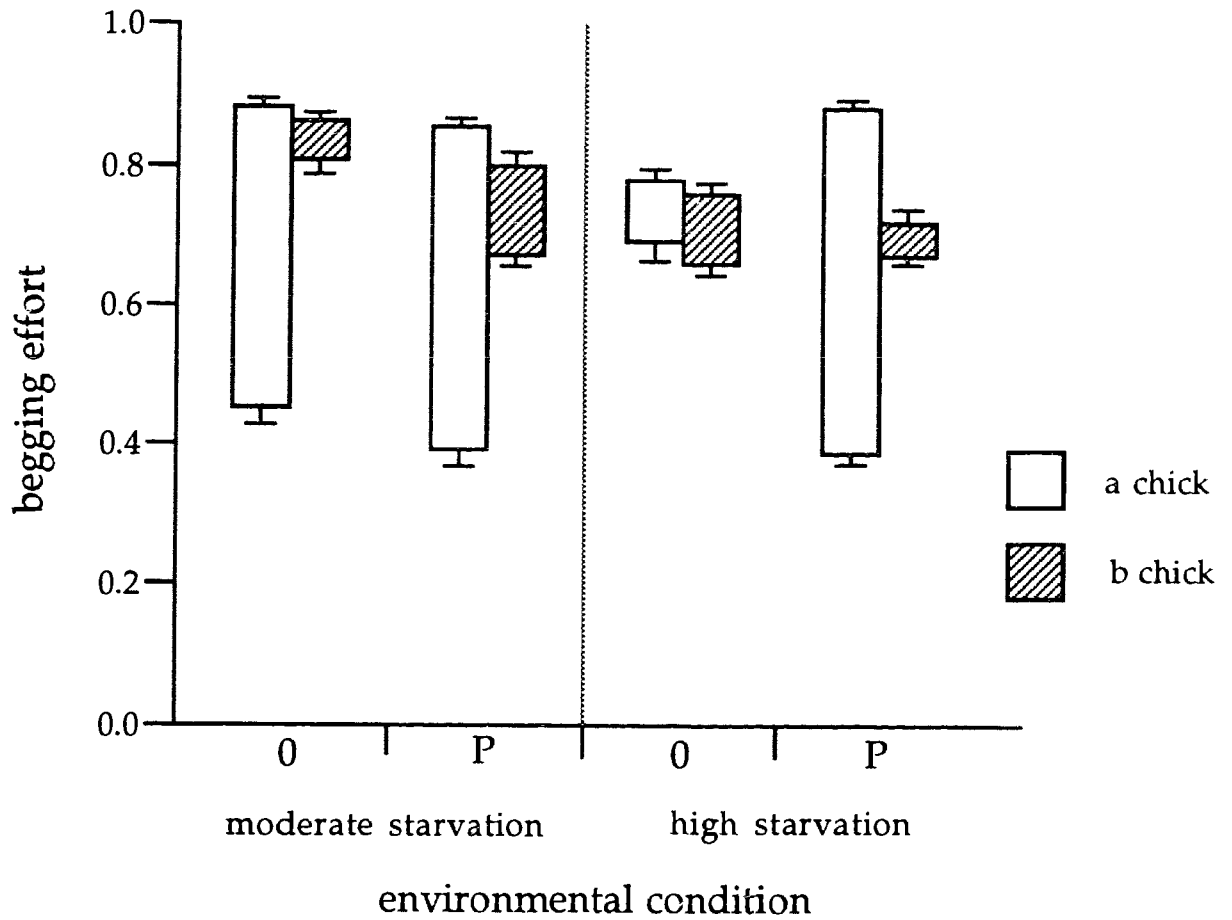


Figure 2.16. Evolved begging strategies under various environmental conditions. Boxes as in Figure 2.10. 0: no predation ( $k = 0$ ); P: predation ( $k = 0.01$ ); under conditions of moderate starvation ( $s = 2$ ), and high starvation ( $s = 1$ ).



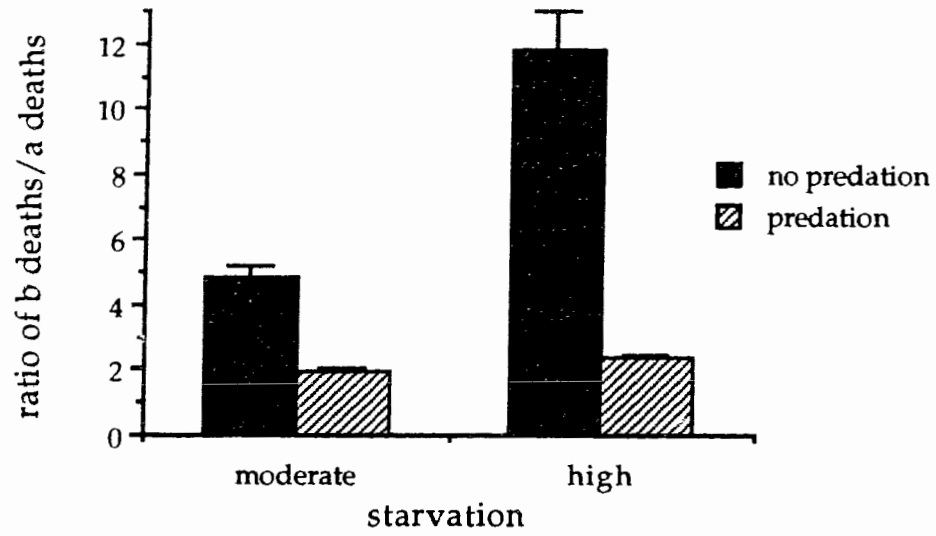


Figure 2.17. Mean ( $\pm$  standard error) ratio of b deaths to a deaths under different starvation and predation regimes. Although more chicks die when predation is included, the proportion of b chicks dying is lower.

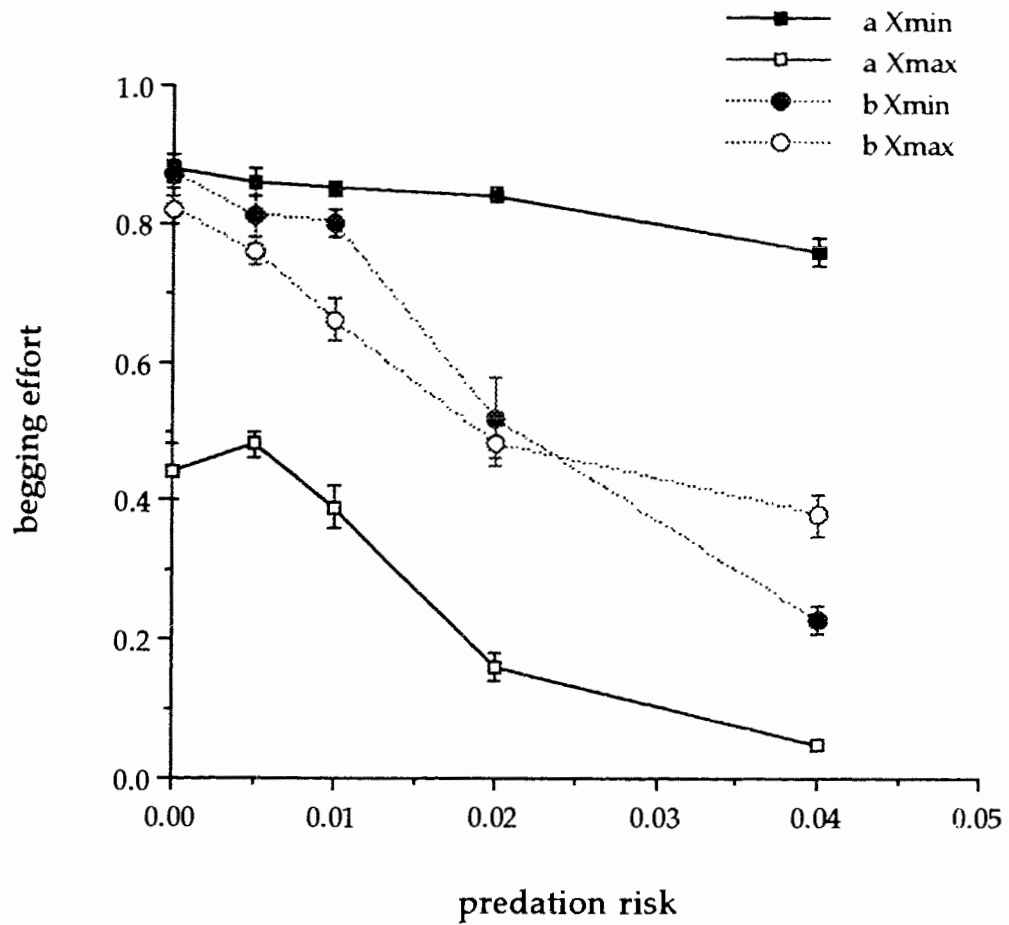


Figure 2.18. Evolved begging strategies of asymmetric chicks (mean  $\pm$  s.e.) under varying levels of predation risk. Note that **b** chicks switch strategies at high predation to begging more at  $X_{\max}$  (full) and less when at  $X_{\min}$  (hungry).

starve. The total begging level stabilizes at a lower level than it would if both chicks followed the "common-sense" strategy (Figure 2.19). I interpret this behaviour as suicide on b's part: if both beg, both likely die; this way, a has a chance at survival.

#### Predation risk and the "home-free" assumption (parent fixed)

The "home-free" assumption, automatically fledging any chick surviving after its nestmate starves, has no effect on trials without predation cost. It has a rather interesting effect in combination with predation risk, however: chicks beg more loudly when begging carries a predation cost (Figure 2.20). Closer examination of model details reveals that these escalated begging levels frequently lead to the immediate death (within the first five time periods) of one chick (generally the b chick). This pattern is consistent with siblicide, where chicks outcompete and starve their nestmate to ensure their own survival. Under the "home-free" assumption, following the starvation of a nestmate, surviving chicks fledge immediately, experiencing no predation risk. This assumption is realistic only if single chicks no longer need to beg to receive food. This tremendous decrease in exposure to predation risk (from 100 to 5 time periods) increases the chances that one chick will survive. Other model trials avoid the siblicide option by replacing the "home-free" assumption with the assumption that chicks continue to beg for 100 periods regardless of their nestmate's survival.

#### Evolving parental strategies

None of the former conditions allow examination of the evolution of begging *de novo*, since all stipulate that a parent feeds the loudest chick. Models allowing for the evolution of parental strategies result in two

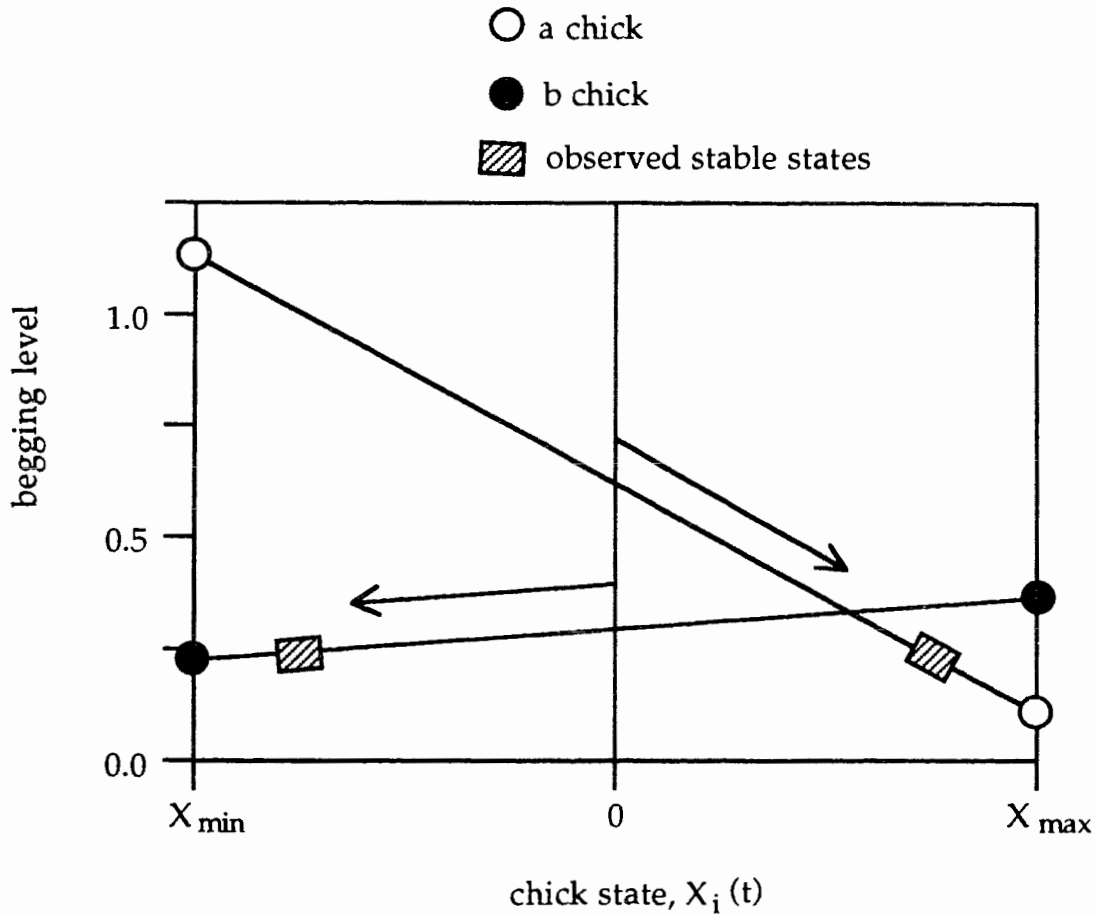


Figure 2.19. Mean evolved begging strategies and resultant states under very high predation risk ( $k = 0.04$ ). Chicks start with state  $X(t) = 0$ , where **a** chicks beg more and are fed. The **a** chicks gain condition and **b** chicks lose condition, until states stabilize and oscillate within the boxes. The **b** chicks have the potential to survive with their reverse strategy, but are still very likely to starve.

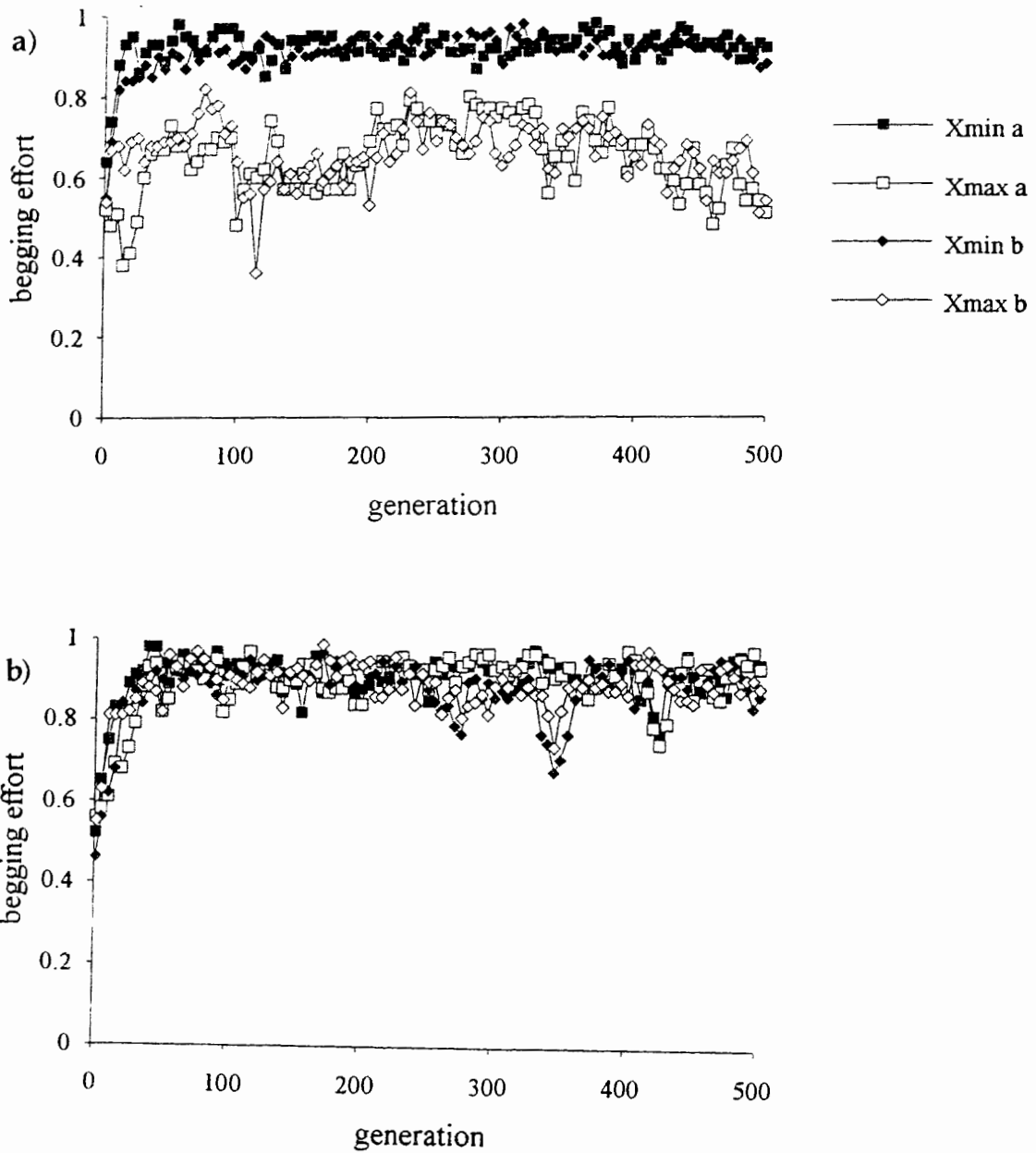


Figure 2.20. Evolution of escalated begging with the "home-free" assumption. a) Run without predation risk. b) Run with predation risk. All other parameters are the same. With added predation risk, more chicks starve.

contrasting patterns of provisioning. In trials with equal chicks, parental strategy evolves to feed beggars, and chicks subsequently beg as described above in about half the cases; in the other half, parents evolve to allocate food to quiet chicks, and chicks beg at low levels when full and tend not to beg when hungry (Figure 2.21). In both cases, begging signals chick state, but in the first, loud begging represents hunger, while in the second it represents satiation. Both provisioning strategies evolve quickly and remain stable over 500 generations, and never flip from one to the other. Conversely, trials with unrelated ( $r = 0$ ) chicks never achieve stability, but continuously switch between the two feeding modes (Figure 2.22). Thus, begging can evolve as a stable signal of chick state, even in cost-free models, provided that nestmates are related.

In asymmetric families (where a chicks beg more effectively), parents tend to evolve the strategy to feed quiet chicks more frequently (symmetric nestlings: parents fed quiet chicks in 10/20 runs; asymmetric nestlings: parents fed quiet chicks in 15/20 runs). In these runs, the a chick unilaterally increases its begging level without increasing its value to the parent. In asymmetric nests without parental choice, b chicks often die, and hence the a chick sets up the survival pattern of the brood. With choice of allocation, parents can evolve retaliation against any such escalation strategies. By feeding quiet chicks, parents eliminate a's advantage, and equal numbers of a and b chicks die (ratio of b/a deaths: parents feed loud chicks =  $2.2 \pm 0.3$ ; parents feed quiet chicks =  $1.1 \pm 0.1$ ). Provisioning strategies also vary with starvation level. If starvation risk is moderately high ( $s=2$ ), parental strategies fluctuate; if it is low ( $s=10$ ), a and b chick survival is similar, and results approximate those for equal chicks. The instability observed with high

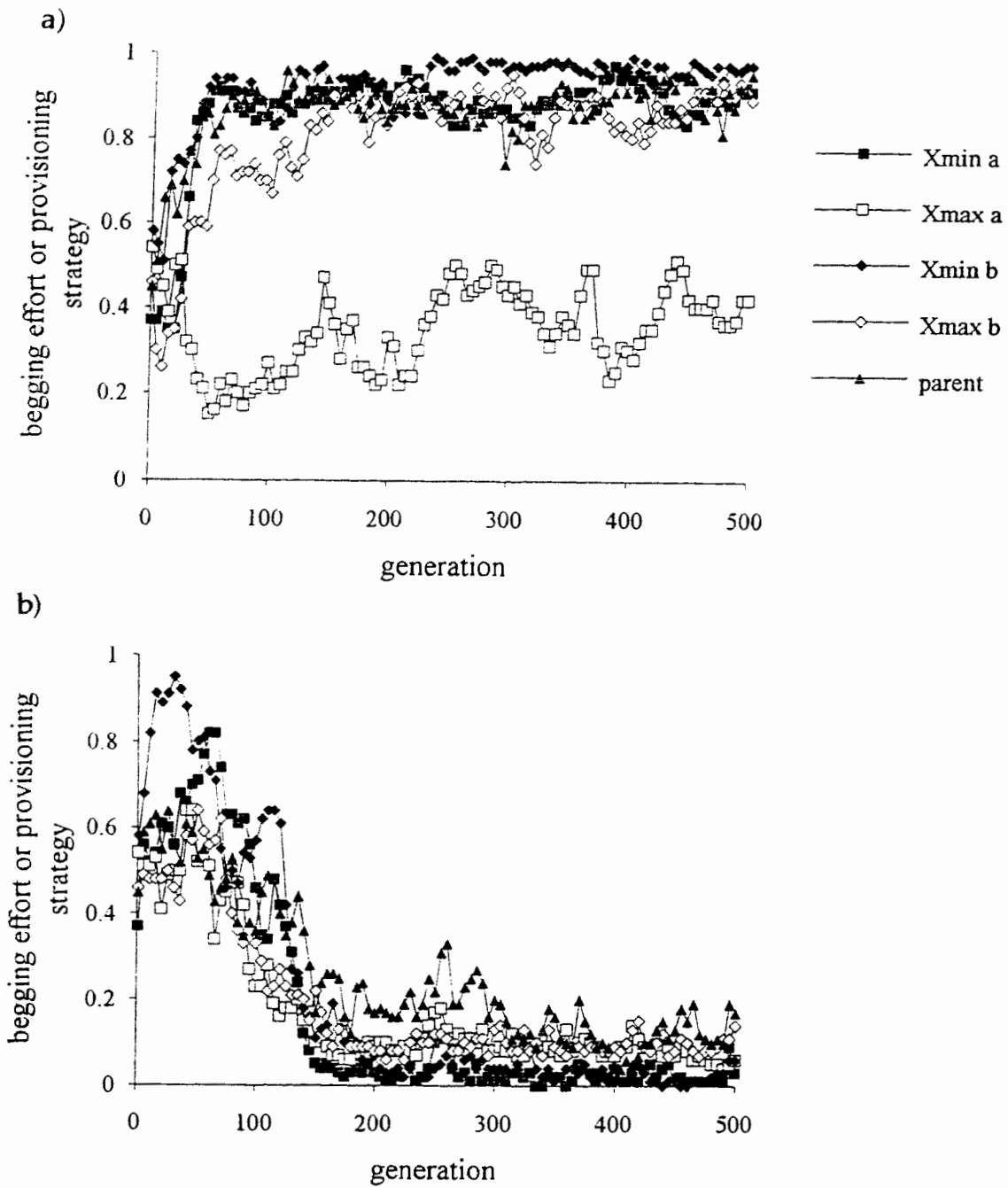


Figure 2.21. Evolution of parental provisioning strategy and begging strategy over time. a) Parents evolve to feed the loudest beggars. b) Parents evolve to feed the quietest beggars. Both runs use the same parameter set.

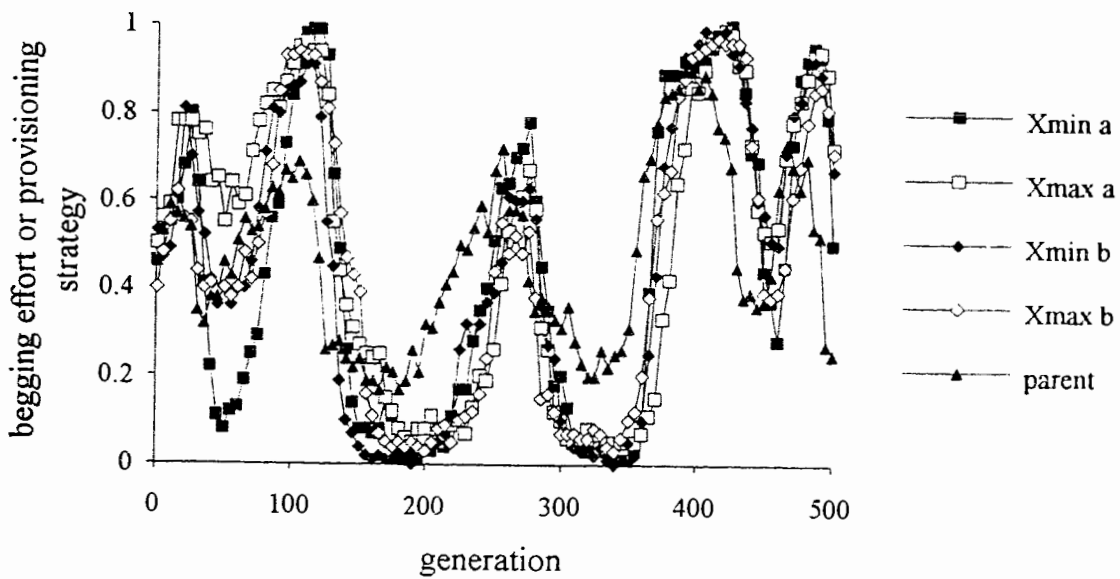


Figure 2.22. Evolution of provisioning and begging strategies over time in broods of two unrelated ( $r = 0$ ) chicks. Note that chick strategy tracks parental strategy with a gap of several generations.



starvation likely arises from the difficulty in achieving a provisioning strategy in which both chicks can survive.

If a chicks have a higher value ( $b$  chick starvation risk is higher), correlating with their louder begging, parents occasionally will switch strategies from feeding the quiet to feeding the loud chick. Trials with these parameter combinations, however, are frequently unstable and hence difficult to interpret.

## Discussion

I have presented a model which examines the evolution of begging as a state-dependent signal, allows both begging and provisioning strategies to evolve, and compares the strategies of equal and unequal chicks when faced with energetic and predation costs to begging. The model suggests that relatedness, asymmetries in competitive ability and need, and energetic and predation costs all affect begging strategy.

The model demonstrates that begging can signal short-term need (hunger or body condition) without an associated cost, provided that nestmates are related. Several authors have suggested that cost-free begging will always escalate unmoderated by kin selection (e.g., Stamps et al. 1978, Macnair and Parker 1979, Parker et al. 1989). My results do not dispute this claim, but point out that evolutionary escalation does not necessarily remove information from begging by siblings. Experimental evidence supports this claim, showing that, in several species, hungry chicks beg more (Chapter 4, Smith and Montgomerie 1991, Litovich and Power 1992). Brood parasites are unrelated to their nestmates, and beg at high levels (e.g., Gochfeld 1978). The model predicts that begging by brood parasites (with  $r = 0$ ) should reflect their hunger less than the begging of their hosts (with  $r > 0$ ).

My results dealing with asymmetries in competitive ability agree with those of Parker et al. (1989). Chicks given a begging advantage (able to beg more loudly for the same effort) showed increased state-sensitivity, begging relatively less when satiated, at least under conditions of low to moderate starvation. Chicks with a high begging ability had a higher mean fitness (fewer died per generation), remained closer to satiation than their siblings, and invested less effort into begging. The model predicts that siblings with a low competitive ability should beg more near satiation, and that siblings with a high competitive ability should beg more (because they can) near starvation.

The model manipulated chick long-term need by giving one chick a higher chance of starvation. I found little effect of long-term need as long as chicks had equal competitive abilities. For needy chicks to improve their chances of survival, they must improve their state. Given no change in food availability, for b chicks to improve condition, a chicks must lose condition. Competition between nestmates makes this strategy unlikely if a has no increased ability, and is hence unable to guarantee food when hungry.

I investigated the begging strategies of large/old versus small/young chicks and of male versus female chicks by creating asymmetries in both ability and need. Larger or older chicks begged less at low hunger levels than their smaller, younger nestmates, whereas male chicks never begged less than their female siblings. Large males used their competitive advantage to increase their survival chances, while large less needy chicks rarely died, and begged less to give a better chance to their juniors. Begging had no associated cost in these runs. I derive three predictions from these results. First, I predict that in sexually dimorphic species, the faster growing gender will beg more loudly than the slower growing gender when both are full or in good condition. Second, I predict that smaller or younger chicks will beg more

than their larger, older siblings when both are full or in good condition. Finally, I predict that larger chicks should always beg more than small chicks when both are hungry or in poor condition.

With sufficient food for two chicks begging at the mean effort, the addition of energetic costs usually resulted in the evolution of escalated begging effort, but occasionally increased the spread between begging levels at satiation and starvation. In the first case, the added food was insufficient to cover the evolved high begging costs; in the second, the same amount of food acted as a surplus. In both cases, begging strategies, once evolved, remained stable. This result illustrates how two alternative strategies, with different mean fitnesses, can be maintained given the same parameter values. Unfortunately, it also creates difficulties in interpreting results of runs including energetic costs, since similar resource abundance is crucial to comparisons between trials.

Energetic costs applied to asymmetric broods decreased the relative leniency of the large sibling, since both chicks decreased their begging efforts when full. In species with high energetic costs to begging and no predation costs (perhaps species in which chicks are quiet, but move extensively), the model predicts that small and large siblings should beg similarly for a given hunger level.

Predation costs led to different strategies depending upon the relative risks of predation and starvation. In asymmetric broods experiencing moderate starvation risk, predation risk merely caused the *b* chick to beg a little less when full. Under high starvation risk, in the absence of predation, both chicks begged loudly regardless of their hunger level. With the addition of predation risk in this scenario, *a* chicks increased their state-sensitivity while *b* chicks did not.

This result demonstrates that predation risk can influence begging behaviour (as suggested by Zahavi 1977) particularly when chicks must trade off starvation risk against predation risk. Since I observed this effect in "parent-fixed" models, I propose a scenario in which predation risk affects sibling interactions rather than parent-offspring interactions: the **a** chick reduces its begging loudness, and avoids escalation, to improve its chances of survival. I do not suggest by this that the **b** chick is "manipulating" its sibling, but only that each chick begs at a level determined by its state, risk of starvation and risk of predation. The constant begging by the **b** chick raises the predation risk felt by its sibling, however, and is one factor in the **a** chick's decision. The evolution of decreased begging by the **a** chick moderates the predation risk felt by both nestmates. Experimental evidence for any effect of predation on begging is rare. David Haskell (Cornell University, personal communication) found that pseudonests on the ground were depredated more frequently when associated with played-back begging calls. Redondo and Castro (1992) found that larger, noisier nests suffered from higher predation rates. I was unable to detect any relationship between begging and predation risk in yellow-headed blackbirds despite predation rates of 40% of nests (Appendix 1).

Other model results show that predation risk is not necessary for the evolution of observed begging patterns, and that several environmental factors may lead to stable begging strategies. The model suggests several explanations for the observation that small chicks beg more (e.g., Chapter 6, Bengtsson and Ryden 1983). First, at stable begging levels, small chicks are more frequently hungry. If hunger level is controlled, small chicks may still beg more because their larger siblings show leniency under low starvation risk, or because their larger siblings show leniency under high starvation risk

coupled with predation risk. Begging patterns should vary between environments with different starvation and predation regimes. The model predicts that species in safe nests subject to high starvation rates (e.g., cavity nesters) should show relatively state-insensitive begging, while those in dangerous nests, also subject to high starvation rates should show state-sensitive and rank-sensitive begging levels. Chicks with asymmetries in competitive ability, experiencing low predation and low starvation risks, should also show state- and phenotype-sensitive begging.

Paradoxically, under very high predation, small chicks begged less when hungry than when full. This strategy frequently led to starvation, but increased the chances of one sibling surviving by decreasing the overall begging level. This reverse begging pattern only showed up under extremely high levels of predation. It may represent suicide on the part of the b chick (O'Connor 1978). Suicide should be rare in small broods, but perhaps plausible in large broods of relatives.

Limited experimentation with the "home-free" assumption (where the death of a sibling results in immediate fledging of the survivor) led to interesting results which suggested the potential for the evolution of siblicide within the model. When a chicks had the option to starve their junior quickly and fledge after only five periods, they did so, evolving a strategy of escalation at all hunger levels. Faced with predation risk, a big sibling has two options: to increase its state-sensitivity, begging only when hungry and letting its junior feed regularly, or starving its junior, and reducing overall begging levels by eliminating competition. The latter option seems unlikely under natural conditions in broods of greater than two, since survivors have to compete for food with remaining nestmates by begging until fledging. The model suggests that some species with two-chick broods may show increased

levels of sibling starvation under conditions of high predation, although competition with future siblings may also lead to continued begging by singletons.

I found that a parental response to begging can evolve, but that feeding the quiet chick evolves as often as feeding the noisy chick, assuming no cost to begging and no signal value other than short-term need. Begging can evolve purely to indicate hunger level, at least when nestmates are related. When a chicks escalated begging (i.e., had a higher begging ability), parents retaliated by feeding quiet chicks, reducing the fitness of a chicks. If escalated begging correlates with an increase in chick quality, the model suggests that parents might evolve to feed the more valuable chick. Further modelling should deal with this issue. Adding evolving parental strategies considerably complicates the model and narrows the parameter space yielding stable results.

Parker and Macnair (1979) modelled two retaliatory strategies in which parents either feed chicks in proportion to demand or ignore solicitation. The first strategy assumes an increase in feeding rate with an increase in begging level. I did not start with this assumption, but found that parents did feed in relation to begging, though only half the time in the predicted direction. Parker and Macnair (1979) found limited stability for ignoring strategies particularly when they carried costs; random feeding (the equivalent of ignoring begging) never evolved in my model, likely because parents always paid a fitness cost for ignoring the information carried in begging.

This model does not allow parents to retaliate to begging by choosing different allocation criteria. Stamps et al. (1989) found that while male budgerigars fed chicks in relation to their begging level, females preferentially

fed small chicks. The model could be extended to offer parents information about chicks other than via begging.

Harper (1986) let parental strategy evolve, but did not consider cases in which parents feed quiet chicks. If begging signals only short-term need, and carries no costs, there is no reason to assume that feeding loud chicks should be more likely than feeding quiet chicks. If begging carries predation costs, parents may even decrease predation risk by feeding quiet chicks. That parents feed loud chicks (Chapter 4, Litovich and Power 1992, Smith and Montgomerie 1991) suggests that begging signals more than short-term need. Once parents feed beggars, the strategy appears stable. As long as chicks are related, they should beg less when full (given sufficient food) keeping the signal honest. Unrelated chicks always compete, and their strategies track the feeding strategy of their parent. It is reasonable, then, to examine strategies of chick competition assuming that parents will continue to feed beggars, though it would be worthwhile to check this assumption periodically.

This model combines aspects of Harper's (1986) and Parker et al.'s (1989) begging models. Parker et al. (1989) extended previous models (including Harper 1986, Parker and Macnair 1979, Macnair and Parker 1979) by examining the effects of asymmetries in competitive ability, but did not allow for the evolution of parental strategy. Harper (1986) allowed allocation and begging strategies to evolve, but only in broods of equal chicks. There is some confusion about the use of relative begging levels between the authors (Harper 1986, Parker et al. 1989). While both models (and previous begging models, e.g., Parker and Macnair 1979, Macnair and Parker 1979) examine begging level relative to a mean nestmate level, as stated by Parker et al. (1989) and as questioned by Harper (1986), they compare the evolution of different aspects of begging. Parker et al. (1989) look at the evolution of begging

escalation (Figure 2.23a), which could be interpreted as absolute begging level, while Harper (and this model) look at the evolution of the state-dependent slope (Figure 2.23b). The second aspect can be stable without incorporated costs while the first cannot (Parker et al. 1989). Sibling competition should drive absolute levels of begging up until costs set a limit, but begging level can still represent relative chick state.

I follow Parker et al. (1989) in examining begging strategies by asymmetric chicks in two-chick broods, and Harper (1986) in allowing parental strategy to evolve and in looking at the evolution of state-dependent begging levels. I differ from both by using a numerical rather than analytical approach to finding stable strategies. While numerical models lose something in elegance and generality, they facilitate examination of such a complex problem as begging. The genetic algorithm approach incorporates relatedness explicitly. Such an approach allows determination of strategies maximizing mean fitness (by examining results with identical chicks—the equivalent to removing competition while retaining the allocation decision). The approach also benefits from its flexibility, although interpretation of a simulation model within a genetic algorithm model can be difficult.

The model could easily be extended to deal with non-linear relationships, particularly the relationship between begging and state. The enforced linearity constrains begging strategies and often results in counterintuitive escalation. Satiated chicks should not beg, yet they do. If hungry chicks should beg maximally, and chicks in average condition ( $X(t) = 0$ ) compete by begging maximally, linearity constrains them to also beg maximally when full, provided the costs of doing so are not overwhelming. Assumptions about linearity, brood size and mode of information transfer (vocal vs. non-vocal) limit the model at present, but could be relaxed. Even



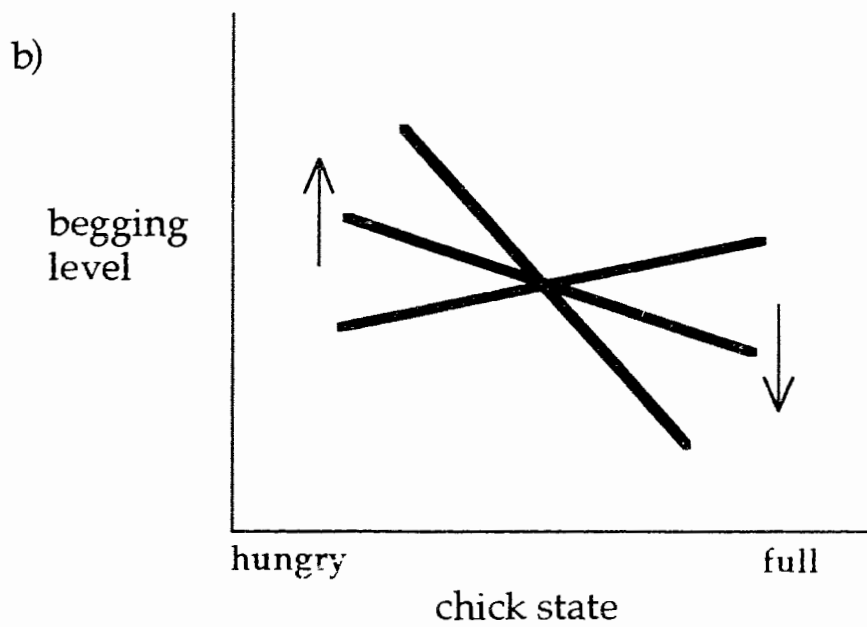
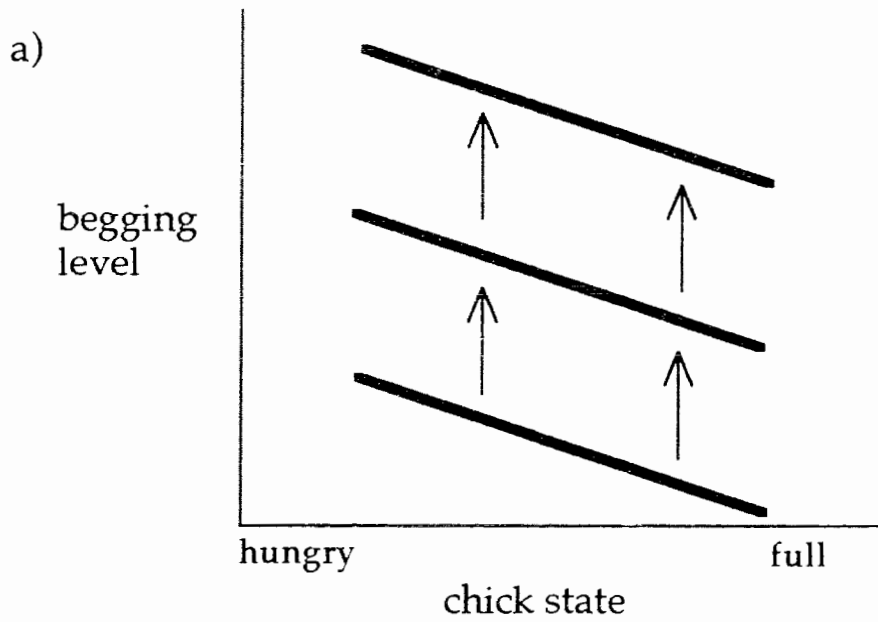


Figure 2.23. Two components of begging level: a) overall level can escalate, b) the slope of the begging-state relationship can change.

in its present form, the model leads to interesting predictions about the begging dynamics of different chicks in different environments.

The following chapters test some of the predictions arising from the model. In the model, parents evolved provisioning strategies based on their nestlings' begging. Chapters 3 and 4 look at the relationship between provisioning and begging in yellow-headed blackbirds. Chapter 3 deals with changes in allocation to the whole brood (an aspect not incorporated into the model), and Chapter 4 addresses within-brood provisioning to chicks of differing short- and long-term need and quality. The model predicts that begging will reflect hunger and that parents will feed according to begging, but does not predict whether parents will feed the quietest or the noisiest chicks.

The model suggests that strategies will evolve where siblings compete for food by begging. Chapter 5 tests the prediction that the level of begging is related to the level of competition within a brood, and Chapters 4 and 6 see if chicks increase begging in response to a nestmate's increase. Finally, and most interestingly, the model suggests that the sensitivity of begging to short-term need will vary with chick ability and long-term need. In particular, it predicts that males, even when in good condition or full, will beg more than females and that large chicks should sometimes beg less than small chicks even though they have a higher ability. While predictions about provisioning and competition are not unique to this model, and may be considered common lore, predictions about variation in sensitivity to state are unique. I test some of these predictions in Chapter 6.

## Chapter 3

The benefits of begging. I: Do parents bring more food?



## Introduction

Begging behaviour is generally believed to benefit nestlings because it induces their parents to bring more food. Studies covering several orders of birds show that parents respond to perceived whole-brood begging level. In particular, played-back begging calls elicited increased parental feeding visits (Muller and Smith 1978, Khayutin and Dmitrieva 1979, Harris 1983, Bengtsson and Ryden 1983); experimentally-muted gull (*Larus delawarensis*) chicks and intoxicated starling (*Sturnus vulgaris*) broods received deficient provisioning (Miller and Conover 1979, Litovich and Power 1992); and deafened parent doves (*Streptopelia risoria*) fed their young less (Nottebohm and Nottebohm 1971). These studies show that parents will visit more often when begging levels increase. The amount of food delivered, however, may not necessarily increase and may even decrease (Welham 1993). Studies of parents faced with hungrier or extra chicks show that they respond to the increased demand by bringing less food more often, by changing prey types or by changing allocation within a brood (e.g., Royama 1966, Tinbergen 1981, Lifjeld 1988, Whittingham and Robertson 1993).

Benefits to begging chicks may also vary over time. Parents may increase provisioning in response to short-term increases in begging, but may be less flexible over longer periods. In an observational study, Stamps et al. (1989) found no significant relationship between begging level and provisioning level of broods over a 12 day period, once the effects of brood sex-ratio were removed. The relationship between brood begging rates and feeding rates likely varies between families (Harper 1986, Hussell 1988); hence experimental studies within families may be necessary to detect responses to begging over long as well as short periods. Experimental studies of whole-

brood begging levels within families have not considered differences in parental response over periods longer than a day. A comparison of parental response to whole-brood begging levels across time scales, along with observations of how parents change provisioning, will provide a more complete view of the benefits that chicks receive from begging.

Yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) nest in marshes and lose many broods to predators (Young 1963, Ricklefs 1969, Clark and Wilson 1981). There is a distinct size hierarchy in the nest and brood reduction by starvation is common (Willson 1966, Richter 1984). Yellow-heads are highly sexually dimorphic, and males fledge at a significantly greater mass than females. The difference in size first appears several days after hatching (Willson 1966, Richter 1983). Broods of two to five nestlings beg quietly at first and increase their volume and persistence as fledging approaches at about 11 days (personal observation). Parents feed their nestlings, and themselves, primarily with emergent damselflies and dragonflies (Willson 1966, Orians 1966). Mothers bear the brunt of provisioning; males generally assist only at their primary nest (Willson 1966, Patterson et al. 1980, Gori 1988, personal observation).

This chapter investigates the parental response of yellow-headed blackbirds to experimentally enhanced whole-brood begging (via playback of recorded calls). I ask if parents change their provisioning schedule, and if they change the amount of food brought per visit or their allocation of food within a brood. I look at parental responses to both short-term (2 h) and longer term (5 day) increases in begging level.

## Methods

### Short-term playback experiment

I studied the begging and provisioning of yellow-headed blackbirds during May to July, 1991, at the Creston Valley Wildlife Management Area, a 7000 ha managed marsh in southeastern British Columbia, Canada. I used three study sites containing islands of cattail (*Typha* spp.) growing in 0.5-1.2 m of water. Two colonies of about 100 and 150 birds each nested at Leach Lake, and one colony of about 350 birds nested at Corn Creek.

By regularly searching the study area, I located nests as they were built and marked them with numbered wooden stakes. I tied small pieces of flagging tape (with the knot of the tape facing the nest), at least 8 m from the nest to aid in nest relocation while attempting to minimize investigation by aerial predators. I noted chick hatching date and order for each nest, and monitored clutch progress daily. All nestlings received paint marks on the head at hatching and coloured leg bands at 6-7 days. I measured chick mass, tarsus and outermost primary length daily. I did not band parents.

I recorded the begging calls of 7-11 day old nestlings from 6 nests in 1990 using a directional microphone. I edited the tapes to remove alarm calls and parental song, and copied the begging calls on to 6-min loop tapes, so that each tape played continuous calls from one brood only. I chose a tape randomly for each trial. Yellow-headed blackbird parents readily accepted foster chicks (personal observation), and I assumed that they would also accept recorded begging from unrelated chicks.

I selected 12 experimental nests (seven in colony A, two in colony B, Leach Lake, and three in Corn Creek) randomly from among those with chicks between 7-11 days old and with observable nests (some nests were built too high or in cattails too dense to see through without breaking down cover).

The brood size of experimental nests (i.e., chicks alive on the day of the trial) ranged from one to four with a mean of  $2.6 \pm 0.2$  chicks (all means are given  $\pm$  standard error). Six of the nests were likely the primary nests of a male (judged from their early initiation within a nest clump; without banded adults, I could not be certain). Trials ran on 12 days between June 3 and June 25, with each nest experiencing a single trial during this period.

Playback equipment consisted of a small speaker, tape player, timer, amplifier and 6 volt gel cell battery within a green aluminium box, mounted on a metal pole driven into the marsh substrate and camouflaged with wet cattails. Each unit faced its respective nest at a distance of 20-40 cm.

The 12 trials ran from 7:00 to 11:00 a.m. and consisted of 2 h of begging playback and 2 h of control (speaker on, but no playback). Six randomly chosen nests received the begging playback first, and six received it in the second period. During the experimental playback, begging was broadcast for 3 min in each 14 min period, and ran independently of parental visits. Playback volume was set at the level of a nest of three 9-10 day old chicks (approximately 70 dB at 3 m). Four nests were observed using a video camera, and eight using binoculars from a floating blind. I approached each nest three times (at the start, middle and end of the trial) to weigh the chicks and to turn the tape on or off. I did not record data for 30 min following these disturbances, since males, and sometimes females, frequently gave alarm calls during this time, and chicks were quiet. Hence, I collected 90 min of data for each 2 h treatment for each nest. To allow parent blackbirds to habituate to the experimental equipment, I placed the playback unit and either a floating blind or a mock video camera in position on the day before each trial.

I recorded the number of visits by each parent to the nest, the provisioning load size (on a scale of 1 to 5, where a load of size 1 did not show

outside the bill, 2 projected over less than a quarter of the bill, 3 projected out of a quarter to half the bill, 4 projected out of half to three-quarters, and a load of 5 projected along the entire bill) and the identity of the fed chick. Loads generally contained several items and prey frequently could not be identified reliably (particularly without video observation). I also recorded the presence or absence of noisy begging by chicks.

I analysed data using repeated measures analysis of variance (SYSTAT; Wilkinson 1988), with the number of provisioning visits by each parent, load size, or mass change during each treatment as the dependent variable; and treatment order and site as independent variables.

#### Long-term playback experiment

In 1993, I broadcast begging calls, using similar equipment, over 5 days at 11 nests in the two Leach Lake colonies, and set up dummy speakers as controls at another 11 nests (randomly assigned treatments). Equipment was removed for recharging at about noon one day and replaced the same time on the following day. While in place, tapes played for 5 min out of every 30 min during daylight, controlled by a timer and light sensor. Hence, begging was broadcast from noon until dusk on one day, and from dawn until noon on the next day. I did not observe parental visits over the experiment. I weighed and measured nestlings prior to equipment placement and after 5 days. I compared mean chick growth over the 5 days between experimental and control nests to probe for any long term parental response to enhanced begging. Since gender and age affect growth rate, I included the number of males per brood and the mean brood age at the start of the experiment (in days), as well as brood size, as covariates.



## Results

### Short-term playback experiment

Parents of both sex visited the nest about twice as often during the playback of begging calls as during the control treatment (Figure 3.1; treatment effect:  $F_{(1,8)}=13.35$ ,  $p=0.006$ ). Female parents visited more often than did males in both treatments (sex effect:  $F_{(1,8)}=7.87$ ,  $p=0.02$ ; sex by treatment interaction:  $F_{(1,8)}=2.38$ ,  $p=0.16$ ). Results were similar between the three sites, regardless of treatment order, with no significant interactions. No nest was visited less frequently during the playback treatment, and only one nest was visited equally during the two treatments.

Nestlings rarely stopped noisy begging during parental visits in the control period, but were frequently silent during the playback period (proportion of visits without loud begging by any chick in the nest; during playback = 0.24; during control = 0.06;  $z = 2.31$ ,  $p = 0.02$ , Wilcoxon matched pairs). During these silent visits, chicks appeared satiated and did not gape, rear or call at the appearance of a parent. Three parents tried to force food into a chick's closed bill. Following rejection, the parent frequently flew in a small circle, revisited and tried once more to feed a chick. In the nest with only one chick, the female flew around and tried to feed her chick 17 times before being successful with one load of food. On at least three occasions, parents approached the speaker very closely and appeared to peer into it while it was broadcasting begging.

During the control period, males fed nestlings at 6 of the 12 nests (those assumed to be primary nests). Of five other families with males available (one died before a trial) three were visited by the male only during the begging playback period. Two of these males were seen feeding their primary (non-experimental) family during the control period and the experimental

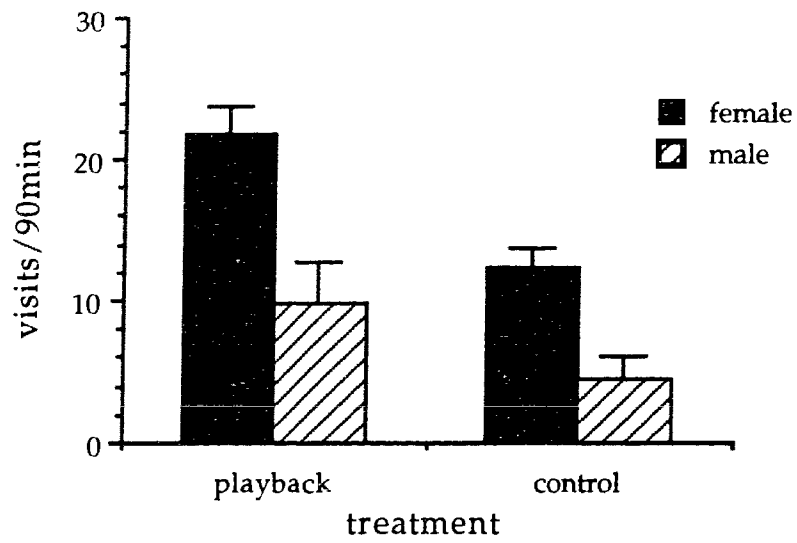


Figure 3.1. Parental provisioning visits (by females and males) to 12 yellow-headed blackbird nests during playback and control treatments (mean  $\pm$  se).

family during the begging playback. The behaviour of the third male away from the experimental nest is unknown, since he was watched by camera. Hence, some males changed not only the frequency of visits to a nest during the playback period, but switched from feeding one nest to feeding another.

Nestlings gained more mass during the 2 h begging period than during the control period, suggesting that the increased visits did represent an increase in provisioning (begging:  $+1.63 \pm 0.24$  g; control:  $0.00 \pm 0.28$  g; treatment effect  $F_{(1,7)}=11.85$ ,  $p=0.01$ , no effect of order or site, using mean mass change per nest, one nest excluded due to missing data). Within treatments, however, there was no relationship between mass change and number of feeding visits to individual chicks (during playback:  $r=0.18$ ,  $p=0.37$ ; during control  $r=-0.05$ ,  $p=0.81$ ; Pearson correlation between feeds and mass change per chick, no corrections made for gender, age or behaviour).

Load size did not change with treatment (begging:  $2.02 \pm 0.28$ ; control:  $2.02 \pm 0.22$ ; treatment  $F_{(1,7)}=0.22$ ,  $p=0.65$ , one nest was excluded because the female always blocked the view of her load). Parents tended to bring smaller loads later in the morning regardless of treatment (i.e., order by treatment effect:  $F_{(1,7)}=3.58$ ,  $p=0.10$ ). The increase in visits during playback therefore represented an increase in food brought to the nest. Loads varied from a single spider, caterpillar or damselfly up to 3 large dragonflies or 7 damselflies, and included combinations of prey types. I was able to determine prey type in both treatments for only 5 nests (and for only 59% of visits to those nests). There are no obvious trends in the amount of each prey type brought (Table 3.1), but the data are insufficient for further analysis.

While parents increased provisioning to both large and small broods during the begging treatment, the number of feeds per chick increased relatively more in small broods than in large broods (Figure 3.2;  $r=-0.57$ ,

Table 3.1

Number of each prey type fed to nestlings per visit during playback and control periods (mean for 5 nests; includes only those visits with identified prey)

treatment	adult dragonflies	adult damselflies	larval Odonates	small flies	others
playback	0.15 ± 0.08	1.31 ± 0.36	0.12 ± 0.05	0.17 ± 0.09	0.04 ± 0.03
control	0.07 ± 0.04	1.79 ± 0.60	0.16 ± 0.10	0.17 ± 0.14	0.11 ± 0.11



Figure 3.2. Increase in the number of parental provisioning visits per chick during the playback treatment, relative to the control treatment, for different brood sizes. Each point represents one brood.

$p=0.05$ ; Pearson correlation between brood size and per chick increase in feeding visits).

Once at the nest, parents did not allocate provisions between nestlings significantly differently during begging playback than during the control period: larger chicks received food at more visits than their smaller siblings (Figure 3.3; treatment effect:  $F_{(1,26)}=9.94$ ,  $p=0.004$ ; rank effect:  $F_{(1,26)}=7.36$ ,  $p=0.01$ ; treatment by rank interaction term:  $F_{(1,26)}=2.83$ ,  $p=0.11$ ; no effects of site or treatment order).

### Long-term playback experiment

Chicks in nests with playback broadcast over five days gained significantly more mass than did control chicks (Figure 3.4;  $F_{(1,16)}=6.00$ ,  $p=0.03$ ). Mass gain was also significantly related to age and gender covariates as well as to an interaction between brood size and treatment (the difference in mass gain between playback and control nests was greatest for broods of two;  $F_{(1,16)}=5.26$ ,  $p=0.04$ ). Tarsus growth tended to be greater in playback nests (Figure 3.4;  $F_{(1,16)}=3.41$ ,  $p=0.08$ ), and was also related to brood age. Primary growth reflected only brood age, and was equal between the two treatment groups ( $F_{(1,16)}=0.16$ ,  $p=0.69$ ). Since the playback broods contained more males (nestlings were too young to sex before the experiment) and were slightly younger at the start of the experiment (both differences non-significant), the experiment is potentially confounded (although I have attempted to control for potential biases statistically), and the results should be interpreted cautiously.

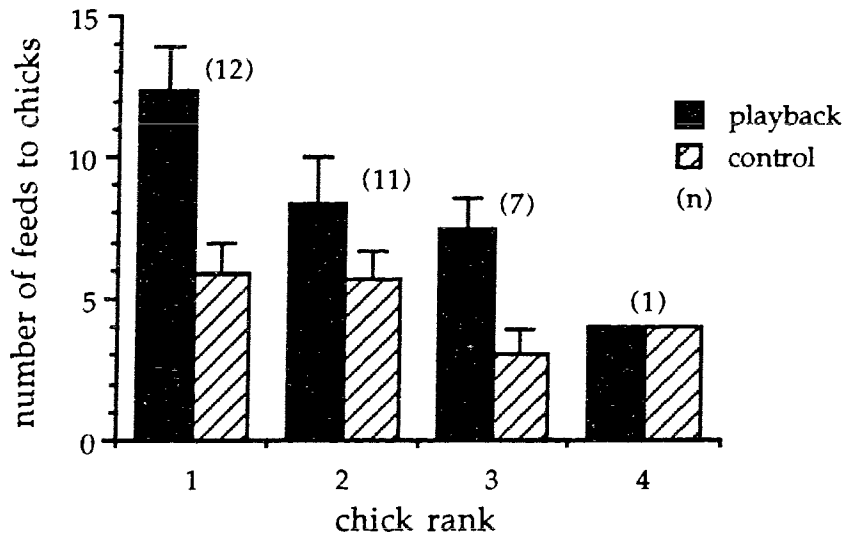


Figure 3.3. Allocation of food to individual nestlings of each size rank within a nest during playback and control periods (mean  $\pm$  se).

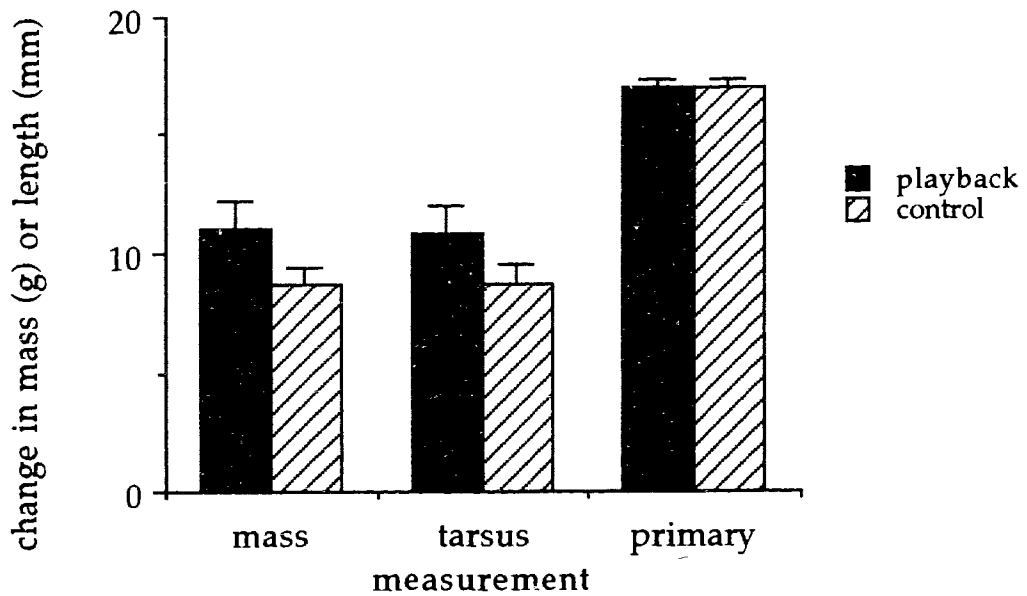


Figure 3.4. Growth of nestlings over 5 days in control and playback treatments in the long-term playback experiment (mean  $\pm$  se).

## Discussion

Parent yellow-headed blackbirds increased their total provisioning when faced with experimentally-inflated begging levels for 2 h. Both males and females almost doubled their feeding visits without changing load size, and broods gained more mass. Some males also changed their provisioning tactics, switching from feeding their primary to a secondary or tertiary nest, a result supporting the recent findings of Whittingham and Robertson (1993) for male red-winged blackbirds (*Agelaius phoeniceus*). The short-term playback experiment demonstrates that, over a two-hour period, nestlings benefit from increased whole-nest begging levels.

The results of the long-term playback experiment suggest indirectly that parents also work harder over longer time periods. Nestlings with enhanced begging grew more (mass and perhaps tarsus) over 5 days when compared with control broods. Primary length, which increases linearly with age in yellow-headed blackbirds, did not vary between treatments. Two possible confounds reduce the strength of these results. First, an unexpected interaction between treatment and brood size complicates interpretation. The largest chick fledged prior to the end of the 5 day treatment period in two of the control broods, reducing brood size from three to two. Since the largest chick in a brood may have grown the most, my mean measurements for these nests may be underestimated. Second, experimental nestlings, upon hearing playback, may have reduced their energetic expenditures by begging less. If part of the decision about when to beg depends on providing a minimum overall begging level to parents (Miller and Conover 1979, Nottebohm and Nottebohm 1971), nestlings with freely-broadcast begging may have reduced their begging levels independently of a decrease in hunger level. Recent evidence suggests that energetic costs of begging are low (John

McCarty, Cornell University, personal communication), but quieter chicks could conceivably channel more energy into growth.

Whittingham and Robertson (1993) found that red-winged blackbird parents increased the number of provisioning visits to broods of experimentally-deprived nestlings, but that they brought less food per load. The birds reduced their travel distance by shifting their foraging site from distant woodland to the marsh around the nest. The yellow-headed blackbirds in this study did not appear to change their load size or their foraging site. Yellow-headed blackbirds generally nest farther from marsh edges than do red-winged blackbirds (Willson 1966, Orians 1980, personal observation). Parents in the study population usually foraged for emergent insects within the male's territory and rarely flew beyond the edges of the colony; hence, reducing travel distance seems an unlikely tactic in this population. Other populations of yellow-headed blackbirds forage farther from the nest (Gori 1988), and would provide an interesting comparison.

Although load size did not change between treatments in the short-term experiment, parents may have switched foraging tactics in a manner not obvious from load size alone. Parent starlings faced with enlarged broods, foraged closer to the nest for lower quality prey (Tinbergen 1981). In yellow-headed blackbird nestlings, the difference in mass gain between the playback and control treatments, as well as the satiation of chicks during the begging playback, could result from eating equally-sized but less nutritious food (i.e., mass changes probably reflect stomach contents rather than growth in the short-term experiment). I was unable to describe load contents adequately without video records or collaring nestlings, since yellow-headed blackbirds bring several prey (in combinations of species) at each visit. Parents did not



change prey type in any obvious or consistent manner between treatments in the visits with observed prey type (though admittedly, the sample is small).

Individual chicks in larger broods benefitted less from increased whole-brood begging levels since their parents increased their feeding visits by a smaller amount per chick than parents of small broods. Experimental manipulations of brood size reveal a lower delivery rate per chick in larger broods (Henderson 1975, Nur 1984, Martins and Wright 1993). Parents feeding a large brood may have less flexibility to vary self-feeding rate, and may be less able to respond to short-term increases in brood demand (Martins and Wright 1993).

Parent yellow-headed blackbirds did not change their pattern of food allocation within the brood in response to changed begging levels: large nestlings received more food than their smaller siblings during both the playback and control treatments. Without measurements of individual begging levels, I cannot link allocation patterns to begging in this experiment. All chicks vocalized less frequently during the playback treatment, but I cannot tell whether this decrease in begging followed satiation first of the large, and then of the small chicks, as suggested by Bengtsson and Ryden (1983). I found no relationship between the number of feeds to nestlings and their mass gain within a treatment. Identification of prey type and estimation of the energy fed to each chick, coupled with corrections for the growth rates of chicks of different ages, sexes and conditions, seem necessary to determine whether such a relationship exists.

The results described in this chapter show that parents respond very strongly to short-term increases in overall begging level, with chicks becoming satiated and silent in many cases, and suggest that parents might also respond to long-term begging rates. Other studies show varied responses

to increased chick demand. For example, while kestrel (*Falco tinnunculus*) males increased provisioning to enlarged broods (Masman et al. 1989), osprey (*Pandion haliaetus*) males did not (Green 1993). Rhinoceros auklets (*Cerorhinca monocerata*) increased provisioning to a fostered larger chick during the middle but not the end of the nesting period (Bertram et al. 1994). Red-winged blackbirds in the eastern U.S.A. were almost entirely unresponsive to played-back begging calls (Anne Clark, Wen-Hsiu Lee, SUNY, Binghamton, personal communication). Parents likely increase provisioning only when the benefits of doing so outweigh the costs, but just when this should be the case needs further work.

## Chapter 4

### The benefits of begging. II: Intra brood allocation



## Introduction

Parents of altricial nestlings must decide how to allocate provisions within as well as between broods. Begging is one potential avenue through which offspring can try to influence this decision. Increased begging by the brood as a whole increases overall provisioning (Chapter 3). The begging model presented in Chapter 2 suggests that parents should be responsive to the begging levels of individual chicks. In this chapter, I ask whether the level of begging by individual nestlings can change the allocation patterns within a brood.

Contemporary siblings share the benefits of higher overall provisioning (Chapter 3), but they disagree about how provisioning should be allocated. Parents view similar chicks as equally worthy of investment, but for a chick, the marginal value of a food item to a full-sibling is devalued by half relative to self (Trivers 1974). This genetic conflict may manifest itself as competition between siblings (Hamilton 1964, Parker et al. 1989). Such rivalry is frequently asymmetrical since broods rarely include chicks of equal competitive ability. In extreme cases, dominant chicks may control access to provisions by threatening or killing their juniors (reviews in O'Connor 1978, Mock 1984).

From a parent's perspective, larger, older or healthier nestlings may be more valuable (via higher survival probability; e.g., Clark and Wilson 1981, Richter 1982) and may therefore receive more investment. Parents may also provision according to the need of their nestlings (a basic tenet of parental care; Clutton-Brock 1991). Begging potentially contains information about both need and value (see Chapters 1, 2). Provisioning may be influenced by both types of information: the difficulty lies in considering how need and ability (or quality) interact. A large hungry chick should be able to influence

food allocation by increasing its begging, but can a small hungry chick do the same?

Several studies have observed a positive correlation between some aspect of begging (vocalization or positioning in the nest) and provisioning (Ryden and Bengtsson 1980, Reed 1981, Greig-Smith 1985, Gottlander 1987, Stamps et al. 1989, Teather 1992). Smith and Montgomerie (1991) deprived nestlings of food and found an increase in begging level coupled with an increase in provisioning level. Litovich and Power (1992) manipulated begging levels downwards by satiating or intoxicating chicks and found that parents fed these chicks less. These results demonstrate that chicks can affect food allocation via begging, but they do not consider the effects of chick ability or quality.

Studies in asynchronously hatched broods, with chicks of differing ability and quality, have found the opposite pattern: late-hatched nestlings generally beg more than their larger siblings (Khayutin and Dmitrieva 1977, Ryden and Bengtsson 1980, Bengtsson and Ryden 1981, Fujioka 1985, Greig-Smith 1985, Drummond et al. 1986, Stamps et al. 1989) but are fed less (Lockie 1955, Ryden and Bengtsson 1980, Bengtsson and Ryden 1981, Richter 1984, Fujioka 1985, Greig-Smith 1985, Drummond et al. 1986, Litovich and Power 1992) with the exception of budgerigars (*Melopsittacus undulatus*; Stamps et al. 1989). As an added complexity, Smith and Montgomerie (1991) found that siblings increased their begging in response to the increase in the begging of manipulated chicks. Larger siblings might be able to swamp the begging efforts of their juniors.

Redondo and Castro (1993) found a general relationship between intrabrood begging and subsequent mass gain in magpies (*Pica pica*), but found that this relationship was highly variable, and unpredictable between

broods. They suggest that factors other than begging may be important in provisioning decisions (including offspring size, as well as parental sex and nestling position), and point out that parental response to begging may not be straightforward. My study attempts to unravel some of this complexity.

In this chapter, I evaluate the benefits of vocal begging to individual chicks in broods of yellow-headed blackbirds (*Xanthocephalus xanthocephalus*) to test the hypothesis that begging benefits individuals in broods of chicks with different quality, ability and need. Yellow-headed blackbird broods hatch asynchronously, and nestlings vary considerably in size (Willson 1966, Richter 1984). Relatively small chicks in a brood often starve, and hence have a lower potential reproductive value.

I manipulated begging levels by changing chick hunger and monitored parental response to begging. In experiment 1, I altered the hunger level of one or two chicks within a brood and compared the begging and feeding of these chicks to that of their unmanipulated siblings, predicting that hungry chicks would beg more and be fed more, and that satiated chicks would beg less and receive less food. In experiment 2, I deprived each chick of a brood in turn, and compared the begging and feeding of these deprived chicks, predicting that small chicks, who might be out-competed by their siblings, or subject to negative parental bias, would benefit less from begging than their larger siblings. In both experiments, I measured food allocation before and after treatments to determine whether chicks can influence provisioning via begging.

## Methods

### Experiment 1

I manipulated the hunger level of 16 nestling yellow-headed blackbirds in 11 nests in 1991, choosing broods randomly from among those with three or four nestlings, known histories, and with accessible, visible nests. Nestlings ranged from six to ten days old, old enough to beg vigorously and young enough not to fledge prematurely when handled. I placed a floating blind within 10 m of the nest on the afternoon before each trial to give parents time to habituate. Each trial was observed from the blind, using binoculars, by one of two observers.

Experimental chicks were removed from the nest and held in the blind for an hour. During this period they were either deprived of food or fed to satiation with a piece of moistened dog food every 5 min. One hour of food deprivation always elicited increased levels of begging in three hand-reared nestlings (not involved in this experiment), and was not longer than chicks commonly wait between feeds (personal observation). I assumed an hour without food would result in a hunger level within the natural range experienced by yellow-headed blackbird chicks. Nestlings were kept in a covered, heated container, sitting inside a plastic strawberry punnet lined with toilet paper. Fecal pellets were removed promptly. Experimental chicks were returned to their nest after an hour, immediately following a parental visit to minimize any disturbance.

I removed one nestling from broods of three ( $n=6$ ), and two nestlings from broods of four ( $n=5$ ), leaving two nestlings in the nest during the treatment period. In broods of four, one chick was deprived and one was fed, and in broods of three, the removed chick was randomly assigned to be deprived or fed. All broods had two "control" chicks, ten had a "deprived"

chick, and six had a "fed" chick. I chose experimental nestlings randomly from the three largest in each nest; the smallest nestlings in four-chick broods were frequently in poor condition, and were extremely hungry without manipulation. I did not replace removed chicks with foster chicks from other nests during the one hour manipulation period due to the difficulty of finding similar chicks nearby and the added disturbance of walking around the study area during an experiment.

I recorded the begging level of each nestling and the frequency of feeding by parents during two observation periods (60 min pre-treatment and 30 min post-treatment; by 30 min after a treatment, nestling hunger levels reflected parental feeding levels rather than the experimental treatment). Measured aspects of begging level included intensity, loudness, type, who vocalized first, who vocalized longest after the visit, and the number of begging episodes when the parents were absent ("extra" begs; Table 4.1). Nestlings' vocal response to a "model parent" was measured when experimental nestling(s) were removed from the brood, and again when they were replaced. I initially used a stuffed adult as my model, but found that chicks responded similarly to my hand. I rustled the surrounding cattails and poked towards the chicks three times.

For analysis, I subtracted measurements of begging and feeding during the last 30 min pre-treatment from the post-treatment values, leaving net response to the treatment as the variable of interest. I divided the control chicks into two groups (small and large) and used a randomized block analysis of variance (nests as blocks) with missing values.



Table 4.1

Aspects of begging in yellow-headed blackbird nestlings measured in experiment 1 (1991) and experiment 2 (1992).

aspect	level	criteria
intensity		mean begging effort
	0	no visible response
	1	movement, no vocalization
	2	single vocalization
	3	$\leq 1$ vocalization per second
	4	$> 1$ vocalization per second
loudness		mean volume over treatment period, no zero values
	1	quiet
	2	moderate
	3	loud
first		proportion of visits in which chick begs first, ties included
start*		mean rank order that a chick starts to vocalize
last		proportion of visits in which chick stops begging last after visit, ties included
extra beg		number of vocalization bouts in absence of parents
type	II	total number of bouts of "exaggerated" begging **
length*		total number of seconds vocalizing in presence of parent, during treatment period
extra length*		total number of seconds vocalizing between visits, during treatment period

\* measured in experiment 2 only

\*\* (type II calls are loud calls  $\geq 1$  s apart given immediately after a feeding visit or between visits; see Muller and Smith 1978)

## Experiment 2

The second experiment compared the begging and feeding of three siblings when each was deprived of food. In 1992, I deprived each chick of seven three-chick broods in turn, and the three largest of three four-chick broods in turn, again selecting broods from among those with known history. Nestling ages ranged from five to eight days, younger than in experiment 1 to give a wider range of nestling sizes within a nest (growth rate decreases after eight days; Richter 1984). I used a video camera to record the experiment, allowing me to measure the duration of vocalizations and the order in which chicks started begging. I set a mock camera in place at least an hour before recording to allow for habituation. Parents adjusted to the presence of a camera much faster than to the presence of a blind, even though the camera was closer to the nest.

I recorded begging and feeding during four periods: 30 min before any treatment (period 1), and 30 min following the first provisioning visit after the return of each of the three chicks to its nest (periods 2, 3 and 4 respectively). Each nestling, in random order, was removed from its nest and held in a heated container without food for 20-80 min. Rather than equal periods of food deprivation, in this experiment I aimed for equal motivation to beg, so that I could examine the parental response to differently-sized begging chicks. To this end, I tested the nestlings' begging response every five minutes, using light and noise as stimuli. Full chicks did not respond to either stimulus; hungry chicks responded to light and noise; very hungry chicks responded to noise alone. When a nestling begged continuously and loudly in response to a tap in the dark on two consecutive tests, it was returned to the nest.

I ranked chicks as "big", "mid" and "small" by their mass and tarsus length (and refer to the four observation periods as control, big deprived, mid deprived and small deprived). Big chicks had a mean mass ( $\pm$  s.d.) of  $33.69 \pm 7.18$  g, mid chicks  $27.05 \pm 7.34$  g and small chicks  $20.51 \pm 6.45$  g. Most chicks were too young to sex; hence I could not choose nests to control for gender effects. More big chicks turned out to be male (6/10); more mid chicks were female (7/10). Of the small chicks that survived long enough to be sexed, half (3/6) were female.

The video recordings were transcribed by an observer blind to the order of chick deprivation. Measured aspects of begging included intensity, loudness and type, as described above, and also the order that nestlings started to vocalize, and the total length of vocalization both during parental visits and between visits (Table 4.1).

I analysed data with repeated measures analysis of variance, using begging and feeding of each chick pre-and post-deprivation as dependent variables, and treatment and size as levels.

## Results

### Experiment 1

During the hour before manipulation, chicks fed by their parents more frequently vocalized first ( $z=-1.75$ ,  $p=0.04$ ), begged more intensely ( $z=-2.52$ ,  $p=0.006$ ), and called louder ( $z=-1.75$ ,  $p=0.04$ ) than unfed chicks on any given parental visit to the nest (Wilcoxon matched pairs, one-way test,  $n=11$ , using mean values for each visit for the fed chick, and the mean of the mean value for other nestlings). Fed chicks did not beg more frequently in the absence of parents prior to each visit ( $z=-0.10$ ,  $p=0.46$ ) and uttered fewer type II, exaggerated calls ( $z=2.39$ ,  $p=0.01$ ).

Unmanipulated begging levels were related to a chick's relative size within a brood, with smaller chicks begging first less often, begging last more often and giving more type II and extra begs (Table 4.2). Loudness and intensity were not significantly related to chick rank. Larger chicks received more feeding visits from their parents (Figure 4.1).

After the one hour hunger manipulation, deprived nestlings begged more in response to a model parent; satiated and control nestlings begged less (Figure 4.2). During the one hour treatment period, control nestlings, who remained in the nest, received more food than usual (i.e., parents did not reduce visits in proportion to the temporary brood reduction), and were probably less hungry as a result.

Large and small control chicks begged similarly during observation periods; hence my comparisons use pooled controls in orthogonal comparisons. Fed nestlings begged less intensely than controls, but did not differ in other aspects. Deprived nestlings begged more intensely, louder, were first and last more frequently, and uttered more type II and extra begs (Table 4.3).

With sexes combined, parents responded to the treatment by feeding satiated chicks considerably less often and feeding deprived chicks twice as often ( $F_{(3,24)}=15.4$ ,  $p<0.001$ ; Figure 4.3). Males and females each fed deprived chicks significantly more (females:  $F_{(1,24)}=34.73$ ,  $p<0.001$ ; males:  $F_{(1,24)}=3.53$ ,  $p=0.035$ , one-tailed), but analysed separately, neither fed satiated chicks significantly less.

To examine the relationship between begging levels and feeding levels, I plotted the change in provisioning rates after treatment against the various measures of change in begging. With treatments pooled, increased provisioning rates were positively correlated with changes in nestling begging

Table 4.2  
 Begging in unmanipulated nestlings in relation to size (mean  $\pm$  se).

aspect	size rank				F <sub>(1,26)</sub> *	p **
	1	2	3	4		
first	0.39 $\pm$ 0.06	0.25 $\pm$ 0.04	0.30 $\pm$ 0.04	0.11 $\pm$ 0.05	5.94	0.02
last	0.20 $\pm$ 0.04	0.17 $\pm$ 0.05	0.42 $\pm$ 0.10	0.44 $\pm$ 0.12	6.31 <sup>^</sup>	0.02
extra beg	0.82 $\pm$ 0.33	1.36 $\pm$ 0.39	3.27 $\pm$ 0.49	4.60 $\pm$ 1.81	25.56	0.001
type II	0.18 $\pm$ 0.12	0.27 $\pm$ 0.20	0.27 $\pm$ 0.14	1.40 $\pm$ 0.51	6.94	0.01
intensity	2.07 $\pm$ 0.14	2.13 $\pm$ 0.13	2.09 $\pm$ 0.15	1.79 $\pm$ 0.39	0.78	0.38
loudness	2.07 $\pm$ 0.11	2.07 $\pm$ 0.10	2.05 $\pm$ 0.11	2.25 $\pm$ 0.25	0.69	0.41

\* analysis of variance, blocked by nest, rank as continuous, proportional data transformed

\*\* one-tailed

<sup>^</sup> F<sub>(1,22)</sub>, missing value for one nest

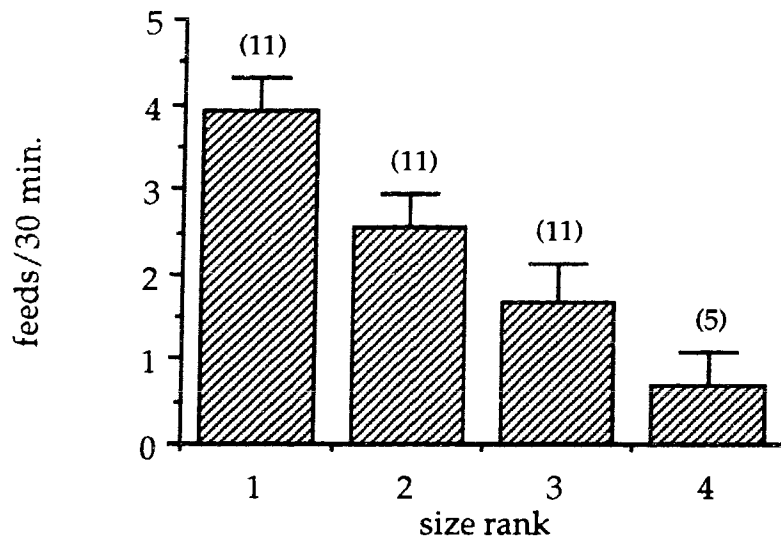


Figure 4.1. Mean number of feeding visits to chicks of each size rank during 30 min prior to manipulation. Larger chicks receive more food ( $F_{(3,24)}=14.36$ ,  $p<0.001$ ; blocked by nest).

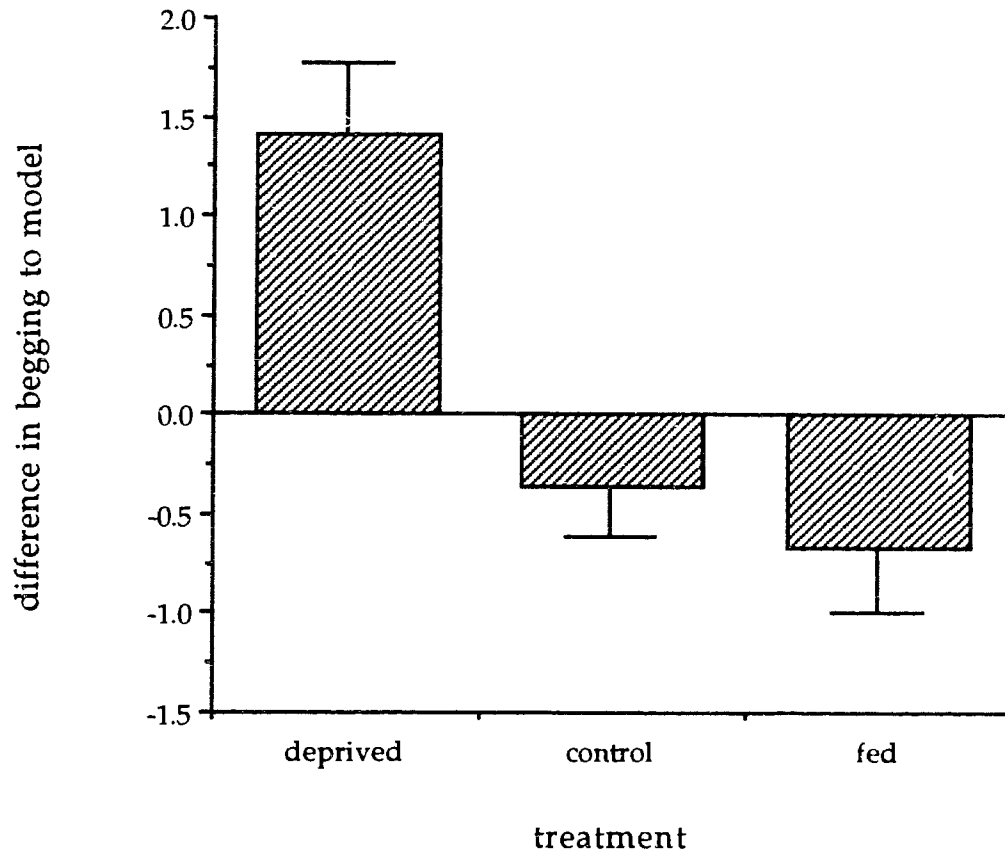


Figure 4.2. Nestling vocalization in response to a model parent (scored out of three). Columns represent the mean change in begging (i.e., score after treatment minus score prior to treatment) and bars show standard errors. Deprived chicks increased their begging ( $z=2.39$ ,  $p=0.01$ , one-tailed Wilcoxon matched pairs), fed chicks significantly decreased ( $z=-1.63$ ,  $p=0.05$ , one-tailed) and control chicks did not change begging ( $z=-1.38$ ,  $p=0.17$ , two-tailed). Treatment significantly affected begging level (KW=13.86,  $p=0.001$ ,  $df=2$ , Kruskal-Wallis non-parametric analysis of variance).

Table 4.3

Change in begging after manipulation of hunger (mean  $\pm$  se).

measure	treatment			F <sup>^</sup>	p	df <sup>^^</sup>
	controls*	deprived	fed			
first	-0.13 $\pm$ 0.04a**	0.39 $\pm$ 0.12b	-0.21 $\pm$ 0.05a	13.8	0.001	3,20
last	-0.09 $\pm$ 0.09a	0.32 $\pm$ 0.13b	-0.15 $\pm$ 0.09a	4.12	0.02	3,16
intensity	-0.47 $\pm$ 0.15a	0.07 $\pm$ 0.11b	-1.43 $\pm$ 0.33c	5.01	0.008	3,24
loudness	-0.15 $\pm$ 0.07a	-0.04 $\pm$ 0.11b	-0.15 $\pm$ 0.12a	2.07	0.14	3,18
type 2	-0.14 $\pm$ 0.25a	2.30 $\pm$ 1.78b	0.00 $\pm$ 0.45a	2.01	0.14	3,18
extra begs	-1.86 $\pm$ 0.39a	1.80 $\pm$ 0.71b	-3.33 $\pm$ 1.76a	8.09	0.001	3,24

\* pooled small and large controls

\*\* means followed by different letters are significantly different (orthogonal contrasts except for begging intensity, where I used Bonferroni corrections)

<sup>^</sup> analysis of variance, randomized block with missing values, blocked by nest, proportional data transformed

<sup>^^</sup> missing values for some nests, due to poor visibility



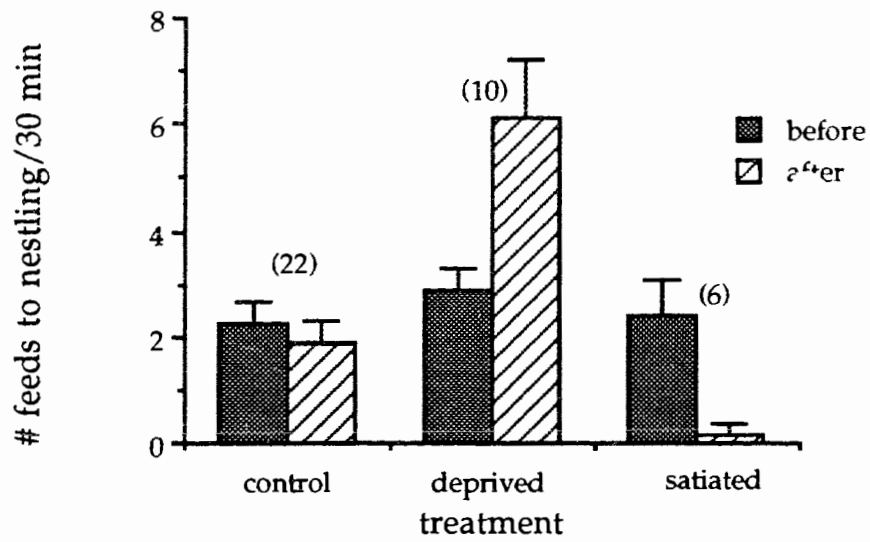


Figure 4.3. Feeding visits to deprived, control and satiated chicks, before and after hunger manipulation. Deprived chicks were fed more often ( $F_{(1,24)}=29.52$ ,  $p<0.001$ ); satiated chicks were fed less often ( $F_{(1,24)}=7.32$ ,  $p=0.01$ ).

intensity as well as with the frequency of begging first and last, and the number of type II and extra begs (Figure 4.4). The change in provisioning was not related to change in loudness. These correlations must be interpreted with caution since they include data from several chicks within a nest, violating assumptions of independence. I thus examined the correlations within treatments. In this reduced sample, changes in begging and provisioning were not significantly correlated, though 18 of 24 measurements were positive (and four of the six negative correlations applied to satiated chicks). Low power renders judgment inconclusive.

## Experiment 2

Before deprivation, chicks receiving food begged significantly more intensely and tended to start vocalizing relatively earlier and to beg for longer than unfed chicks (Table 4.4). Fed chicks did not beg more loudly, utter more type II begs, or vocalize more frequently in the absence of parents prior to each visit.

Food deprivation significantly changed several aspects of begging, resulting in relatively earlier starts to vocalization, more intense begging, and longer periods of vocalization both during and between parental visits (Table 4.5). Deprived nestlings did not call significantly more loudly, or beg last significantly more frequently, though trends were in the predicted direction. Size also affected begging. Smaller nestlings begged significantly more intensely than larger nestlings, started to beg sooner, and begged last more often. Relative nestling size was not related to loudness or length of vocalization. Chicks of different size did not respond to the hunger treatment differently in any of the measured aspects of begging (i.e., there were no significant treatment by size interaction effects).

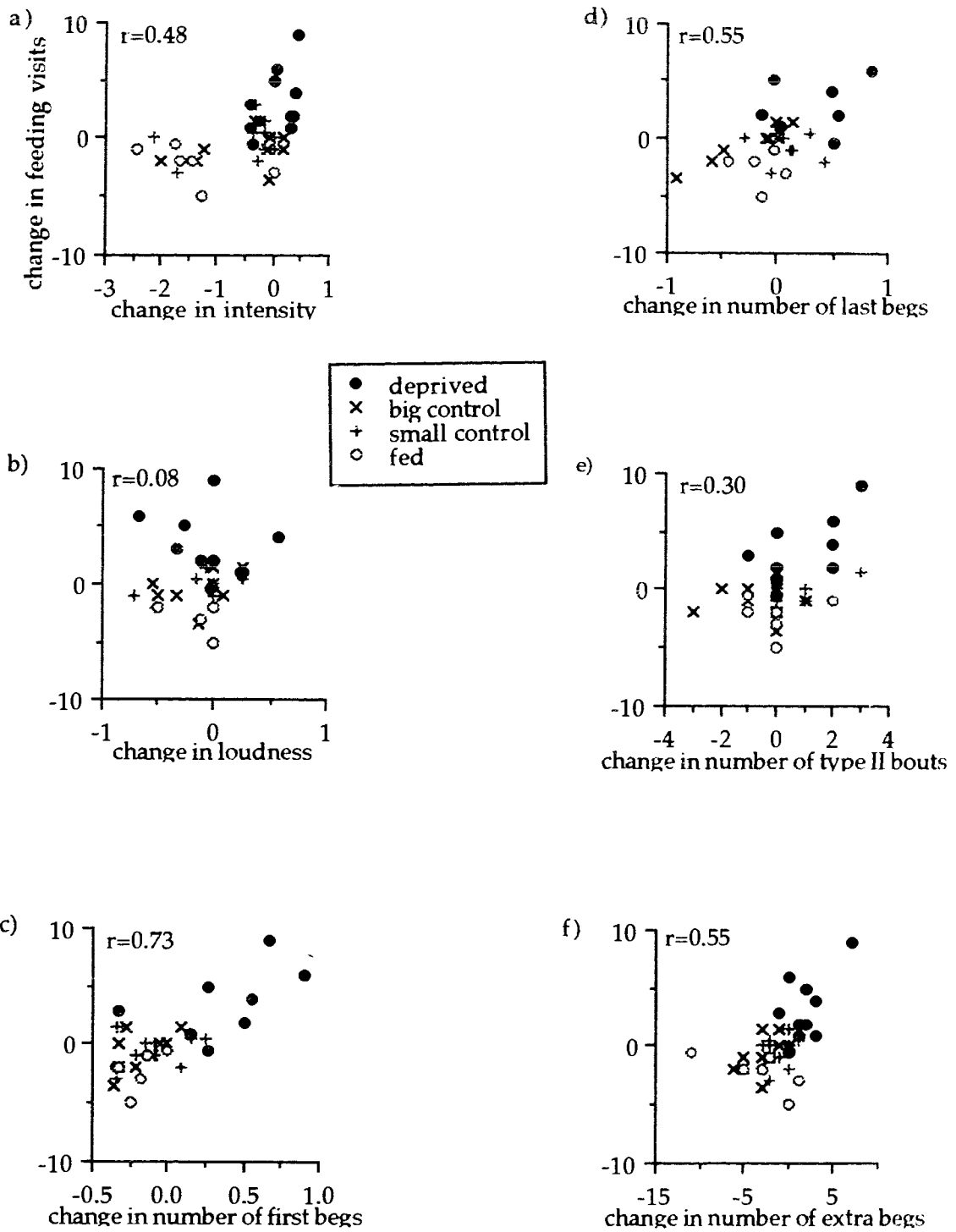


Figure 4.4. Change in the number of feeding visits against change in various aspects of begging level: a) intensity, b) loudness, c) first begs, d) last begs, e) type II begs, f) extra begs.

Table 4.4  
 Begging levels of fed and unfed chicks before manipulation in 1992  
 (mean  $\pm$  se).

aspect	fed	not fed	Z*	p**
intensity	3.01 $\pm$ 0.16	2.69 $\pm$ 0.27	-1.69	0.045
length	16.93 $\pm$ 2.13	14.48 $\pm$ 2.82	-1.24	0.11
loudness	2.37 $\pm$ 0.19	2.27 $\pm$ 0.24	-0.67	0.25
start	1.36 $\pm$ 0.17	1.84 $\pm$ 0.14	1.54	0.06
last	0.47 $\pm$ 0.10	0.45 $\pm$ 0.10	0.06	0.43
type II	0.03 $\pm$ 0.03	0.04 $\pm$ 0.03	0	0.5
extra begs	0.29 $\pm$ 0.12	0.30 $\pm$ 0.11	0.31	0.38

\* Wilcoxon matched pairs, n=9 (no provisioning to one nest)

\*\* one-tailed

Table 4.5  
 Begging by big, mid and small chicks before and after deprivation, 1992,  
 (mean  $\pm$  se).

size	aspect of begging					
	intensity	loudness	start	last	length	extra length
<b>before</b>						
big	2.42 $\pm$ 0.27	2.11 $\pm$ 0.33	1.64 $\pm$ 0.13	0.30 $\pm$ 0.11	75.50 $\pm$ 20.66	14.50 $\pm$ 7.11
mid	2.83 $\pm$ 0.22	2.17 $\pm$ 0.23	1.70 $\pm$ 0.09	0.46 $\pm$ 0.09	74.50 $\pm$ 17.50	25.20 $\pm$ 12.53
small	2.91 $\pm$ 0.28	2.09 $\pm$ 0.34	1.86 $\pm$ 0.15	0.59 $\pm$ 0.08	88.56 $\pm$ 26.24	24.89 $\pm$ 9.02
<b>after</b>						
big	2.90 $\pm$ 0.17	2.35 $\pm$ 0.20	1.22 $\pm$ 0.06	0.45 $\pm$ 0.09	120.00 $\pm$ 18.01	37.30 $\pm$ 15.17
mid	3.21 $\pm$ 0.14	2.42 $\pm$ 0.21	1.42 $\pm$ 0.10	0.54 $\pm$ 0.08	138.00 $\pm$ 19.51	88.73 $\pm$ 29.30
small	3.30 $\pm$ 0.18	2.40 $\pm$ 0.20	1.54 $\pm$ 0.13	0.73 $\pm$ 0.10	147.40 $\pm$ 25.56	45.4 $\pm$ 14.52
<b>hunger</b>						
F(1,8)	5.80	1.62	23.03	4.77	25.02	5.75
p	0.04	0.24	0.001	0.06	0.001	0.04
<b>size</b>						
F(2,16)	3.89	0.24	3.6	4.86	0.1	2.55
p	0.04	0.78	0.05	0.02	0.45	0.11
<b>interaction</b>						
F(2,16)	0.24	0.42	0.54	0.59	0.29	0.82
p	0.79	0.67	0.59	0.56	0.76	0.46

The number of provisioning visits to nestlings increased following deprivation and increased with relative chick size (hunger effect:  $F_{(1,7)}=4.41$ ,  $p=0.04$ ; size effect  $F_{(2,14)}=3.74$ ,  $p=0.03$ , both one-tailed; Figure 4.5). Parents did not respond differently to the deprivation of large versus small chicks (interaction term:  $F_{(2,14)}=0.91$ ,  $p=0.43$ ).

Although small chicks received more feeding visits after deprivation than before, parents rarely altered the qualitative pattern of food allocation within a brood. In nine of ten families, big chicks were fed more than their siblings in the "big deprived" period, whereas small chicks were only fed more than their nestmates in two of ten families in the "small deprived" period. Small chicks generally received a higher proportion of parental feeding visits, but did not receive more than their larger siblings (size effect:  $F_{(2,14)}=6.62$ ,  $p=0.01$ ; treatment effect:  $F_{(3,21)}=0.89$ ,  $p=0.46$ ; interaction:  $F_{(6,42)}=0.18$ ,  $p=0.58$ ; proportional data transformed; Figure 4.6).

To determine if the inability of small chicks to beat their siblings was due to competing behaviour of their siblings, I plotted the change in begging of each deprived chick against the mean change in begging of its siblings for four aspects of begging that increased following treatment (vocalization length during and between visits, begging intensity and early begging; Figure 4.7). Since rank measurements are not independent, I calculated the proportion of visits when each nestling begged first (including ties). Deprived chicks vocalized longer (see Table 4.5), but their siblings also begged longer during the same periods. Deprived chicks begged more intensely, but their siblings also increased their begging intensity. The six correlations between vocalization length of the experimental chick and of its siblings (during and between parental visits, separate correlations for each treatment period) were all positive, five of them strong ( $r \geq 0.65$ ). Two of the three correlations

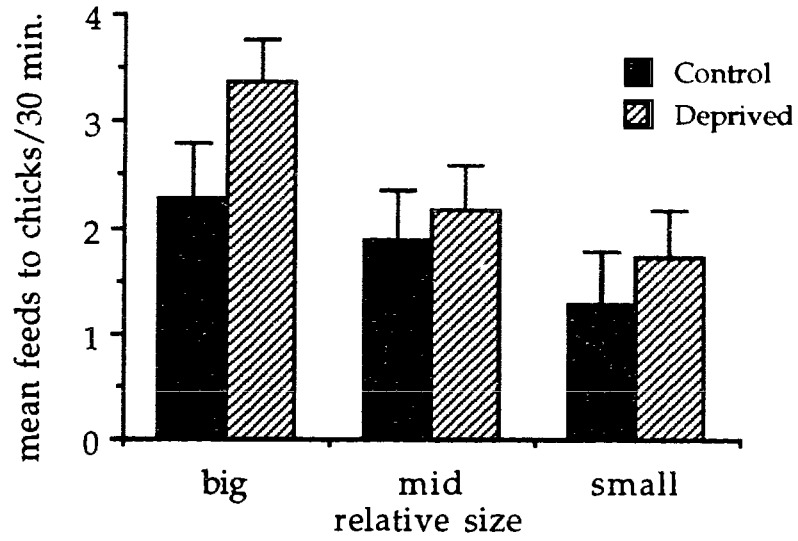


Figure 4.5. Feeding visits to chicks during the control period (30 min) and the periods during which each was deprived (mean  $\pm$  standard error).

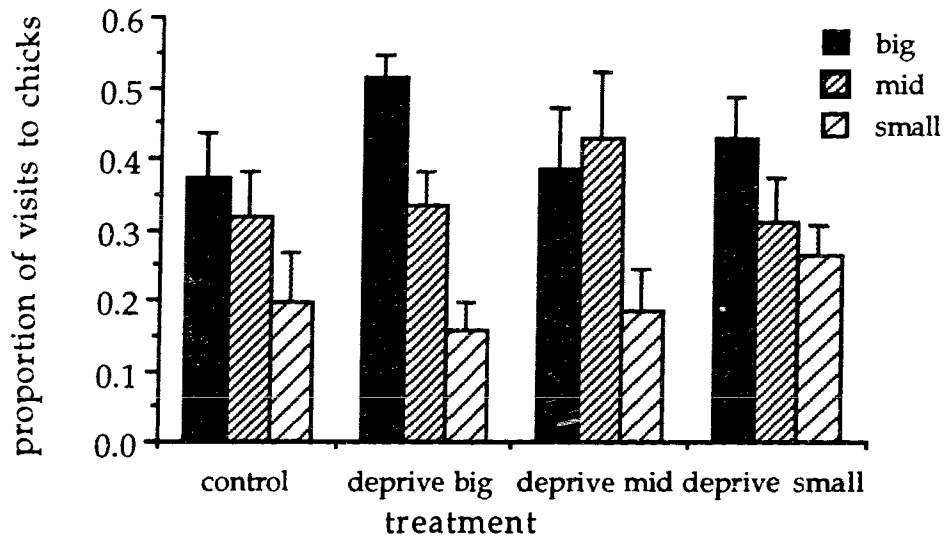


Figure 4.6. Proportion of visits to all chicks during control period and following the deprivation of each chick (mean  $\pm$  standard error). Proportions are calculated including visits to the smallest chick in 4-chick broods, and hence columns may total less than one.



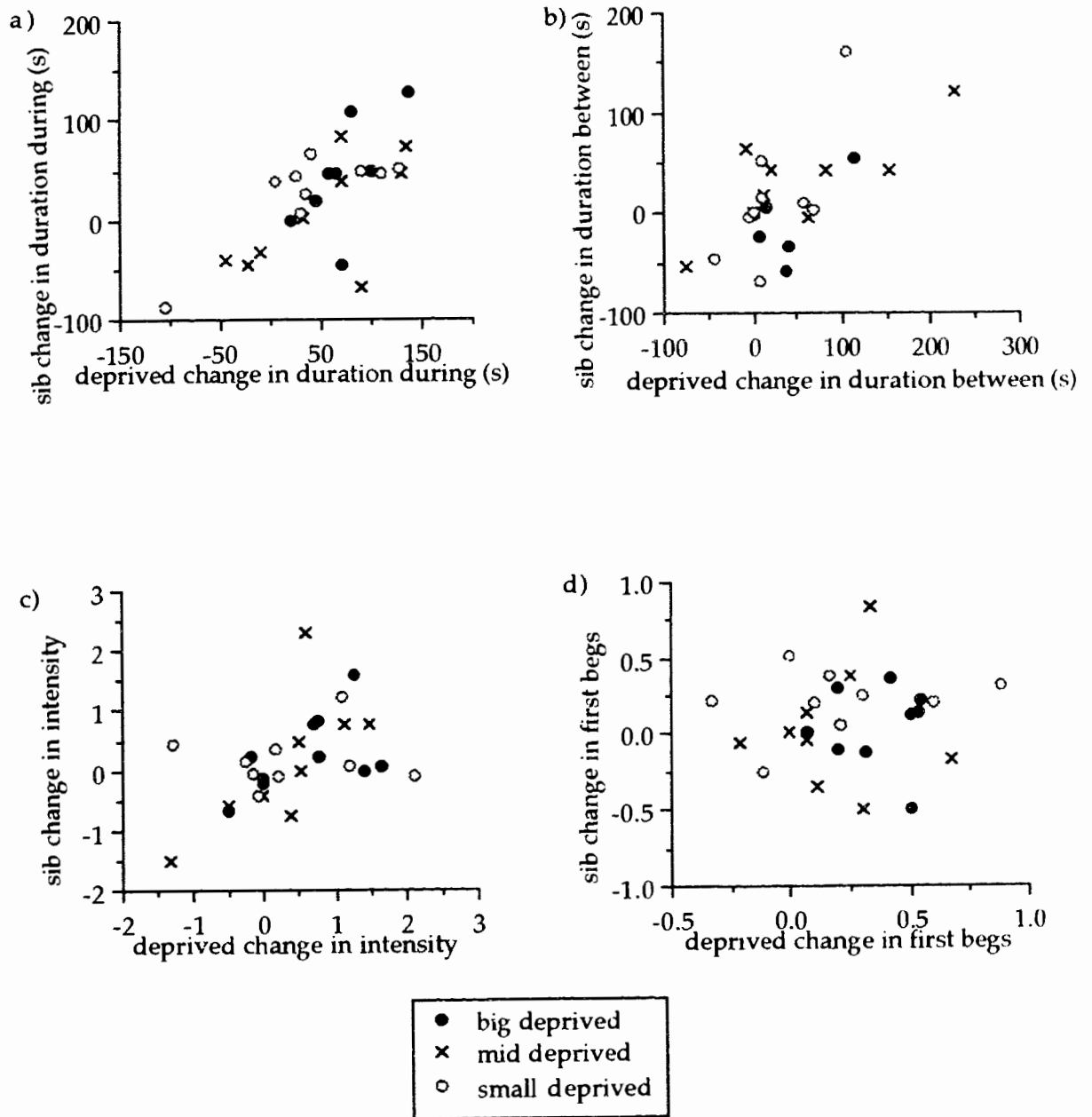


Figure 4.7. Relationship between the change in begging of each deprived chick and the mean change of its siblings' begging. a) length of vocalization during parental visits. b) length of vocalization between visits. c) intensity of begging. d) number of first begs.

between begging intensity of the deprived chick and of its siblings are also positive, showing that nestmates tend to increase their begging in relation to the increase in begging of their hungry sibling. There was no relationship between the proportion of visits when a deprived chick begged first and the proportion its siblings did so in any treatment period (possible if siblings begged simultaneously, tied for begging first).

## Discussion

Experiment 1 demonstrates that parent yellow-headed blackbirds change their allocation of provisions in response to changes in the begging levels of their offspring. Nestlings who were deprived of food increased many aspects of begging and received more food. Other nestlings, held away from the nest for the same period, but who were satiated, begged less intensely and received less food. These results agree with the experimental findings of Smith and Montgomerie (1991) in robins (*Turdus migratorius*), Litovich and Power (1992) in starlings (*Sturnus vulgaris*), and Redondo and Castro (1993) in magpies (*Pica pica*), and with the model results in Chapter 2. They support the assumption of positive relationships between hunger, begging and feeding used as the basis for many theoretical models of begging (reviews in Parker 1985, Harper 1986, Hussell 1988).

Experiment 2 shows that while parents increase their provisioning to hungry chicks, they also allocate food based on relative offspring size. When small nestlings were deprived of food, they increased many aspects of begging and received more food than they had previously, but generally still received less food than did their larger siblings. In asynchronous broods, with a hierarchy of chick sizes, increased begging may change food allocation quantitatively rather than qualitatively. Whether this effect results from

sibling competition or from parental bias towards high quality chicks, it should be incorporated into any models of the evolution of begging behaviour. To date, I know of only one published model of begging which incorporates varying chick value or competitive ability (Parker et al. 1989).

In both experiments, small chicks stopped begging last more frequently than did their larger siblings. Small chicks gave more type II calls and begged more in the absence of their parents in experiment 1, and begged more intensely in experiment 2. Large chicks out-begged their juniors in only one measured aspect: they started begging earlier at the approach of a parent. Yet, parents fed large chicks more in both experiments. Big chicks do not seem to be thwarting their sibling's efforts by begging earlier: they did not beg earlier in response to early begging by their deprived small siblings.

While preferential feeding of big chicks was not related to higher levels of any of the measured aspects of begging, I cannot be certain that parents were biasing their feeding independently of begging. Offspring might convey hunger via vocal components of begging, and might transmit information about size via non-vocal components. Larger chicks should be able to rear higher and to gape wider. Larger chicks may beg at a different sound frequency. Older chicks may be able to respond more quickly to parental presence, and to position themselves closer to the nest edge (Khayutin and Dmitrieva 1977, Muller and Smith 1978, Gottlander 1987). Discovering which aspects of begging are related to size and which to hunger, as well as learning how begging will change with competition, requires controlled laboratory experiments (e.g., Chapter 6). Learning which aspects of begging parents respond to is more difficult since manipulation of begging remains crude and indirect. I was unable to tease apart the various aspects of begging because all measured components increased with hunger.

Smith and Montgomerie (1991) found evidence for sibling competition in their manipulation of individual chick hunger level. In experiment 1, I found no effects of sibling competition: control nestlings did not increase their begging levels in response to the increased begging of their deprived sibling. Five of these broods were reduced from four to two chicks for an hour, and the control nestlings received a food bonus during this time. Their satiation may have cancelled out any effects of competition. In experiment 2, I did see increased vocalization length and begging intensity in response to increased begging by the deprived siblings. These broods were reduced by only one chick, and so were less likely to be satiated. Conversely, part of the observed relationship might be an artifact of experimental design. In experiment 2, I visited nests repeatedly (seven times in the course of each trial). Some parents became agitated and stayed away from their nests for up to 20 min in a treatment period, resulting in a whole brood of hungry chicks. In these cases, deprived nestlings and their hungry siblings would likely all beg more intensely and for longer. Since this pattern was not evident in which nestling begged first, however, such an artifact seems unlikely.

In experiment 2, nestlings assigned to "big" and "mid" groups were biased by gender, with more fast-growing males in the "big" group, and more slow-growing females in the "mid" group. In yellow-headed blackbirds, the first two nestlings hatch at a shorter interval than later chicks. Hence a second hatched male might overtake its older sister in mass and tarsus by six or seven days. My sample was too small to test for gender differences within size class. Inspection of the data revealed no obvious outliers, but I cannot be certain that the effects I saw were due only to size and not to sex. Gender-biased feeding and begging occur in other species. Male red-winged blackbirds (*Agelaius phoeniceus*) beg more vigorously than their female siblings

(Teather 1992) and female-biased budgerigar (*Melopsittacus undulatus*) broods receive more food (Stamps et al. 1987).

The experiments presented in this chapter suggest that parent yellow-headed blackbirds respond to both the hunger level and size of their offspring. I conclude that begging nestlings can benefit from changed food allocation, but that the extent of these benefits may vary between siblings in broods with a size hierarchy.

## Chapter 5

### Begging as competition for food



## Introduction

Theoretical models suggest that chicks compete with one another for food by begging (Chapter 2, Macnair and Parker 1979, Harper 1986, Parker et al. 1989). Several comparative studies support this idea by illustrating a positive correlation between brood size and begging level interspecifically (e.g., Cotingidae, Harper 1986), and between brood size and the ratio of begs to feeds intraspecifically (e.g., budgerigars, *Melopsittacus undulatus*, Stamps et al. 1989; egrets, *Bubulcus ibis*, Fujioka, 1985), although Henderson (1975) found no brood size effect in glaucous-winged gulls (*Larus glaucescens*).

Stronger evidence that chicks change their begging behaviour in relation to sibling competition comes from Smith and Montgomerie's (1991) experimental study of begging in robins (*Turdus migratorius*). Smith and Montgomerie deprived individual nestlings of food and then returned them to their broodmates. Deprived chicks begged relatively more and were fed more than their "control" nestmates, who had remained in the nest during the deprivation period. The "control" chicks also altered their begging level, however, apparently in response to the changed begging of their hungry nestmate. Smith and Montgomerie (1991) did not monitor parental provisioning to "control" chicks during the deprivation period, however, and the response of these "controls" may have been confounded by changes in hunger level. Similarly, yellow-headed blackbird (*Xanthocephalus xanthocephalus*) chicks tended to increase begging following the deprivation of a nestmate (Chapter 4), but again, the behavioural change might have followed changes in hunger level. I found that parents fed big chicks more even when their small siblings were hungry (Chapter 4). I could not tell if this provisioning was based on competition (where chicks with high ability could beg more) or on parental bias towards high quality chicks, judged

independently of begging. Zebra finches (*Poephila guttata*) increased begging upon hearing played-back begging calls (Muller and Smith 1978), but yellow-headed blackbirds did not, likely because they were well-fed and satiated (Chapter 3).

In this chapter, I investigate whether broods of yellow-headed blackbirds change their begging level when faced with increased competition for food in the form of an extra nestmate.

## Methods

I performed two addition experiments using yellow-headed blackbirds in Creston, B. C. In 1992, I added a nestling to natural broods of chicks in the field; in 1993, I added a nestling to artificially-created broods in the laboratory, and attempted to control for hunger.

### Field experiment

I used eleven broods of yellow-headed blackbird nestlings in two nesting areas as experimental subjects. I placed a mock video camera in front of the nest one day prior to experimenting to allow parents to habituate, and replaced it with a video camera on the day of the trial. I chose families randomly from among those observable by camera (i.e., not in the centre of a clump of cattails), and with three nestlings alive on the day of the experiment. Some broods hatched from clutches of three ( $n=7$ ); others were reduced from four by starvation of one chick ( $n=4$ ).

I added a chick to each brood for half of a two-hour observation period, and observed the natural three-chick brood during the other half (treatment order randomly assigned). The added nestling came from a nearby brood of similarly-aged chicks, and was selected to weigh less than the heaviest but



more than the lightest chick in the experimental brood. I never added apparently sick or starving chicks, or those infested with mites. I marked all chicks with paint for identification (colour randomly assigned).

The video tapes were transcribed by an observer naive to the purpose of the experiment, but experienced with watching nests of yellow-headed blackbirds. Measured aspects of begging included the intensity (0-4 scale representing the perceived effort of begging; see Chapter 4), loudness (1-3 scale) and total duration (s) of vocalizations during and between parental visits. I calculated brood means and totals for each measurement of begging (looking only at the three siblings) for the two treatment periods, and analysed these data with blocked analyses of variance.

### Laboratory experiment

I repeated the addition experiment the following year (1993) under laboratory conditions, where I could control for chick hunger level. I removed eight chicks from the colony on each of five days, for use in ten experimental trials. I used only apparently healthy birds from 7-10 days old, removing one chick from natural broods of three or four chicks (except two from one brood of four) to change the natural broods as little as possible. I painted each chick's head for identification, and returned all experimental chicks to their family at the end of each day. Parents accepted all chicks upon their return.

The eight chicks made up two artificial broods of four (three plus the "addition" chick). Each brood of three sat nestled inside a strawberry punnet which was lined with clean tissue paper and placed inside a heated container. The addition chicks sat in similar containers alone. I fed all nestlings to satiation with moistened pieces of cat food until 30 min prior to experimental

trials. I defined satiation as the point when a nestling either refused to gape in response to sound on two consecutive attempts 5 s apart, or accepted food and did not swallow it within 10 s.

Each trial again consisted of two hours of observation (via video camera), one hour with three chicks and one hour with four chicks. In this experiment, treatments were randomly assigned in half hour blocks, to allow each brood to experience augmentation and reduction repeatedly, and to decrease any bias due to trends in hunger over the two hour period.

Feeding "visits" occurred every 5 min throughout the trials. I fed each chick sequentially (one quarter or one third piece of moistened cat food, according to chick size), so that each received food every fifteen minutes. Prior to feeding, I passed a shadow over the "nest", and tapped the container. As soon as begging started, I fed the chosen chick as quickly as possible, and tapped the container again to simulate continued parental presence. In the four-chick treatments, I fed the three broodmates as before, and fed the added chick at the same time as feeding one of the regular chicks (i.e., with forceps held in each hand), so as not to increase the length of the feeding "visit", while keeping feeding rate constant.

I calculated the mean begging intensity and loudness (see Table 4.1), and the total duration of vocalizations during and between feeding visits for each half hour period. I also measured rearing height, estimated as the distance the base of the bill moved vertically. I removed one nest from analysis due to an inconsistent feeding protocol which resulted in chicks not begging at all during most of the visits (15/18) over three of the four periods. I analysed the data for the remaining nine trials using an analysis of variance blocked by trial number and by time period, predicting that chicks would beg more in broods of four than in broods of three.

## Results

### Field experiment

The three experimental nestlings vocalized for longer during parental visits when a fourth chick was present, but did not beg for longer between visits (Figure 5.1; during visits:  $F_{(1,10)} = 7.39$ ,  $p=0.02$ ; between visits:  $F_{(1,10)} = 0.11$ ,  $p>0.5$ ; analysis of variance, blocked by trial; mean increase of  $51.1 \pm 18.8$  s per chick). When accompanied by an extra chick, nestlings also begged more intensely (3-chick broods: mean intensity =  $2.68 \pm 0.16$ ; 4-chick broods: mean intensity =  $2.96 \pm 0.17$ ;  $F_{(1,10)} = 12.36$ ,  $p=0.01$ ), and more loudly (3-chick broods: mean loudness =  $2.21 \pm 0.15$ ; 4-chick broods: mean loudness =  $2.42 \pm 0.16$ ;  $F_{(1,10)} = 9.45$ ,  $p=0.02$ ).

Parental provisioning rate did not increase to broods of four (3-chick broods: number of visits =  $11.82 \pm 1.95$ ; 4-chick broods: number of visits =  $11.64 \pm 1.61$ ;  $F_{(1,10)} = 0.02$ ,  $p>0.5$ ; including visits where the addition nestling was fed): hence the number of feeds per chick tended to decrease (3-chick broods:  $4.0 \pm 0.5$  visits per chick; 4-chick broods:  $3.5 \pm 0.4$  visits per chick;  $F_{(1,21)} = 2.63$ ,  $p=0.12$ ; repeated measures analysis of variance, blocked by nest, on feeds to the three siblings).

### Laboratory experiment

Nestlings begged for significantly longer during the four-chick treatment (3-chick broods:  $187.72 \pm 18.63$ s per chick; 4-chick broods:  $205.11 \pm 16.86$ s per chick;  $F_{(1,23)}=12.14$ ,  $p=0.002$ , blocked by trial and period). The high error associated with begging length results from strong trial and period effects. Eight of nine broods begged less during the first half-hour treatment than during the following three periods. Chicks responded less readily to tapping on their container during the first period, and may have taken time

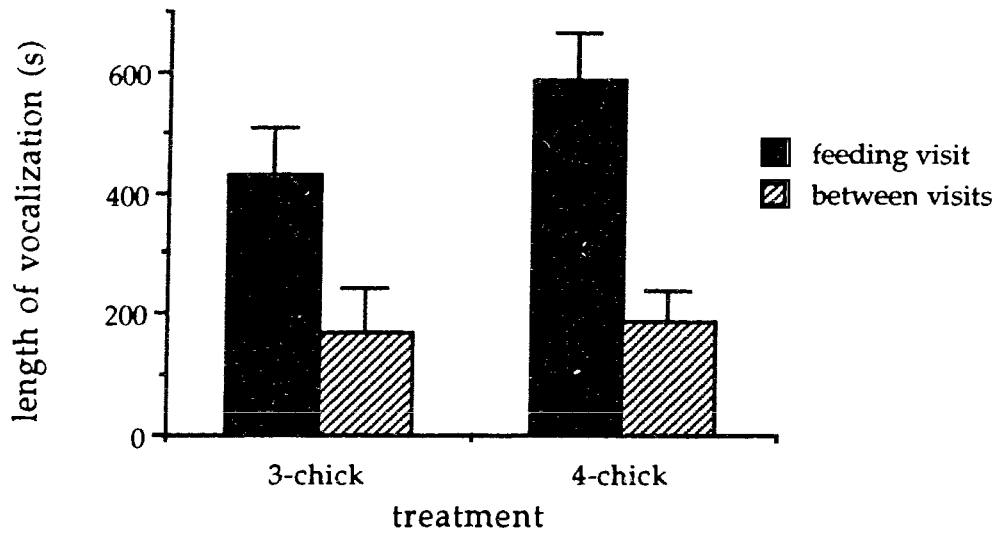


Fig. 5.1. Time spent vocalizing by broods of three siblings (summed per nest) with and without an extra nestmate. Bars show the mean length of vocalization in ten broods (plus standard error) during parental visits and between visits.

to learn the relationship between an unfamiliar sound and a feeding visit. Figure 5.2 controls for period and trial effects graphically by representing the begging duration for each treatment and period standardized by the total begging duration for each brood.

Chicks tended (non-significantly) to beg more loudly in four-chick broods (mean loudness: 3-chick broods:  $2.27 \pm 0.13$ ; 4-chick broods  $2.32 \pm 0.13$ ;  $F_{(1,23)} = 2.41$ ,  $p=0.13$ ). They did not change their begging intensity, the length of between-visit begs, or rearing height (mean intensity: 3-chick broods:  $2.08 \pm 0.12$ ; 4-chick broods:  $2.02 \pm 0.08$ ;  $F_{(1,23)} = 0$ ,  $p=1$ ; between-visit beg duration: 3-chick broods:  $38.83 \pm 15.96$  s per chick; 4-chick broods:  $42.89 \pm 9.93$  s per chick;  $F_{(1,23)} = 1.16$ ,  $p=0.29$ ; mean rearing height: 3-chick broods:  $40 \pm 3$  mm; 4-chick broods:  $37 \pm 2$  mm;  $F_{(1,23)} = 0$ ,  $p=1$ ).

## Discussion

In the field, chicks faced with an added competitor in the nest increased their begging length, loudness and intensity. Since feeding visits in the field did not compensate for the presence of an extra mouth, chicks in the field were likely more hungry during this period. Hungry chicks beg more (Chapter 4, Litovich and Power 1992, Smith and Montgomerie 1991); hence the change in begging may have reflected an increased hunger level rather than potential food competition.

Two observations suggest that the change in begging does not solely follow from changes in hunger. First, I showed in Chapter 4 that hungry chicks increase the duration of their begging both during and between parental visits (Table 4.5). In the addition experiment, chicks did not increase the length of their between-visit begs, suggesting that they were not much hungrier. Second, the slope of the relationship between begging level and

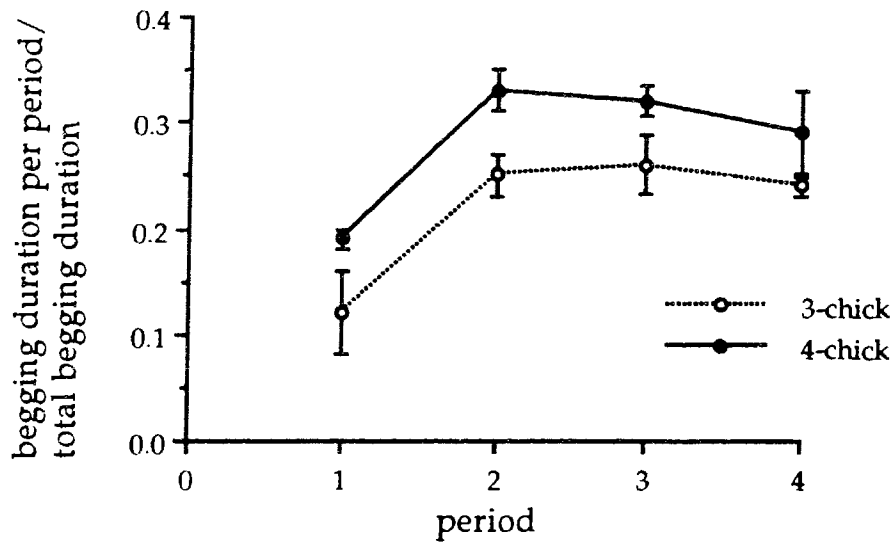


Fig. 5.2. Begging duration by nestlings in 3-chick and 4-chick broods. The data are expressed as the time spent begging in a period as a proportion of the total time spent begging over all four periods for each nest (mean  $\pm$  standard error for nine nests).

hunger level measured in laboratory experiments was 0.69 (see Chapter 6, Table 6.2). The number of provisioning visits in the addition experiment decreased from 4 to 3.5 feeds per chick, a proportional reduction of 0.125 (i.e.,  $-0.5/4$ ). Assuming that the change in hunger is directly proportional to the change in the number of visits, this translates into a potential increase in begging due to hunger of  $0.69 \times 0.125 = 0.09$ . The actual increase in begging per chick in this experiment was 0.36; hence, the calculated change in hunger could account for only  $0.09/0.36 = 25\%$  of the actual change in begging level. Obviously, these calculations are somewhat crude, but they do show that the observed effect is consistently larger than the effect expected from the potential change in hunger level alone.

The laboratory experiment provides stronger evidence that nestlings increase their begging level in response to an increase in brood size, independently of hunger level. Chicks significantly increased their begging duration during visits, and tended to increase their begging loudness. They did not increase begging intensity, the length of between-visit begs or rearing height. Chicks changed their begging behaviour as the experiment progressed, particularly between the first and subsequent periods, possibly due to insufficient deprivation prior to the experiment, and possibly due to increased familiarity with the laboratory feeding system over time. A 30 min learning period would perhaps have been helpful in removing this complication.

Stamps et al. (1989), in an observational study, found an effect of brood size on begging level comparing singletons and larger broods. They were unable to detect any effect in broods of more than two, but since they did not manipulate brood size, variation in provisioning between families may have obscured any pattern. The addition experiments presented in this chapter

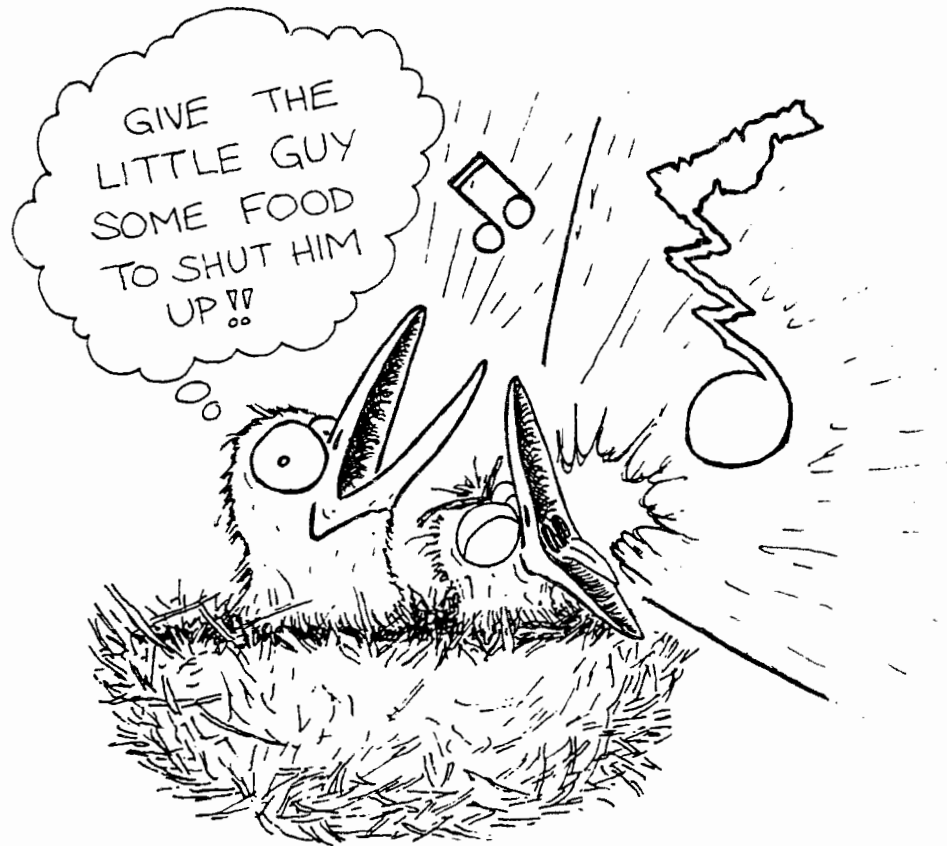
show that within families, yellow-headed blackbird nestlings in broods of three do beg more in response to the presence of an extra nestmate.

Siblicidal egrets do not reduce aggression directed at siblings if food availability increases (Mock et al. 1987), but do fight less in reduced broods (two versus three chicks; Mock and Lamey 1991). Food levels are unpredictable from day to day in egrets, and brood size may be a better indicator of future food demands than hunger level (Mock and Lamey 1991). Non-aggressively brood-reducing species faced with unpredictable food supplies may also use the number of nestmates as an indicator of future competition. Yellow-headed blackbirds fall into this category since they provision their young with emergent insects—a resource depending strongly on unpredictable weather patterns. The increase in begging with increased brood size shown in this chapter suggests that yellow-headed blackbirds can assess the potential competition within their brood and that they respond to increased competition with increased begging.



## Chapter 6

### Strategic aspects of begging



## Introduction

Previous chapters have established that nestlings benefit from begging by changing both the total provisioning level to a brood (Chapter 3, Bengtsson and Ryden 1983, Harris 1983, Muller and Smith 1978) and the food allocation within a brood (Chapter 4, Smith and Montgomerie 1991, Litovich and Power 1992). Because begging nestlings likely pay mortality and energetic costs for these benefits (Redondo and Castro 1992, Gochfeld 1978, David Haskell, Cornell University, personal communication, John McCarty, Cornell University, personal communication), chick state (including age, body condition, gender and rank in a brood), as well as hunger, may alter the relative costs and benefits and thus the observed level of begging—food may be more valuable to some chicks. In this chapter, I investigate how much chicks of differing states beg.

Begging potentially signals nestling need for parental care (Godfray 1991). Nestling need can take two forms: short-term need (or hunger) is dynamic and can change between parental visits, and long-term need reflects static or slowly changing aspects of state, including body condition, gender and size rank (see Chapter 1). In many species, chicks in poor body condition are susceptible to starvation (e.g., Richter 1984, Litovich and Power 1992) and need more food to survive and fledge. In dimorphic species, the faster-growing sex, with higher energy demands, needs more food (Fiala and Congdon 1983, Teather 1987, Teather and Weatherhead 1988). Many studies have documented differences in survival between early and late hatched chicks in asynchronously hatching species, especially under conditions of low food availability (Parsons 1975, Husby 1986, Slagsvold 1986, Anderson 1989, Lessells and Avery 1989, Bryant and Tatner 1990). Particularly in species that experience a pressure to fledge quickly (e.g., yellow-headed blackbirds; see

Appendix 2), late-hatched, relatively small chicks will need more food than their larger, older nestmates to fledge successfully. Hungry chicks beg more (Chapter 4, Smith and Montgomerie 1991); and begging therefore contains information about short-term need for care. If chicks also beg to signal their long-term need, relatively small chicks, those in poor condition or of the faster-growing sex should beg more than their larger, heavier, slower-growing conspecifics for a given hunger level.

Begging may also contain information about nestling quality. Information about long-term need may be correlated with information about quality, for example, chicks in poor body condition have high need and low quality (both due to their lower probability of survival). Relatively large chicks in good condition may be more valuable to parents, prompting increased provisioning. As well as feeding in relation to begging level, parent yellow-headed blackbirds feed chicks in relation to their size (Chapter 4). Other studies have found preferential feeding of larger young (Drummond et al. 1986, Litovich and Power 1992, Ryden and Bengtsson 1980, Fujioka 1985), though budgerigar mothers bias feedings to small chicks (Stamps et al. 1985).

Large chicks, able to bear higher energetic costs, may be able to out-compete their needier siblings by begging more (Ryden and Bengtsson 1980, Fujioka 1985, Greig-Smith 1985). There is evidence that chicks compete by begging: nestlings beg more when their siblings beg more (Chapter 4, Smith and Montgomerie 1991) and when an added chick increases potential competition for food (Chapter 5). If large chicks out-beg their smaller siblings, or if parents skew feeding towards nestlings with high reproductive value, begging will no longer contain stable information about chick long-term need, but will instead contain information about chick competitive ability or quality. High quality chicks will benefit from advertising their quality, and

small chicks, or those in poor condition, will not be able to beg more than their large siblings. The predictions derived above will be reversed, and relatively large, good condition chicks will beg more than their needy siblings.

The case for gender is less clear: from the chick's perspective, the faster-growing sex needs more food, but may also have a competitive advantage simply by being larger, while from the parents' perspective, one sex may be costlier to raise, but may have a higher reproductive potential. In Chapter 2, I described a model in which I was able to create chicks with asymmetrical needs and abilities, representing males (with high ability and high need) and females. The model predicted that males should beg more than females even when both are in good condition or full.

Many authors discuss the honesty of begging as a signal (reviews in Chapter 1, Litovich and Power 1992). I believe a more relevant question is "What information does begging carry?": a dishonest signal of need may be an honest signal of quality or competitive ability, and parents may benefit from interpreting either type of message. In a theoretical model, Godfray (1991) suggests that begging can reliably signal some type of need, but does not discriminate between short-term need and long-term needs that are susceptible to collapsing into signals of quality. Indeed, most theoretical considerations of begging do not model chicks with varying qualities or long-term needs (Parker 1985, Harper 1986, Hussell 1988, Godfray 1991). Parker et al. (1989) developed a model of begging incorporating chicks of differing long-term need, but were unable to test their predictions that small, late-hatched chicks should beg more. The model described in Chapter 2 looked at the evolution of begging strategies by large and small chicks and suggested that, under some circumstances, small chicks should beg more.

Several empirical studies report higher levels of begging by relatively small chicks (who may also have been in poor body condition; Chapter 4, Ryden and Bengtsson 1980, Greig-Smith 1985, Khayutin and Dmitrieva 1979, Fujioka 1985, Stamps et al. 1989). Teather (1992) found that male red-winged blackbirds (*Agelaius phoeniceus*) begged more than females. None of the studies looking at size or gender effects controlled for nestling hunger level. That smaller chicks or males beg more because they are hungry does not constitute evidence that begging can carry information about long-term need. Drummond and Chavelas (1989) found that small blue-footed booby (*Sula nebouxi*) chicks begged more in control nests, but big chicks begged more in experimentally food-deprived broods. Small chicks were sometimes prevented from begging by their aggressive senior siblings. In blue-footed boobies, then, begging announces hunger level, but may not reveal chick long-term need.

Three further studies suggest that begging does not signal long-term need. Stamps et al. (1989) observed apparently contradictory evidence that late-hatched budgerigar (*Melopsittacus undulatus*) chicks begged more than their older siblings, but that chicks in poor condition (measured by mass at a given age) did not beg more over a long period at the end of nestling phase. However, if few wild budgerigar nestlings starve (Wyndham 1981), and if there is little pressure to fledge early, chicks with a relatively low mass for their age are not necessarily needy. Redondo and Castro (1993) saw no relationship between begging and mass gain over the previous 24 h in magpies (*Pica pica*). They did not control for nestling hunger level in these measurements, and probably collected insufficient data to detect any effect beyond immediate hunger level. Litovich and Power (1992) found that parent starlings (*Sturnus vulgaris*) preferentially fed "best-beggars" and

concluded that begging cannot carry information about long-term need (as felt by runts in their study). They did not present data relating begging levels to chick state; hence their conclusions are difficult to evaluate. To determine if begging can signal long-term chick need in natural systems, I attempted to control for nestling hunger level, and investigated begging vocalizations in broods of unequal chicks.

This chapter describes three studies performed on yellow-headed blackbird nestlings designed to examine the effects of chick state on begging. Yellow-headed blackbirds nest colonially in marshes, building readily accessible nests. Yellow-headed blackbird chicks hatch asynchronously (Richter 1984) and are sexually dimorphic at fledging (Richter 1983). The younger chicks in a brood often die (Richter 1984, Appendix 2). Using this system, I was able to look at the effects of chick body condition, gender and size rank within a brood on begging. First, I compared the begging calls of a variety of nestlings at different hunger levels to test the predictions that males (the faster growing sex) would beg more than females, and that nestlings in poor body condition would beg more than their heavy conspecifics (study 1). Since I could not manipulate gender or body condition, this study was largely exploratory. Second, in a cross-fostering experiment in the field (study 2), and in a controlled experiment in the laboratory (study 3), I tested the prediction that relatively small chicks would beg more than their large nestmates. In addition to looking at the effects of chick size, the laboratory experiment was designed to examine the effects of nestmate begging competition, to confirm, under controlled conditions, the suggestion from Chapter 4 that chicks increase begging when their nestmates beg more.

## Methods

### Study 1: Effects of gender and body condition

In 1993, I investigated the effects of nestling gender and body condition on begging under laboratory conditions. For these observations, I used yellow-headed blackbird chicks who had been temporarily removed from their nests for participation in size-rank (study 3, this chapter) or addition (Chapter 5) experiments. The three or eight chicks selected on a given day met the size and age criteria for their respective experiments, and hence do not constitute a random sample. They were selected from within a small area of the marsh each day to minimize collection time. The short nestling season (four weeks in 1993) and long collection time precluded using an independent sample of chicks for this investigation.

A total of 70 (30 male and 40 female) nestlings spent up to 8 h in a heated room away from their nests. I generally removed one chick per nest (in one case, I removed two chicks from a brood of four), leaving at least two chicks. All chicks were marked for identification with dots of acrylic paint. Nestlings sat in plastic strawberry punnets lined with toilet paper placed inside heated containers. They were fed to satiation with moistened pieces of cat food (bulk dried pieces of similar size) at collection and at return, and throughout the day except during trials. All nestlings were returned to their nests in the afternoon, and none were rejected by their parents. I never removed apparently sick, starving or mite-infested birds.

I weighed each chick and measured its tarsus and outermost primary length. I continued to measure nestlings in their nests for two to four days after the experiment to establish gender. I also recorded chick age (days since hatching) and size rank within the nest.

I measured the begging level and hunger level of every chick at least once, immediately after the completion of an addition or size-rank experiment, where chicks had experienced a variety of hunger levels, brood sizes and nestmate competition. I made no attempt to standardize hunger for this first measurement. I measured 44 nestlings an additional one to three times, following food deprivation periods of 30, 60 or 90 min. Many chicks did not beg after only 30 min of deprivation.

To record vocalizations, I placed nestlings singly in a heated container beneath a microphone set 25 cm above the chick's bill. I used a Sony Professional Walkman to record all calls. I stimulated begging by passing my hand over the chick, touching its beak with a pair of tweezers, and tapping five times on the container. Following the cessation of begging, I measured each chick's hunger level by feeding it pieces of moistened cat food (quartered pieces of uniform size, about 5 x 5 mm), one piece per 5 s. Without a 5 s pause, chicks took in more pieces than they could swallow. I defined satiation as the point at which a chick did not open its bill in response to taps on the side of the container within 15 s from swallowing the previous piece of food.

I analysed several aspects of begging from the recorded tapes: total calling duration (time from first sound to end of last sound); loudness (maximum decibels, recorded with a sound-level-meter placed at a constant distance from the speaker); number of begs; and mean duration of each sound within a begging bout (measured from printed sonograms; Figure 6.1). I only measured sonograms if chicks had given at least two begging calls; hence my data for this measurement are a subset (particularly for the 30 min deprivation period). I explored the entire data set using regressions of begging level against hunger, body condition and gender, and fitted models including



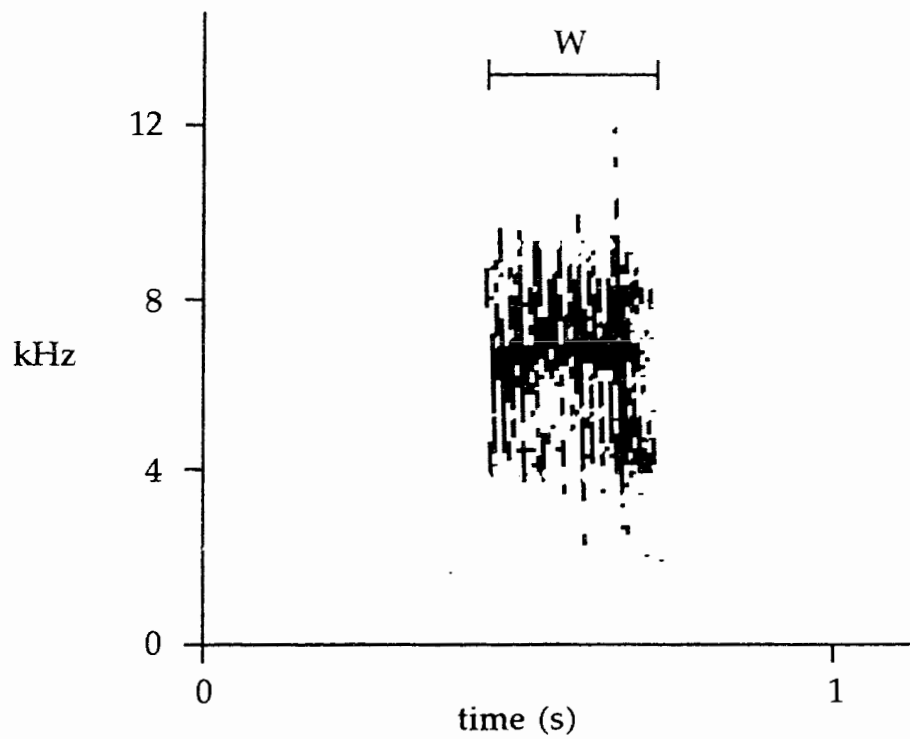


Figure 6.1. Sonogram of a begging call given by a yellow-headed blackbird nestling.  $w$  shows the measurement of the call duration.

chick age, rank and interaction terms as independent variables. I then analysed the begging levels of the 44 experimentally-deprived nestlings using repeated measures analyses of variance.

### Study 2: Effects of rank: field experiments

In 1991, I measured nestling begging response to a model blackbird, assigning a subjective level of calling from zero to three (0=no vocalization, 1=one quiet call, 2=several quiet calls, 3=several loud calls) to each chick. I used 19 nests and measured each brood on three to seven days. I calculated the mean response for each chick, and compared begging levels between chick ranks.

In 1992, I manipulated chick rank in 20 yellow-headed blackbird broods. I found pairs of broods where the smallest chick in one nest (excluding runts in four-chick nests) was of similar size to the biggest chick in the second nest. I exchanged these two chicks between nests so that the small chick was larger than its new nestmates and *vice versa* (10 "small to large" and 10 "large to small" treatments). In this way, by using the same chick, within a treatment (before and after fostering), I could compare the effects of nestling size rank on begging while controlling for other aspects of chick state (e.g., age, condition, sex). To control for the effect of exchanging nestlings between nests, I found ten nests with equally-ranked (either large or small) chicks of similar size, and exchanged these chicks ("equal to equal" treatment). All 30 experimental broods had at least three chicks (six had four). If more than one brood fitted the selection criteria, I chose the experimental brood randomly. On many days there were no options.

Trials ran for two hours (one hour before manipulation, and one hour of cross-fostering) and were observed by video camera. I placed tripods and

mock cameras in position several hours before each trial to allow for habituation. I remained in a floating blind, close to, but not in sight of, the experimental nests to minimize disturbance during the manipulation. Blinds placed in sight of nests attract predators (particularly mink, personal observation). All nestlings received stripes of acrylic paint on their head and under their bill to facilitate identification. The pairs of experimental chicks were painted with the same colour.

I analysed begging prior to manipulation to look for effects of chick rank on begging within a brood, and then compared the begging levels of experimental chicks between natal and foster nests. Since begging varies considerably between broods, I compared rank levels of begging within a brood rather than using absolute levels. To illustrate, one nest may be very quiet normally—a chick fostered there from a noisy nest may decrease its begging relative to its previous level, but might still be begging more than its foster siblings. I examined several vocal components of begging (Table 6.1).

### Study 3: Effects of rank: laboratory experiment

In 1993, I investigated the effects of relative chick size and of nestmate behaviour on begging. For each trial, I selected three chicks (small, mid and big) from different nests. Big chicks had the highest mass, longest tarsus and longest primary (i.e., were bigger and older); small chicks were smaller and younger. I did not use chicks who were bigger in one category and smaller in another (e.g., a healthy, large, but young male and a smaller but older female). Small chicks weighed 20-26g, mid chicks 28-34g and big chicks 37-52g. I selected chicks from a pool of over 200 nests, using measurements taken on the afternoon prior to experimentation. Sometimes chicks changed in size or condition overnight by so much that I had to choose replacements. I

Table 6.1

Aspects of begging in yellow-headed blackbird nestlings measured in field rank experiment (study 2; 1992).

aspect	level	criteria
intensity		begging effort
	0	no visible response
	1	movement, no vocalization
	2	single vocalization
	3	≤1 vocalization per second
	4	>1 vocalization per second
loudness		volume (no zero values)
	1	quiet
	2	moderate
	3	loud
start		rank order that a chick starts to vocalize
last		proportion of visits where chick stops begging last after visit, ties included
extra beg		total number of vocalization bouts in absence of parents
type	II	total number of bouts of "exaggerated" begging *
length		total number of seconds vocalizing in presence of parent, during treatment period

\* single loud bursts of sound  $\geq 1$  s apart (see Muller and Smith 1978)

removed chicks from the marsh in a heated container, fed them to satiation with pieces of moistened cat food, and brought them into a heated building.

I used the mid chick as the experimental subject, pairing it with either the big or small chick as a nestmate. The mid chick experienced four treatments: a big satiated nestmate (BF), a big hungry nestmate (BH), a small satiated nestmate (SF), and a small hungry nestmate (SH). Because hungry nestlings beg more (Chapter 4), the treatments effectively placed the experimental chick with either a mostly silent or noisy partner. By manipulating nestmate hunger, I was able to manipulate begging competition.

I ran trials on 11 trios of nestlings, with the treatment order randomly assigned. Each treatment lasted one hour, consisting of a 30 min adjustment phase followed by 30 min of observation. A pair of nestlings was placed together at the start of the adjustment phase. I fed each nestling two pieces of moistened cat food immediately, at 15 min, and at 30 min. The portions ranged from one-eighth to half of a prepared piece to satiate the "full" chicks and not the "hungry" chicks (2.5 x 5 mm, to the experimental chick and to the nestmate in the BH and SH treatments; 5 x 10 mm, to the nestmate in the BF or SF treatments). I assumed that during this period, especially at feeding times, chicks would be able to assess their size relative to that of their nestmate. I fed both chicks the same number of times so as not to set up any apparent feeding bias.

During the observation phase, I fed each chick one piece of food every five minutes (for a total of five episodes within the 30 min; one-sixteenth of a piece, 2.5 x 2.5 mm to the experimental chick and to "hungry" nestmates; half a piece to "full" nestmates) and measured the length of vocalizations immediately after feeding. I then stimulated the nestlings to beg again by

waving my hand over the chick and tapping the container five times. I recorded whether or not a chick responded to my shadow, the length of its vocalization, maximum loudness (three point scale), maximum intensity (four point scale: 0 = no response, 1 = movement, but no vocalization,  $2 \leq 1$  vocalization per second,  $3 > 1$  vocalization per second), and the rearing distance (a crude estimate measured against lines drawn at 1 cm intervals on the wall of the container) of the experimental chick, and recorded the maximum begging intensity of its nestmate.

I compared the begging levels of experimental chicks when they were paired with small versus large nestmates to look at the effect of relative size, and compared their begging when paired with hungry versus full nestmates to examine the effect of nestmate behaviour. For analysis, I used the mean of the five begging episodes as the begging measure for each treatment. I analysed each measure of begging using a two-way analysis of variance, blocked by trial, looking at the effects of nestmate size and nestmate hunger level.

## Results

### Study 1: Effects of gender and body condition

I regressed chick mass against tarsus length for each sex (Figure 6.2) and used the residuals as a measure of chick body condition. Mass and tarsus are highly correlated ( $r=0.90$ ,  $p<0.001$ ; Pearson correlation, all p-values Bonferroni corrected) and, at least over the studied range, the plots appear linear (i.e., plots of residuals show no trends). The condition residuals are not significantly correlated with chick age ( $r=-0.13$ ,  $p=1.00$ ), tarsus ( $r=0.06$ ,  $p=1.00$ ) or hunger level ( $r=0.17$ ,  $p=1.00$ ). They are correlated with chick rank within a

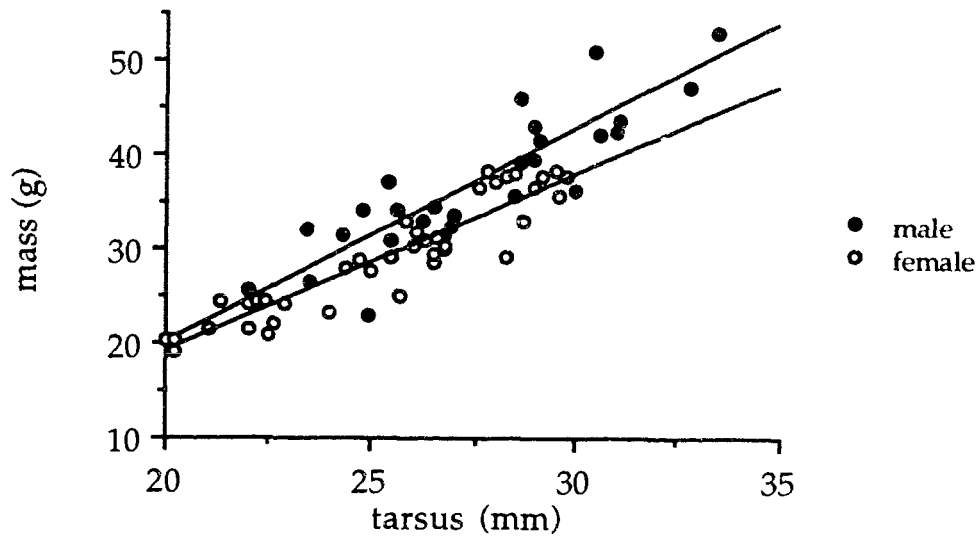


Figure 6.2. Regression of yellow-headed blackbird chick mass against tarsus used to calculate chick body condition (residuals from the regression for each sex). Females:  $\text{mass} = -18.41 + 1.87 (\text{tarsus})$ ,  $r^2=0.87$ ,  $n=40$ ; males:  $\text{mass} = -25.28 + 2.26 (\text{tarsus})$ ,  $r^2=0.80$ ,  $n=29$ , (one male too young to use).

nest (lower rank chicks are in poorer condition;  $r=-0.37$ ,  $p<0.001$ ). Sex and size-rank are also significantly correlated (i.e., males are larger;  $r=0.26$ ,  $p=0.03$ ).

Inducing a predetermined hunger level was not possible without prior calculation of hunger by deprivation-time curves for chicks of varying age, condition and sex. Rather than creating hunger classes and looking at begging distributions for each class, I determined hunger level immediately following each begging episode, and related measures of begging to hunger. I measured hunger as the number of pieces of food a chick would swallow, with 5 s pauses between each offering. Males ate more food than females, especially after long deprivation periods (Figure 6.3). Since hungrier chicks beg more, I could not compare the begging levels between genders using deprivation time as the independent variable.

I performed exploratory multiple regression analyses on total begging duration, loudness, the number of begs per bout and individual call duration (see Methods for a description of begging measures) using hunger level, sex, body condition, age and rank in the natal brood as independent variables describing a chick's state. I examined models with two- and three-way interactions and selected those with a low Mallows'  $C_p$  (a statistic used for selecting the best small, unbiased models; Draper and Smith 1981) and adjusted multiple  $r^2$  for further work. I used condition indices and variance proportions to check for multicollinearity (Wilkinson 1988) and restricted my selected models to those including the main effects and without such complications in interpretation and stability.

Total begging duration increased with hunger level, and decreased with increasing body condition (Table 6.2). Males tended to beg for longer than females. A sex difference was apparent as an interaction between



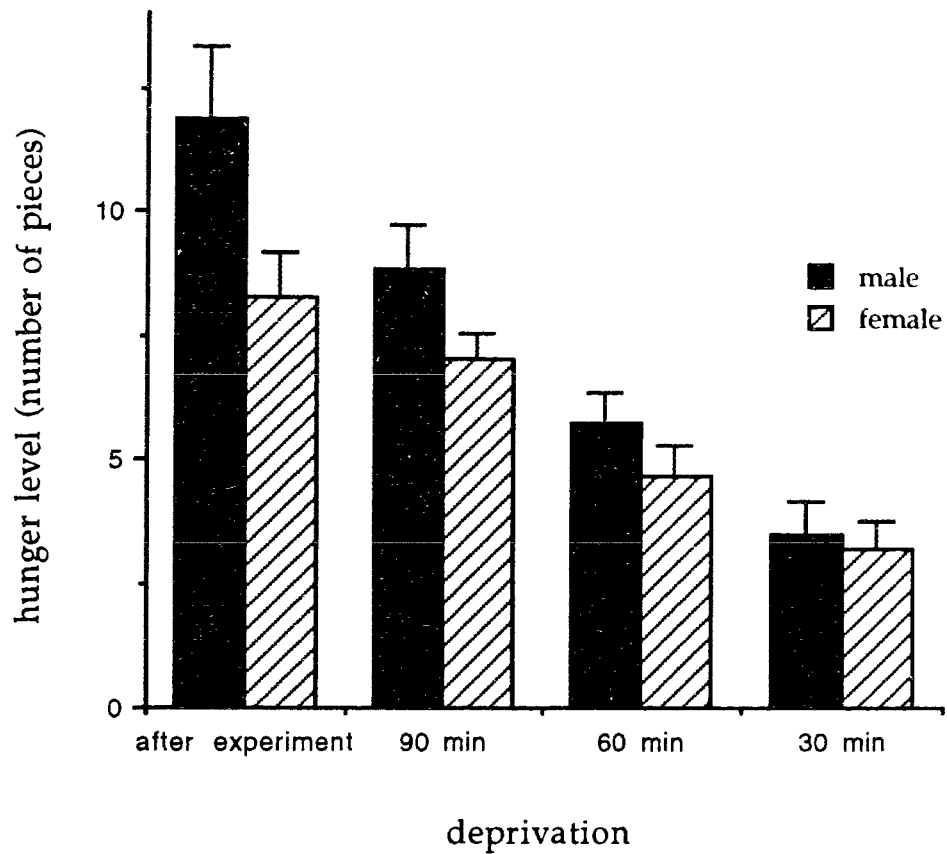


Figure 6.3. Hunger levels of males and females after various deprivation times in study 1 (mean  $\pm$  standard error; after experiment refers to a measurement taken under various hunger levels following the completion of an unrelated laboratory experiment). Males ate more than females for a given deprivation time (overall,  $F_{(1,33)}=7.96$ ,  $p=0.008$ , repeated measures analysis of variance with sex as an independent effect, using chicks who were tested four times).

Table 6.2. Selected multiple regression model for total begging duration.

variable	coefficient	t	p
constant	5.28	6.14	<0.001
hunger	0.69	6.82	<0.001
sex	1.31	1.38	0.17
condition	-0.74	-2.60	0.01
condition*sex	0.59	1.70	0.09

Table 6.3. Selected multiple regression model for begging loudness.

variable	coefficient	t	p
constant	57.04	17.44	<0.001
hunger	0.65	5.78	<0.001
sex	2.50	2.50	0.013
age	1.21	2.77	0.006
condition	-1.84	-6.29	<0.001
condition*sex	1.63	4.55	<0.001

Table 6.4

Selected multiple regression model for number of vocalizations per bout.

variable	coefficient	t	p
constant	1.70	0.58	0.56
hunger	0.66	6.66	<0.001
sex	0.46	0.51	0.61
age	0.36	0.92	0.36
condition	-0.86	-3.22	0.002
condition*sex	0.64	1.98	0.05

Table 6.5. Selected multiple regression model for single call duration.

variable	coefficient	t	p
constant	0.12	3.12	0.002
hunger	0.01	3.91	<0.001
sex	0.02	1.44	0.15
age	0.01	2.51	0.013
condition	-0.01	-3.06	0.003
condition*sex	0.01	2.92	0.004

condition and sex. Neither age nor rank were related to begging length. Begging loudness increased with hunger level and with age, and decreased with increasing body condition (Table 6.3). Males begged more loudly than females. Loudness was also strongly related to a condition by sex interaction. The number of vocalizations per bout increased with hunger and decreased with increasing body condition (Table 6.4). Males and females called equally overall, but beg number was related to a condition by sex interaction. Neither age nor rank were related to the number of calls given. The mean duration of calls within a bout increased with hunger and age, decreased with body condition, and again was related to an interaction between sex and condition (Table 6.5).

The interaction between gender and condition was the only interaction term with a strong influence on models which included the main effects. To examine this interaction more closely, I divided all chicks into either "good" (i.e., positive mass versus tarsus residual) or "poor" (i.e., negative mass versus tarsus residual) condition. I then calculated and compared the begging and hunger levels of good and poor males and good and poor females. Males ate more than females, but good and poor chicks ate similar amounts (Figure 6.4). Patterns of begging were rather interesting: while good and poor males begged equally loudly, and for a similar length of time (total duration and call duration within a bout), good females begged more quietly and for a shorter period than poor females (Figure 6.5).

Repeated measures analysis on nestlings who had been deprived for 90, 60 and 30 min intervals confirmed this effect. I performed these analyses on sexes separately since hunger levels after given deprivation times differed between males and females. Males begged for longer with increasing deprivation time (i.e., increasing hunger level;  $F_{(2,26)}=14.42$ ,  $p<0.001$ ; Figure

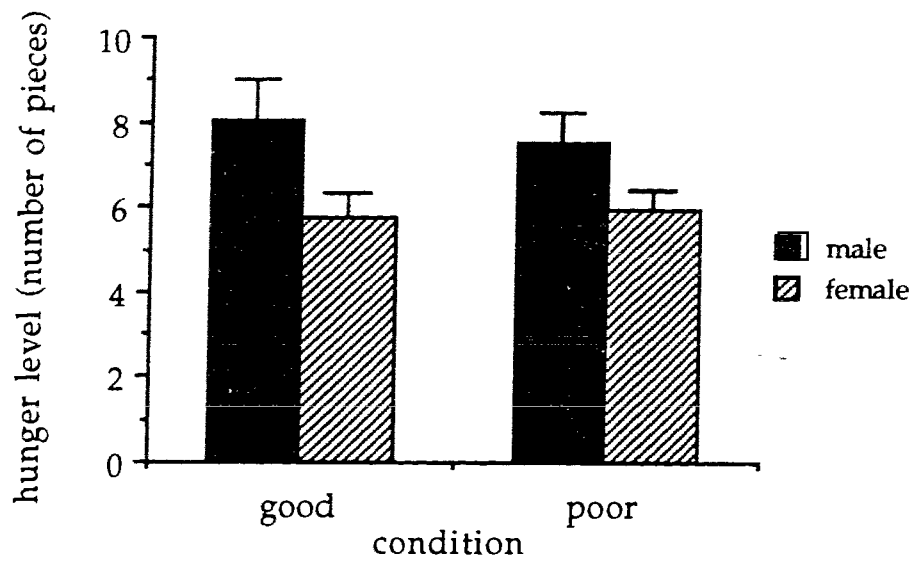


Figure 6.4. Hunger levels of male and female yellow-headed blackbird chicks in good (positive residuals) and poor (negative residuals) body condition in study 1 (mean  $\pm$  standard error).

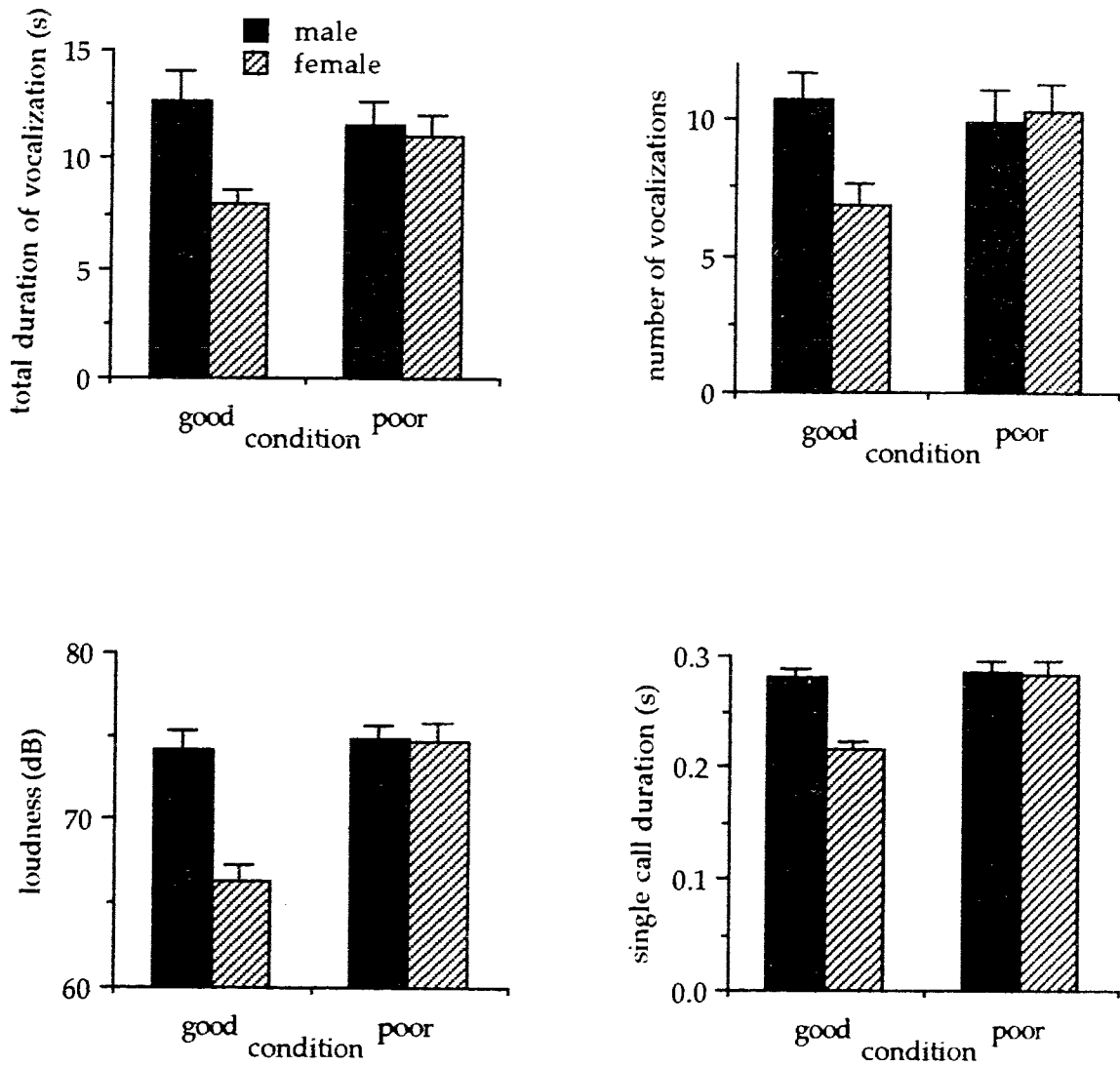


Figure 6.5. Begging levels (total duration, loudness and number of calls, and call duration) by yellow-headed blackbird chicks in good (positive residuals) and poor (negative residuals) body condition in study 1. Figures show means ( $\pm$  standard error) of all data points to examine results of regression analysis.

6.6), but not with decreasing condition ( $F_{(1,13)}=0.02$ ,  $p=0.90$ ). All males, independently of their condition, begged more when hungrier (condition by deprivation time interaction:  $F_{(2,26)}=0.59$ ,  $p=0.56$ ). Females increased begging length with increasing deprivation time ( $F_{(2,28)}=7.65$ ,  $p=0.002$ ; Figure 6.6), but also with decreasing body condition ( $F_{(1,14)}=6.43$ ,  $p=0.02$ ). There was a significant deprivation time by condition interaction in females, with chicks in poor condition increasing begging after 60 min and those in good condition waiting until after 90 min of deprivation time to beg for longer ( $F_{(2,28)}=4.37$ ,  $p=0.02$ ). Males and females both increased begging loudness with increasing deprivation time (males:  $F_{(2,22)}=17.52$ ,  $p<0.001$ ; females:  $F_{(2,26)}=7.06$ ,  $p=0.004$ ), but males showed no effect of condition ( $F_{(1,11)}=0.07$ ,  $p=0.79$ ), while females in good condition always begged more quietly ( $F_{(1,13)}=12.36$ ,  $p=0.004$ ). Very few chicks gave two or more calls following a 30 min deprivation period, hence I removed this treatment from analysis of call duration to increase sample size. Across the 60 min and 90 min deprivation periods, both sexes increased their mean calling length (males:  $F_{(1,13)}=17.38$ ,  $p=0.001$ ; females  $F_{(1,13)}=11.37$ ,  $p=0.005$ ). Again, females in good condition begged less than those in poor condition ( $F_{(1,13)}=5.41$ ,  $p=0.04$ ), while males did not ( $F_{(1,13)}=0.24$ ,  $p=0.63$ ).

### Study 2: Effects of rank: field experiments

In unmanipulated nests, in 1991, low rank (i.e., relatively small) nestlings begged more in response to a model parent than did their larger siblings (Figure 6.7). In a subset of experimental nests in 1992, chick rank prior to manipulation (i.e., in the first observation period) was related significantly to begging length, intensity, loudness and to the number of last, type II and extra begs, with relatively small chicks begging more, but was not

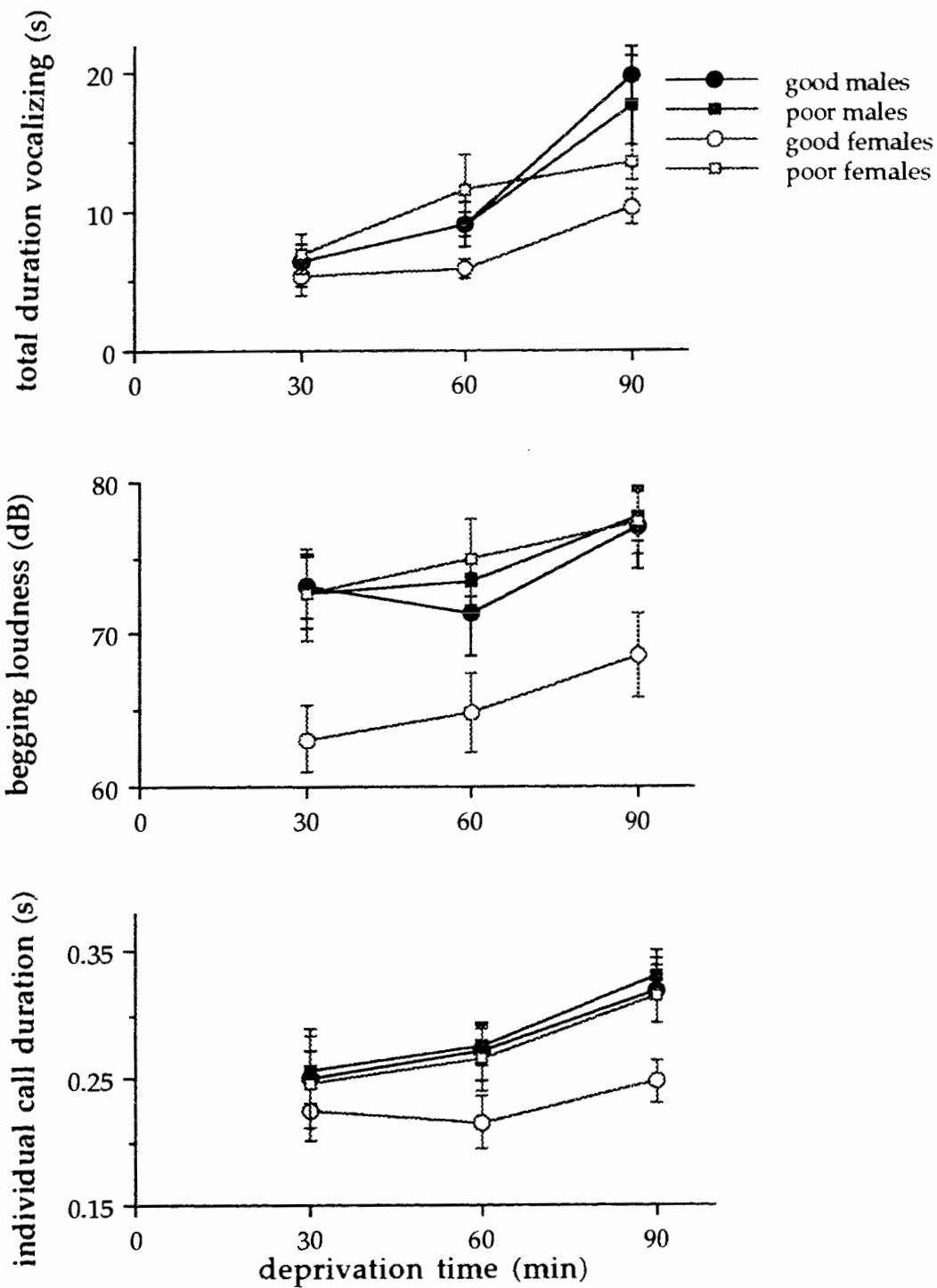


Figure 6.6. Total begging duration, loudness and call duration in yellow-headed blackbird nestlings after 30, 60 and 90 min of food deprivation in study 1. Points are means ( $\pm$  standard error) for males and females in good body condition (positive residuals) and poor body condition (negative residuals).

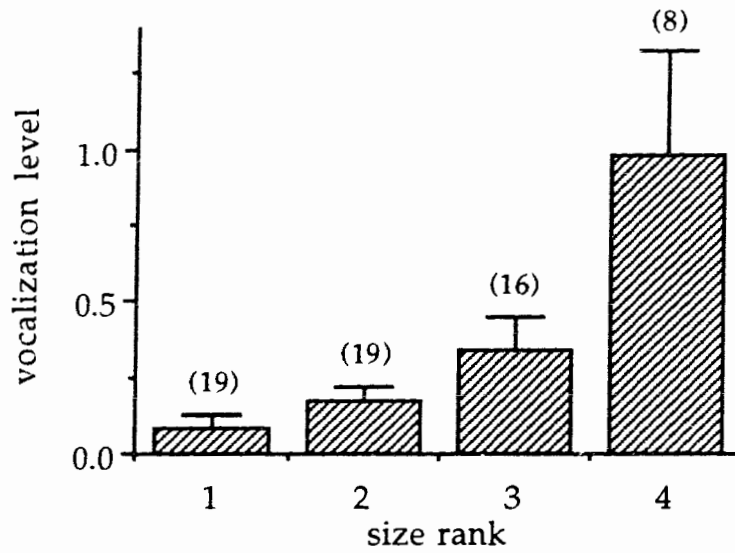


Figure 6.7. Vocalization level (arbitrary scale from 0 to 3) of nestlings in natural broods in response to a model parent (mean  $\pm$  standard error, (n)). Smaller chicks vocalize more intensely ( $F_{(3,40)}=7.83$ ,  $p<0.001$ ; analysis of variance blocked by nest).



related to start rank (Table 6.6). Neither of these observational data sets controls for effects of hunger, body condition or gender.

I analysed data from the 1992 cross-fostering experiment using rank measures of begging rather than actual values, because nests differed tremendously in overall begging level (personal observation; e.g., mean begging time per chick per hour varied from 38 s in one brood to 448 s in another). I compared the begging rank of each exchanged chick in its natal nest with its begging rank in the foster nest, and then looked at the differences between treatments (big to small, small to big and equal to equal). I standardized rank as  $(\text{rank}-1)/(\text{brood size}-1)$  to give a number between 0 and 1, where 0 represents the chick who begged most in a brood and 1 represents the chick who begged least for each measure of begging.

Within treatments, nestlings exchanged from being relatively small in a brood to being relatively large significantly decreased their relative begging time, intensity and loudness, and also decreased their relative last begs and extra begs (Table 6.7). They did not start significantly later, or change the relative number of type II begs. Chicks exchanged from large to small significantly increased their relative begging time, and increased the relative number of last, type II and extra begs. They did not significantly increase begging intensity or loudness, and tended (non-significantly) to start begging later rather than earlier. Control chicks, swapped between equal ranks, started to beg significantly later. They did not significantly change begging rank in any of the remaining components of begging, but did show tendencies to decrease begging in five of the six measured components.

The change in begging rank significantly differed between treatments for begging length (Figure 6.8;  $KW=12.57$ ,  $p=0.001$ ; Kruskal-Wallis non-

Table 6.6

Relationship between aspects of begging and nestling size rank prior to experimental manipulation (Table 6.1 describes aspects).

begging aspect	nestling rank				F <sub>(1,40)</sub>	p
	1	2	3	4		
length	146.14 ± 21.68	147.46 ± 25.27	201.73 ± 28.74	386.33 ± 92.16	15.04	<0.001
intensity	2.29 ± 0.16	2.25 ± 0.18	2.52 ± 0.17	3.00 ± 0.15	10.16	0.003
loudness*	1.85 ± 0.16	1.87 ± 0.13	2.05 ± 0.17	2.63 ± 0.23	9.86	0.003
start	1.53 ± 0.06	1.48 ± 0.09	1.44 ± 0.06	1.33 ± 0.09	2.08	0.16
last	0.39 ± 0.07	0.33 ± 0.05	0.72 ± 0.05	0.77 ± 0.19	14.86	<0.001
type II	2.00 ± 1.15	3.96 ± 2.51	13.18 ± 4.65	35.67 ± 35.67	7.06	0.011
extra	4.05 ± 1.17	3.23 ± 0.87	8.73 ± 1.69	7.33 ± 5.36	11.75	0.001

\* F<sub>(1,39)</sub>, one measurement missing

Table 6.7

Begging by cross-fostered nestlings in their natal and foster nests. In treatment S-L, the smallest chick in a nest was fostered to become the largest, in treatment L-S, the largest became the smallest, and in treatment E-E, chicks exchanged nests, but retained their size rank (n=10 for each treatment). Measurements are mean standardized rank for each aspect (see text).

treatment	aspect	natal	foster	z	p
S-L	time	0.13 ± 0.07	0.70 ± 0.13	2.41	0.01
	intensity	0.18 ± 0.12	0.50 ± 0.15	1.7	0.05
	loudness	0.10 ± 0.06	0.38 ± 0.13	2.03	0.02
	start	0.29 ± 0.11	0.46 ± 0.14	0.91	0.18
	last	0.13 ± 0.07	0.58 ± 0.14	2.46	0.01
	type II	0.35 ± 0.11	0.50 ± 0.12	1	0.16
	extra	0.15 ± 0.08	0.56 ± 0.12	2.56	0.01
L-S	time	0.73 ± 0.11	0.38 ± 0.12	-1.9	0.03
	intensity	0.70 ± 0.12	0.43 ± 0.11	-1.28	0.1
	loudness	0.55 ± 0.08	0.38 ± 0.13	-1.07	0.15
	start	0.58 ± 0.14	0.75 ± 0.13	0.86	0.2
	last	0.75 ± 0.11	0.37 ± 0.10	-2.12	0.02
	type II	0.68 ± 0.08	0.36 ± 0.10	-2.11	0.02
	extra	0.63 ± 0.09	0.42 ± 0.10	-2	0.02
E-E	time	0.50 ± 0.11	0.68 ± 0.10	1.69	0.09
	intensity	0.50 ± 0.10	0.62 ± 0.10	1.47	0.14
	loudness	0.58 ± 0.10	0.69 ± 0.12	0.95	0.34
	start	0.43 ± 0.14	0.77 ± 0.08	2.03	0.04
	last	0.54 ± 0.12	0.58 ± 0.12	0.54	0.59
	type II	0.55 ± 0.11	0.69 ± 0.10	1.45	0.15
	extra	0.64 ± 0.14	0.60 ± 0.13	-0.53	0.6

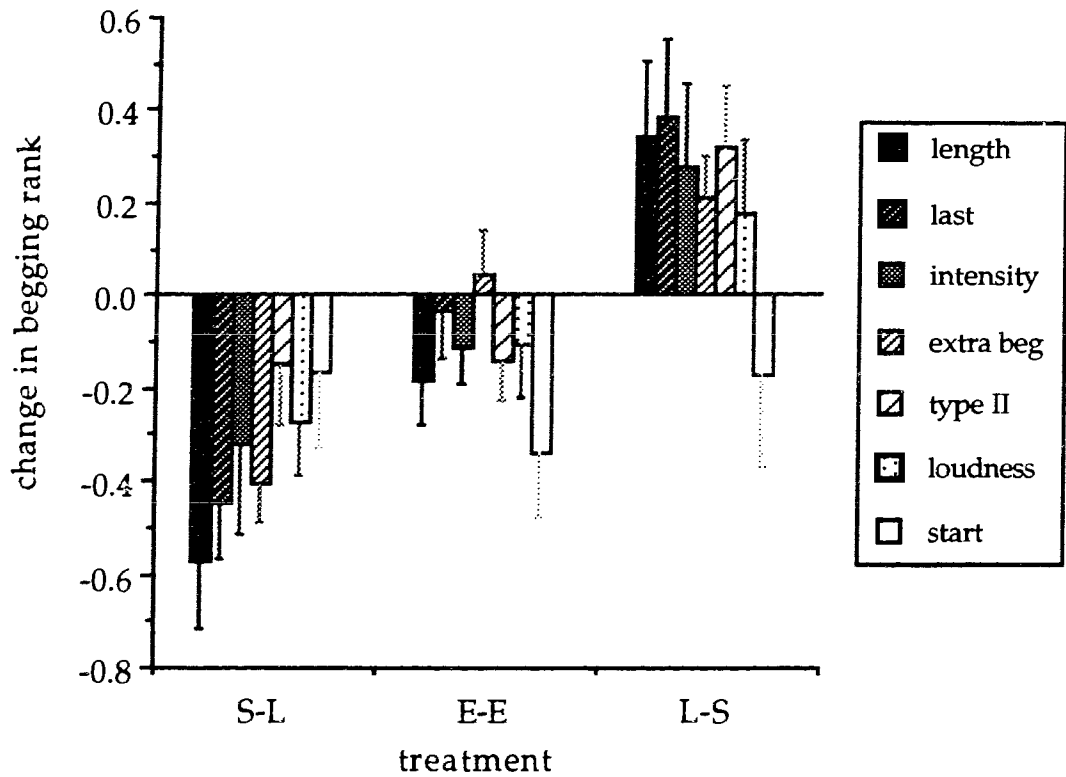


Figure 6.8. Change in begging rank due to treatment for several aspects of begging in study 2. S-L chicks were exchanged from being relatively small to relatively large; L-S chicks were exchanged from being relatively large to relatively small; and E-E chicks were exchanged, but retained their size rank (n=10 for each treatment).

parametric analysis of variance, one-tailed tests) and intensity (KW=7.24,  $p=0.014$ ) and the number of last (KW=11.73,  $p=0.002$ ), type II (KW=7.75,  $p=0.01$ ) and extra begs (KW=13.93,  $p<0.001$ ). Treatments did not differ significantly in begging loudness (KW=2.78,  $p=0.08$ ) or in start rank (KW=0.93,  $p=0.32$ ).

Provisioning ranks also changed within treatments: chicks who became relatively larger were fed relatively more within their foster brood (when small: rank fed =  $0.68 \pm 0.11$ ; when large: rank fed =  $0.38 \pm 0.16$ ;  $z=-1.87$ ,  $p=0.06$ ; Wilcoxon matched pairs,  $df=2$ , two-tailed tests); those who became relatively smaller were fed less (large:  $0.21 \pm 0.07$ ; small:  $0.84 \pm 0.10$ ;  $z=2.68$ ,  $p=0.008$ ), and those of constant rank were fed similarly before and after fostering (before:  $0.26 \pm 0.09$ ; after:  $0.43 \pm 0.16$ ;  $z=0.99$ ,  $p=0.32$ ). The change in feeding visits to experimental nestlings differed significantly across treatments (KW=11.61,  $p=0.003$ ).

Since provisioning changed between natal and foster nests, hunger levels likely varied over time, and may have been responsible for some of the observed changes in begging. As a coarse examination of changes over time, I compared the mean length of time spent vocalizing during the first five parental visits and the next five visits (or the first and second halves if parents visited less than ten times) after fostering. While begging patterns did not change significantly over time (relatively large foster chicks:  $z=1.36$ ,  $p=0.17$ ; relatively small foster chicks:  $z=-1.35$ ,  $p=0.18$ ; Wilcoxon matched pairs,  $n=10$  for both cases), the direction of change was consistent with that expected from decreasing (those fostered as large chicks) or increasing (those fostered as small chicks) hunger. I did not analyse the field data more closely to determine if the observed begging was an effect of my treatments or an effect of changes in feeding pattern (and hence hunger). Instead I tested these alternative hypotheses in the controlled experiment discussed below.

### Study 3: Effects of rank: laboratory experiment

Hungry nestmates (i.e., non-experimental, stimulus chicks) begged more intensely than full nestmates (Figure 6.9;  $F_{(1,30)}=96.46$ ,  $p<0.001$ ; analysis of variance, blocked by trial,  $n=11$  trials). Big nestmates did not beg more intensely than small nestmates ( $F_{(1,30)}=0.53$ ,  $p=0.5$ ), but there was an interaction effect ( $F_{(1,30)}=4.25$ ,  $p=0.05$ ) with small chicks increasing their intensity by more when they were hungry. This interaction was influenced by one big chick who rarely begged (and probably was insufficiently food-deprived).

Experimental chicks begged for significantly longer when their nestmate was bigger (Figure 6.10;  $F_{(1,30)}=20.47$ ,  $p<0.001$ ) and when their nestmate was hungry ( $F_{(1,30)}=15.94$ ,  $p<0.001$ ), with no size by hunger interaction ( $F_{(1,30)}=0.89$ ,  $p=0.4$ ). All eleven experimental chicks begged for the shortest time when paired with a small full chick; eight of eleven begged longest when paired with a big, hungry chick. Experimental chicks also begged significantly more intensely with big, and marginally non-significantly more intensely with hungry, nestmates (size:  $F_{(1,30)}=5.72$ ,  $p=0.02$ ; hunger:  $F_{(1,30)}=3.75$ ,  $p=0.06$ ; interaction  $F_{(1,30)}=0.64$ ,  $p=0.4$ ). They begged significantly more loudly with big nestmates, but did not beg louder with hungry nestmates (size:  $F_{(1,30)}=5.45$ ,  $p=0.03$ ; hunger  $F_{(1,30)}=1.36$ ,  $p=0.25$ ; interaction:  $F_{(1,30)}=0.09$ ,  $p=0.8$ ). They also reared significantly higher with big nestmates, but not with hungry nestmates (size:  $F_{(1,30)}=10.55$ ,  $p=0.003$ ; hunger:  $F=2.31$ ,  $p=0.14$ ; interaction  $F_{(1,30)}=0.49$ ,  $p=0.5$ ). Experimental chicks tended to beg sooner (i.e., they responded to the shadow more readily) when their nestmates were bigger (size:  $F_{(1,30)}=3.34$ ,  $p=0.08$ , hunger:  $F_{(1,30)}=2.64$ ,  $p=0.115$ ; interaction:  $F_{(1,30)}=0.04$ ,  $p=0.8$ ). Conversely, experimental chicks begged for significantly longer after receiving food when their nestmate was hungry, but

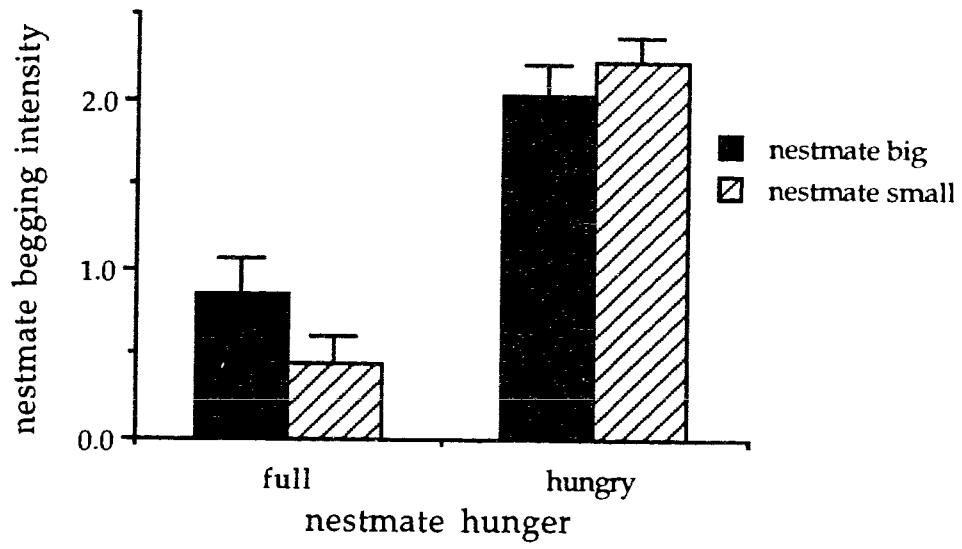


Figure 6.9. Begging intensity of nestmate (i.e., non-experimental chick) in study 3.

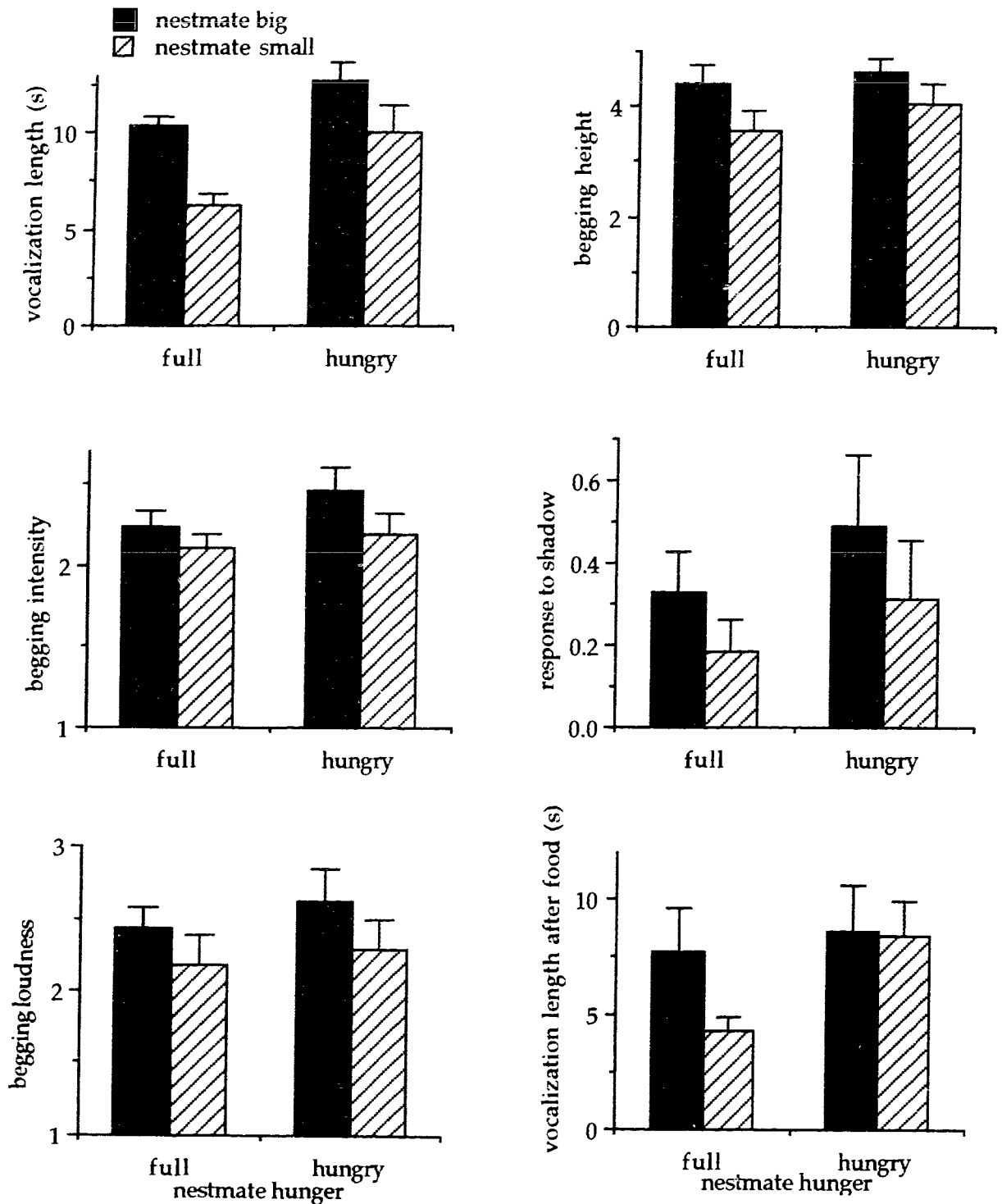


Figure 6.10. Begging level of experimental chick when matched with a big hungry, big full, small hungry or small full nestmate in study 3 (mean  $\pm$  standard error, n=11 for each treatment).



did not beg significantly longer when their nestmate was big (size:  $F_{(1,29)}=2.62$ ,  $p=0.12$ ; hunger:  $F_{(1,29)}=4.99$ ,  $p=0.03$ ; interaction:  $F_{(1,29)}=2.15$ ,  $p=0.15$ ; one treatment in one trial not measured). Across treatments, experimental chicks begged for longer when their nestmate begged more intensely (Figure 6.11), but this pattern was not distinguishable within treatments.

## Discussion

The studies described in this chapter support the hypothesis that begging can carry information about nestling long-term need. I predicted that, in yellow-headed blackbirds (with hatching asynchrony, pressure to fledge quickly, and sexual dimorphism), small chicks, those in poor condition and males would beg more than large, heavy and female chicks. I found that even when I controlled for nestling hunger level (either experimentally in study 3 or statistically in study 1), needy chicks begged more. I found no evidence that chicks vocalized more with increasing quality, although older males (the biggest chicks measured) could beg more loudly (had higher ability), and did so when very hungry. I found evidence for competition in that chicks begged more in the presence of active nestmates.

Litovich and Power (1992) discovered that parent starlings fed the "best-beggars", and argued that runts (last-hatched chicks in poor body condition) could not be the best-beggar due to energetic limitations. They concluded that begging signals nestling value and inferred from this conclusion that parents win any parent-offspring conflict (Trivers 1974) in starlings. I cannot discuss their conclusion that begging did not contain information about chick need because Litovich and Power did not present their data on begging intensity as it related to need, but I can discuss their interpretation. Parents, in deciding how to allocate food, might benefit from knowing which chicks have a high

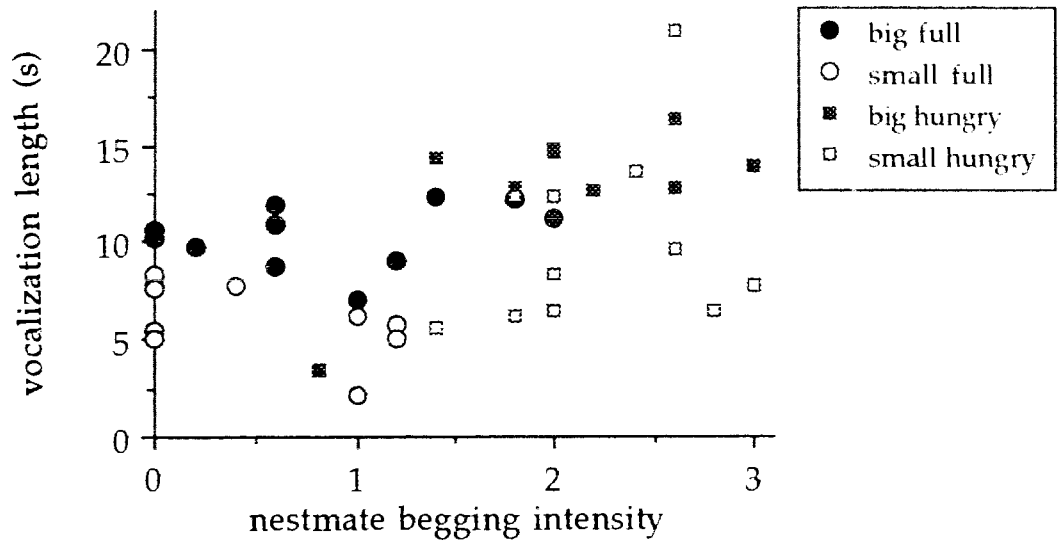


Figure 6.11. Vocalization length given by experimental nestling in relation to its nestmate's begging intensity in study 3 (overall  $r=0.46$ ,  $p=0.002$ ,  $n=44$ ).

need (i.e., would benefit more from being fed), as well as from knowing which have a higher quality. Chicks with high competitive ability (the best-beggars of Litovich and Power 1992) may actually be receiving more food than is optimal for a parent if the increment in reproductive value per unit of food is greater for a needier chick. Hence, their parent starlings are not necessarily "winning" any conflict. Before we can test any predictions regarding parent-offspring conflict using begging, we must be certain about the costs and benefits to both parties of the communication (Mock and Forbes 1992, Clutton-Brock 1991). Knowing what types of information can be transmitted by begging seems a prerequisite to this goal.

#### Effects of gender and body condition

Laboratory observations (study 1) show that gender and body condition affect begging in yellow-headed blackbird chicks. Unlike relative size, investigated experimentally in studies 2 and 3, neither body condition nor gender are amenable to manipulation. Hunger level also proved difficult to control with any finesse. Instead of controlling for hunger level experimentally, I recorded the begging of chicks after several deprivation intervals and used hunger as a variable in my regression models.

Body condition and gender were important variables in regression models of begging length, loudness and number, with begging increasing with decreasing body condition, and with males begging more (particularly males in good condition). Older chicks begged more loudly. Neither relative rank in the brood nor chick mass (other than as a component in condition) influenced begging. Teather (1992) found that male red-winged blackbirds begged more, but did not measure their hunger level. When I controlled for hunger level in regression models, the effect of gender was reduced, but not

eliminated. Hence, male yellow-headed blackbirds do not beg more just because they are hungrier.

The only compelling interaction in models including the main effects was between sex and condition. Closer examination of this interaction showed that while males tended to beg loudly and for a long time regardless of their condition, females only begged loudly and long when in poor condition. Females in good condition (less needy on both accounts) begged least. Females in poor condition increased their vocalization length after 60 min of deprivation, while those in good condition only increased begging length following 90 min without food. Even after 90 min of deprivation, females in good condition begged more quietly than males or females in poor condition. These observations from study 1 supplement the experimental evidence from studies 2 and 3 that begging can carry information about nestling long-term needs, and uphold the prediction that males should beg more (Chapter 2).

The observational results of study 1 should, however, be cautiously interpreted. Nestlings were not randomly selected, and experienced various experimental treatments prior to recording. Chicks taken from a "brood" (created for an experiment) tended to beg more than chicks who had been sitting alone in a container. Some chicks who had begged continuously while waiting to be recorded (in a "brood" with other chicks) would not beg for food when placed singly for recording. Chicks ate more food on their first trial (immediately following another experiment) than following 90 min of deprivation, although none had been deprived for as long as 90 min at this first measurement. Experience prior to recording (in terms of competition or food availability) may affect begging and measured hunger levels of individual nestlings. Stamps et al. (1989) suggest that experience with

nestmates and prior begging success may influence begging by budgerigars. Although prior experience was likely random with respect to gender and body condition in my study, future work should attempt to control for possible biases in prior experience.

### Effects of rank

In the field (study 2), exchanged nestlings begged for relatively longer, more loudly and more intensely when smaller than their nestmates, and begged last more frequently and gave more type II and extra begs. By comparing rank levels of begging within natal and foster broods, I was able to control for any absolute changes in begging resulting from changes in the level of nestmate begging—an effect shown to be important in study 3. While experimental chicks in the laboratory tended to start begging sooner when relatively small (i.e., responded more readily to a shadow stimulus), experimental chicks in the field, in all treatments, tended to start begging later in their foster nest (significantly so in the equal-to-equal, control treatment). No other begging components showed this pattern. Perhaps chicks in foster nests were unfamiliar with the signs of an approaching parent in their new location and were slower to respond.

I cannot rule out hunger as contributing to mean begging levels in the field experiment since swapped chicks received different amounts of food in their natal and foster nests. Comparing begging using the same chick in different nests controls for condition, gender and age, but does not control adequately for hunger levels over time. Nestlings did not change their vocalization length significantly between the first five and next five parental visits, but did change in a direction consistent with that expected from a change in hunger (i.e., newly large chicks tended to beg less over time and

newly small chicks tended to beg for longer). Some chicks seemed to beg immediately at the level appropriate to their foster rank while others did not. As an alternative explanation for any lag in response, chicks might take several begging episodes to assess their relative size. Study 2 taken alone would be unconvincing evidence that nestlings are begging in relation to long-term as well as to short-term need, but it corroborates the results of study 3, and shows that the effect is observable in natural nests.

I did not compare begging between chicks in the same nest in different treatments (e.g., naturally-small vs. fostered-small chicks). Table 6.7 seems to show some interesting trends, with naturally-small chicks tending to beg more than fostered-small chicks in the same nest, and naturally-large chicks tending to beg less than their fostered replacements. At first glance, such a result seems to add to the evidence that needy chicks beg more, since smaller chicks in natural broods are generally in poorer condition than naturally-large chicks (Richter 1984, personal observation). However, between-treatment comparisons would be difficult to interpret since the chicks in question differ in more than body condition—certainly in hunger level, and sometimes in gender.

The laboratory rank experiment (study 3) clearly demonstrates that chicks can assess their relative size and that they alter their begging to reflect this size. Nestlings begged more (longer, louder and more intensely) when paired with a larger rather than smaller nestmate even when their nestmate remained silent. The nestlings used for this experiment varied in age as well as in size, and the observed change in begging level could represent an assessment of age rather than relative size. While an interesting detail, such a result does not discredit the hypothesis that needy chicks beg more, since relatively younger chicks face similar growth goals in order to fledge, and

hence benefit similarly by increased provisioning. Teasing apart the highly correlated effects of relative age and relative size will not be easy: controlling for either one increases variation in body condition—a third variable. By using nestlings who were both larger and older, I controlled for body condition differences to some extent. Study 3, where I manipulated chick long-term need, and controlled for hunger, constitutes my strongest evidence that vocal begging can carry information about long-term need.

### Effects of competition

Experimental chicks in study 3 also increased some measures of begging (vocalization length, begging after feeding, begging intensity) when their nestmates were hungry (and hence begged more). This response, together with the results of Chapter 5, show that a potential exists for sibling competition to drive up begging levels, and raises interesting questions about why big siblings do not beg more (see Parker et al. 1989, Chapter 2, Chapter 7). I concentrated on measuring nestling vocalizations, and may have missed differences in other components of begging. Parents may feed according to some non-vocal criterion (e.g., size, position or height; Gottlander 1987, Smith and Montgomerie 1991, Teather 1992) leaving vocalizations as the only option for small chicks. If vocal begging bears predation costs for all nestmates, large nestlings may renounce their feeding privileges to quiet their small siblings (Chapter 2, Zahavi 1977).

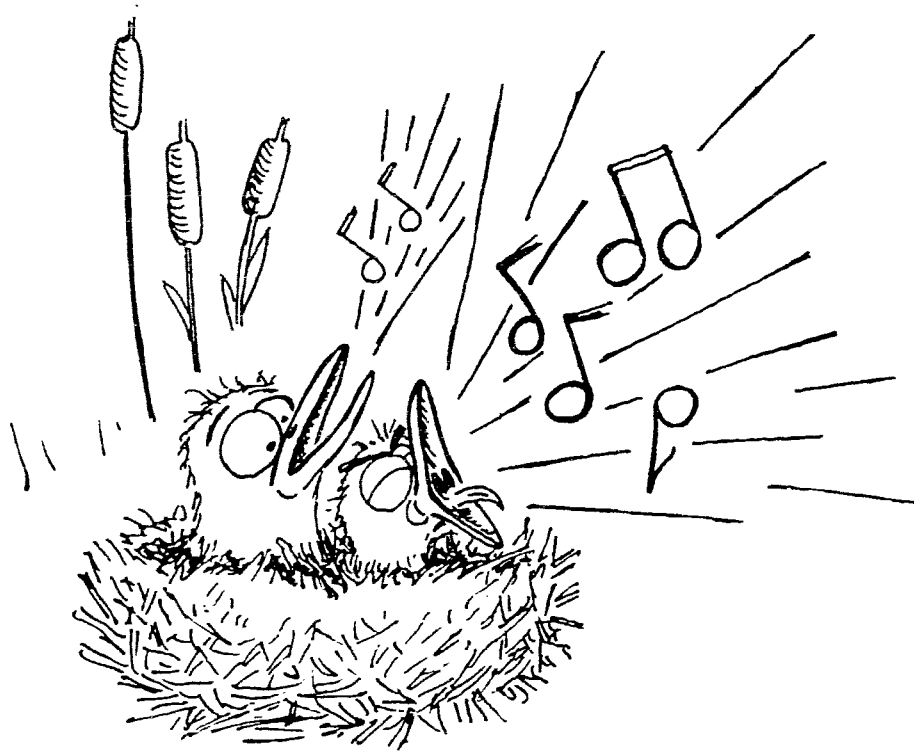
Combining evidence from the three studies, I conclude that vocal begging can signal long-term need as well as short-term hunger level in nestling yellow-headed blackbirds. I examined those aspects of chick need likely to be unstable and susceptible to collapse into signals of quality (i.e., aspects correlated with chick quality or competitive ability). Just how begging

contains stable information about long-term need when nestmates increase begging in the face of competition remains unanswered. The genetic algorithm model developed in Chapter 2 suggests that differences in the hunger state of related large and small nestmates may stabilize the signal of need: large nestmates will be hungry less often, and will incur indirect benefits at these times by allowing their needy siblings to eat.



# Chapter 7

## Conclusions



This thesis has investigated several aspects of the behavioural ecology of begging in yellow-headed blackbirds (*Xanthocephalus xanthocephalus*). Given than loud begging carries potentially high costs, much theoretical interest has focussed on its evolution, either as a form of parent-offspring conflict (leading to escalating costs) or as a form of honest information about a nestling's need or value (requiring costs for stability). In Chapter 1, I summarized the various theoretical arguments for the evolution of costly begging in three sections: begging as manifested genetic conflict between parents and their offspring; begging as communication of value; and begging as communication of need. I concluded that the conflict and cooperative communication perspectives could be easily reconciled, but that predicting whether begging should signal need or value was less obvious.

The interactions involved in decisions about begging and provisioning are complex. Some sort of communication to its parent of a nestling's need seems reasonable. However, parents are related equally to all of their offspring, while nestlings are related more to themselves than to their siblings. Hence, siblings should compete over the limited provisioning forthcoming from their parents. Such competition could result in escalation of begging, perhaps reducing its information content. If all chicks had equal competitive ability and equal quality, escalation would not eliminate information about chick need—begging could still be *relatively* honest if *absolutely* dishonest. Differences in chick ability (likely correlated with differences in chick quality), however, complicate this picture. Competitively superior nestlings may beg more and outcompete their less able siblings for food. Parents may also bias provisioning towards these valuable nestlings. Either scenario reduces the likelihood that begging can remain a signal of

nestling need, particularly if aspects of need (e.g., long-term need) correlate negatively with aspects of quality or ability (e.g., a weak chick needs food, but has a low potential value and less energy available to beg). One of the goals of my thesis, then, was to determine if begging could carry information about nestling need for provisioning in a species with asymmetric abilities, need and values.

To this end, I asked three questions of begging in yellow-headed blackbird nestlings. First, I asked whether nestlings benefit from begging (Chapters 3, 4). If begging acts as communication between chicks and their parents, parents must respond under some circumstances. I looked at two types of parental response: increased provisioning in response to whole-brood begging level and increased allocation to begging chicks within a brood. Second, I tested whether yellow-headed blackbird nestlings compete by begging, i.e., whether chicks change their begging level in response to changes in their nestmates' begging levels, or in response to added competition within the brood (Chapters 4, 5, 6). It was important to discover whether chicks compete by begging to determine the potential that begging could collapse into a signal of quality (e.g., because high quality chicks could fake signals of need). Finally, given positive evidence that begging chicks can change provisioning levels, and that chicks compete by begging, I investigated strategic begging by different classes of nestlings, asking if needy chicks beg more (i.e., when food is worth more to them), or if valuable chicks beg more (Chapter 6). I also examined these questions using a simulation model, designed to look at the evolution of begging and provisioning strategies in families of one parent and two potentially asymmetrical siblings (Chapter 2).

I found strong evidence that parent yellow-headed blackbirds respond to the begging of their chicks: both females and males increased their

provisioning to broods with experimentally-enhanced begging (Chapter 3). This increased provisioning resulted in chicks gaining more mass during two hours of begging playback than during a control period. Broods of chicks with increased begging over five days (via playback) also gained more mass than did broods without (Chapter 3). I conclude that chicks benefit from an increased overall brood begging level.

Parents also responded to changed begging levels within a brood. In unmanipulated broods, nestlings who received food had begged more intensely, started earlier, and begged for longer than unfed nestlings in any visit; after experimental manipulation of hunger level, parents increased their allocation to food-deprived chicks, who begged more (Chapter 4). However, although parents did increase or decrease their feeding visits to chicks with experimentally increased or decreased begging levels, they did not base their food allocation on begging alone. Big chicks always received more food deliveries than their smaller nestmates, even when the small chicks begged more (Chapter 4). Big chicks reacted to parents' visits more quickly (i.e., started to beg sooner) than their smaller siblings. I considered the idea that parents use early starts to begging as a cue to relative size, but did not find support for this hypothesis when siblings did not beg earlier in response to earlier begging by their deprived nestmates. Parents may use non-vocal cues to judge nestling size. Yellow-headed blackbird nestlings can benefit from begging more within a brood by increasing the amount of food they receive, but cannot increase their allocation above that of their larger siblings.

Several of my studies suggest that siblings compete for food by begging, and that their behaviour changes when their nestmates' behaviour changes. In natural broods, chicks increased begging in response to an increase in the begging level of a deprived nestmate (Chapter 4, experiment 2). More

convincingly, in a controlled laboratory experiment, chicks begged more when their single nestmate was hungry and noisy, and less when it was satiated and silent (Chapter 6). Chicks also begged more when an extra nestling was added to the brood, both in the field and in a controlled laboratory experiment (Chapter 5). The begging model (Chapter 2) supports the contention that strategies of escalation can evolve, leading to competition by begging. Full siblings ( $r = 0.5$ ) evolved high begging levels with relatively little sensitivity to their state as compared with identical chicks (i.e.,  $r = 1$ , with no genetic competition), who showed high state-sensitivity. Many more full siblings starved and competition for food via begging decreased mean fitness.

Finally, I found evidence that nestling yellow-headed blackbirds beg strategically in relation to their need, i.e., chicks beg more when food is worth more to them. Evolved begging strategies reflected hunger level in the model (Chapter 2), and experimentally-deprived chicks begged more (Chapter 4). In natural, unmanipulated broods, smaller chicks (who may have been hungrier) begged more (Chapter 4). Under laboratory conditions, where I controlled hunger level, chicks begged more when paired with a large than a small nestmate, and males and chicks in poor condition begged more than females and chicks in good condition (Chapter 6). Interestingly, there was an interaction between gender and body condition, with males begging loudly and for a long time regardless of condition, and females only begging at a high level when in poor condition. In yellow-headed blackbirds, smaller nestlings must grow fast to fledge successfully (Appendix 2), males reach a higher mass at fledging, and chicks in poor condition risk starvation—these groups of chicks should value food highly. Together, the begging levels for these distinct classes of nestlings support the hypothesis that needier chicks beg

more. In the begging model, males (chicks with high need and high ability) evolved to beg more loudly than females regardless of their state, and smaller chicks (with high need and low ability) evolved to beg more than their bigger siblings when both were relatively satiated. I conclude that begging can signal nestling short-term need (i.e., hunger level) and, more surprisingly, that it can also signal nestling long-term need. I found no evidence that begging level signalled chick value (as estimated by size rank or body condition), and cannot support the hypothesis that begging carries information about quality.

I have shown that needy chicks beg more, that parents respond to overall and within-brood begging levels, and that nestlings compete by begging. Integrating these three findings will prove more difficult. If nestlings compete for food by begging, and if parents respond to begging by bringing more food, why do big chicks beg less than their smaller siblings?

In general, big chicks may be less hungry. Ample evidence from this thesis and elsewhere shows that begging can signal hunger level (see Chapters 2, 4, 6). I found that parent yellow-headed blackbirds fed according to size rank (Chapters 3, 4); hence big chicks were probably less hungry. However, in the laboratory, when I controlled hunger level, nestlings still begged less when bigger than their nestmate (Chapter 6): hunger does not tell the whole story.

The begging model suggests that bigger chicks (with a higher begging ability) should be more sensitive to their short-term state (i.e., hunger). For the same high hunger level, big chicks should beg more than their small siblings (because they can), whereas for the same low hunger level, big chicks should beg less than their small siblings (i.e., show leniency; Chapter 2). This prediction is readily tested: if all chicks in a brood are hungry (e.g., following a storm, or early in the morning), big chicks should beg more, whereas, if all

chicks are relatively satiated, small chicks should beg more. The model proposes two conditions under which big chicks should be sensitive to hunger, begging little when at low hunger levels: in the first, under low starvation risk, big siblings increase their inclusive fitness benefits by reducing the risk of their sibling's death; and in the second, under both a high risk of starvation and a high risk of predation, big siblings decrease the chances of predation (and death of both chicks). In both scenarios, the costs of begging outweigh the benefits to the big sibling. The first of this pair of hypotheses suggests that big chicks beg less because their small siblings need food (i.e., begging carries inclusive fitness costs), and hence implies that begging carries honest information about nestling need. The second suggests that big chicks beg less because their siblings have changed the context of their begging decision (i.e., begging increases predation risk), and hence implies that small nestlings may be "manipulating" their nestmates' behaviour. Hence, under different environmental regimes, begging by small chicks may influence the begging of their larger siblings by demonstrating need, or by changing the context of their decision.

Both of these hypotheses suggest that big siblings should be sensitive to the begging level of their siblings as well as to their own hunger level. Closer examination of the responses of big and small nestmates to changes in the begging level of their siblings may help test the ideas. If big siblings beg less in order to increase their inclusive fitness (or to decrease predation risk), they should be responsive (i.e., by reducing begging) to insistent begging by their needy nestmates. I predict that while small chicks will increase their begging level following the deprivation of their larger siblings, big chicks will not increase begging following the deprivation of their smaller siblings. My data in Chapter 4 are insufficient to evaluate any such trends.

I have shown in this thesis that begging by yellow-headed blackbirds carries information about chick long-term and short-term need. Even in a species with large differences in nestling ability and value, and with competition for food via begging, begging remains a reliable signal of need. I have demonstrated that parents use the information about nestling need provided by begging to decide how to allocate food, but that they may also provision according to some cue of nestling value. I have developed a model to explore these ideas which suggests that begging can be both an "honest" signal of need and can be "manipulative" depending upon the starvation and predation regimes of a species.



## Appendix 1

### Predation costs of begging

## Introduction

This appendix documents several attempts to measure the predation costs of begging in yellow-headed blackbirds. Models of begging generally assume, or conclude, that begging is costly (Parker et al. 1989, Parker and Macnair 1979, Harper 1986). Two types of cost have been discussed: energetic costs, borne by the caller alone, and predation costs, which are also felt by the caller's nestmates (see Chapters 1, 4). John McCarty (personal communication) has recently completed an experiment suggesting that energetic costs of begging are minimal. Until recently, support for a predation cost to begging has been entirely anecdotal (Skutch 1949, Perrins 1965, Kilham 1977, Gochfeld 1978). Subsequently, Redondo and de la Reyna (1992) have found correlative evidence for predation costs in magpies, where larger broods were depredated more frequently. In an experimental study, David Haskell (personal communication) has found that pseudo-nests with playback begging were depredated more than those without, at least when the nests were situated on the ground. He found no effect of playback for nests in trees. Yellow-headed blackbird nestlings beg loudly, and can be heard up to 1 km away (personal observation). They may suffer from high levels of predation (mean of 40% of nests in my study populations; mostly by mink *Mustela vison* and ravens *Corvus corax*). Yellow-headed blackbirds seemed a good system to look for predation costs of begging.

## Methods

I played recorded begging calls in several studies designed to look for a predation cost of begging in colonies of yellow-headed blackbirds in Creston, B. C. in 1991, 1992 and 1993. I recorded the begging calls from several broods

of nestlings in 1990, and copied them (minus parental calls) on to 6 min loop tapes.

In 1991, I examined predation response to recorded begging in three sessions (before, during and after the nesting period—early May, late May and early July respectively). Each session consisted of two 3 day trials. In each trial, I placed six pseudo-nests (woven from wet cattail and reed canary grass) containing two quail eggs and a plasticine egg (painted to resemble the quail eggs, and tied to the bottom of the nest) at random locations through a yellow-headed blackbird breeding area, sewing them to the nearest clump of cattails. Poles supporting green aluminum boxes containing playback equipment were driven into the marsh substrate near each of the six nests, and were camouflaged with cattails. Begging calls were broadcast for 3 min out of 14 from three of the six speakers (three playback and three control nests randomly assigned) from dawn to dusk. An assistant and I visited the nests at dawn to place the equipment, and at dusk to remove it for recharging.

In the third session (early July), I modified the experimental design first by using recently-vacated yellow-headed blackbird nests instead of pseudo-nests (as an olfactory cue for mammals), second by placing meat in the nest instead of quail eggs (as a higher food reward), and finally by placing a floating platform of mud underneath the nests (to look for tracks). I also placed quail eggs near an active mink den to see if they would be eaten.

I repeated a similar playback experiment in 1992, playing back calls at five pseudo-nests (and not at five control pseudo-nests) for seven days at each nest, and moving the pseudo-nests three times (total of 15 controls and 15 treatment nests). In a second study, I placed the equipment at active yellow-headed blackbird nests containing chicks, and again played begging calls for 3 min out of 14 at five treatment nests, but not at five control nests. I checked

the nests twice daily (at dawn and dusk) and continued the treatment until the chicks fledged or were depredated, when I moved the equipment to a new nest (total of eight controls and eight treatment broods).

In 1993, I placed speakers (and dummy speakers) at 22 active yellow-headed blackbird nests (11 playback broods and 11 controls) to look at both the benefits and costs of increased whole-nest begging levels (see Chapter 2 for a discussion of the benefits). In 1993, the playback equipment included a light sensor, which turned the speaker on at dawn and off at dusk, and removed the necessity of disturbing nests at these times. Instead, I removed the equipment for recharging at noon, an inactive period both for predators and chick provisioning, and returned it the following noon. Each playback brood experienced playback (broadcast 5 min out of 30) from noon to dusk one day and dawn to noon the next day for five days .

## Results

In 1991, in the pre-nesting period, marsh wrens were the only successful predator (identified by small holes pecked in the plasticine egg). Marsh wrens found and destroyed eggs in seven nests with playback and two without. One plasticine egg had been pecked in 81 places! The colony with this high marsh wren population subsequently failed to hatch any nestlings—marsh wrens destroyed all yellow-headed blackbird eggs. I did not use this colony again. In the second period (during nesting), one nest (with playback) was investigated probably by a mammal (identified by a tipped nest: the plasticine egg was unmarked). In the final period, no nests were disturbed in either treatment, and I found no marks on the mud platform. The quail eggs placed near the mink den were not eaten.

In 1992, one marsh wren and two mammals destroyed the eggs in nests with played back calls, and one marsh wren destroyed the eggs in a control nest. In the second experiment, chicks from three broods (two playback and one control brood) were killed by mammals (identified by a tipped nest, and uneaten legs and feathers). In 1993, one playback and one control brood suffered depredation (the first mammalian, the second unknown, probably avian, since the nest appeared undisturbed with no remains).

Overall from the various experiments, 14 of 52 playback nests and 5 of 52 control nests were depredated or destroyed. Table A1.1 summarizes the data. Ignoring marsh wren destruction (marsh wrens destroy eggs or kill very young hatchlings; they do not kill older, begging chicks), 6 playback nests and 2 control nests suffered predation. Differing methodologies and low power prevent me from drawing any conclusions from these data.

Table A1.1. Predation and destruction by marsh wrens of pseudo-nests containing quail eggs and of yellow-headed blackbird broods with and without broadcast begging calls.

year	n for each treatment	playback		control	
		marsh wren	predator	marsh wren	predator
1991 (eggs)	18	7	1	2	0
1992 (eggs)	15	1	2	1	0
1992 (chicks)	8	-	2	-	1
1993 (chicks)	11	-	1	-	1
total	52	8	6	3	2

## Discussion

My results suggest that if a predation cost to begging exists in yellow-headed blackbirds, it is either small or difficult to document, even in colonies with high levels of nestling predation. That a family of mink refused to eat quail eggs placed at their den suggests that these predators would be unlikely to look for nests containing quail eggs. Yasukawa (1989) found that mink removed plaster eggs in a playback experiment broadcasting female red-winged blackbird calls following the nesting period. Perhaps in a colony of loudly begging yellow-headed blackbird nestlings, mink have ready access to more valuable prey. Rewards of meat also failed to attract mink, and dead yellow-headed blackbird nestlings were not scavenged.

Following my first attempts using quail eggs and meat, I thought that predators investigating nests with begging might expect live chicks in the nest, and might not disturb the nest without seeing such prey. When I repeated the experiment using live broods, however, the predation level in my experimental nests (controls and playbacks) was lower than the predation level in the surrounding colony! Two possible logistical problems may be relevant. Until 1993, I visited the colony at dawn and dusk, disturbing the area at the time that mink are active. In 1993, light sensors removed the necessity of disturbing the colony at these times, but the extra power required for the playback equipment resulted in a loud noise when the begging started every 25 min. This loud noise may have startled any predators approaching the nest. Overall, although yellow-headed blackbirds beg loudly and suffer high predation rates, I cannot offer any evidence for a predation cost to begging. I located nests many times by following begging, and I observed predation of two begging fledglings by a sharp-shinned hawk (*Accipiter*

*striatus*), but my anecdotal observations are not corroborated by my experiments.

## Appendix 2

### Pressure to fledge in yellow-headed blackbirds



## Introduction

This appendix documents observations that late-hatched yellow-headed blackbird nestlings experience pressure to fledge. Hatching asynchrony leads to a hierarchy of chick sizes within each brood (Richter 1984, personal observation). Older chicks (up to two or three days older than their juniors) tend to fledge first, although females, which reach their asymptotic mass sooner, often fledge before males (Richter 1983, personal observation). Yellow-headed blackbirds have a short nestling period of 10-14 days (mean =  $12.20 \pm 0.18$  days for 68 nests over three years in Creston, B. C.), and many broods succumb to predation while in the nest (mean proportion =  $0.40 \pm 0.06$  for three study sites over three years in Creston, B. C.; predation varies considerably between populations from 0.02 (Richter 1984) to 1.00 (Roberts 1909, cited in Richter 1984)).

In asynchronously-hatching species, any pressure to fledge should be particularly noticeable in the behaviour of young chicks at the time when their older siblings fledge. Older siblings may move away from the nest, and parents may refuse to travel back to a nest to feed junior nestlings. Young budgerigars, with a long nestling period (35 days), and a safe nest, do not appear pressured to fledge when their older siblings leave the nest, but receive provisioning in the nest for several days, and continue growing without competition from their fledged siblings (Stamps et al. 1989). In yellow-headed blackbirds, with a short nestling period, and a dangerous nest, younger chicks may be more pressured to fledge at the same time as their siblings. This appendix documents the fate of younger siblings as they approach fledging.

## Methods

I looked at the fate of junior nestlings in several ways from 1990 to 1993. I considered broods with at least two nestlings of fledging age ( $\geq 10$  days) from which at least one chick fledged (identified either by observation of a fledgling or by the presence of fecal matter on cattails around the nest). Possible fates of junior siblings include fledging, dying in the nest (due to starvation or some other cause), drowning, and being eaten. The bodies of chicks who died in their nest around fledging generally remain in the nest (i.e., are not removed by parents or scavenged; personal observation). Drowned chicks float under the nest for one or two days, but then often disappear (possibly due to water movement, scavenging or disintegrating and sinking). In broods with a senior fledgling, I could not distinguish whether junior siblings had been eaten or fledged without seeing signs of nest disturbance or witnessing the junior chick out of the nest.

In 1990, 1991 and 1992, my assistants and I visited respectively 38, 109 and 135 nests every second day to weigh and measure chicks, and every day near fledging to determine fledging date. All nestlings were uniquely marked with paint and coloured leg bands. When faced with an empty nest at the time of fledging, we searched the surrounding cattails for fledglings, checked the nest for dead chicks or signs of predation (remains or a disturbed nest), checked the water beneath the nest for dead chicks, and noted the presence of fecal deposits on the cattails around the nest. In the absence of a sighting, I assumed that a chick had fledged if 1) it had appeared healthy on the previous nest visit, 2) its outermost primary measured  $\geq 20$  mm on the previous visit, 3) there were no remains or signs of nest disturbance, and 4) many feces surrounded the nest. Many fledglings were subsequently identified away from their nests by their coloured leg bands. I categorized dead chicks as

"dead fledglings" if their primary was longer than 20 mm, and tallied the number of broods with nestlings who had either drowned or died in the nest shortly before they were due to fledge. Occasionally, the remains of younger chicks who had previously starved remained in the nest. I did not include these chicks in the present sample, as their death occurred before any siblings fledged. Most starvation occurred before chicks reached 8 days old.

In 1993, we did not follow broods regularly throughout the nestling period, but checked 103 nests at the end of the breeding season. We looked for the remains of nestlings in the nest and for feces around the nest. We could not detect drowned nestlings at this time. I assumed that chicks from nests with no remains had fledged (a conservative estimate of the number of dead fledglings).

In 1990, I also observed nine broods of nestlings from a blind for one to three days until the whole brood had fledged (defined as the time when a chick first stepped out of its nest on to a cattail). I observed the time of fledging for each chick, patterns of parental provisioning and occasions when nestlings returned to their nest.

## **Results**

Of the 385 nests visited over 4 years, I identified nestling fates in 172 of those with at least two chicks alive around fledging. Table A2.1 shows the numbers of broods in each year in which 1) all chicks ready to fledge were assumed to fledge, 2) a "fledgling" died in the nest or 3) a "fledgling" drowned. Nestlings almost old enough and large enough to fledge died in about a quarter of broods. I never found a senior chick drowned or dead in the nest.

Table A2.1. Broods in which junior nestlings fledged or died following the fledging of a senior sibling.

year	fate of junior nestling(s)			proportion with deaths
	fledged	died in nest	drowned	
1990	15	2	3*	0.25
1991	23	4	5	0.28
1992	44	6	4	0.19
1993	51	15	—	0.23

\*I intervened and saved two of these chicks from drowning

My observations from a blind in 1990 suggest that junior siblings died because parents preferentially fed fledglings. Nestlings spent several days in the vicinity of their nest before they could fly, returning to their nest overnight. In three broods, two of three chicks had fledged, leaving the junior sibling in the nest. Although the fledglings remained within 3-5 m of the nest, and although the junior sibling begged continuously (non-stop for 2 h in one case), parents never fed the nestling while it remained in the nest. In all three cases, a parent fed the junior chick within 15 min after it left the nest. Two of the three chicks, in their eagerness for food, reached out too far towards their parent, and fell into the water beneath their nest. Both could have drowned had I not intervened, since they fell into relatively open water with few cattails nearby. I often observed fledglings swimming several strokes and climbing on to vegetation, but did not see them swim beyond 1 m. In another nest, a junior chick who had fledged on one day returned to its nest after receiving food, did not receive any further provisioning, and was dead in its nest the following morning, cause unknown. I never witnessed aggression between siblings that resulted in injury, but I cannot rule out such behaviour from my small sample of broods. Many of the "fledglings" who died in the nest were in poor body condition, and probably starved.

## Discussion

My observations suggest that late-hatched yellow-headed blackbirds experience a pressure to fledge. Parents seem responsible for at least part of this pressure, by preferentially feeding fledglings even when a nearby nestling should fledge the following day given sufficient food. In yellow-headed blackbirds, nesting over water, costs of fledging prematurely include drowning. Nestlings must trade off this cost against the predation cost of remaining in the nest for longer. Junior chicks face a decision to either remain in the nest and possibly starve or to leave the nest and possibly drown. Fledging synchrony, following hatching asynchrony, means that late-hatched nestlings should value food particularly highly while in the nest, to achieve the fastest growth possible.

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