Family conflicts over parental care in the blue tit, *Cyanistes caeruleus*

A thesis submitted to Lancaster University
for the degree of Doctor of Philosophy

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Megan Dickens
BSc (Hons.), University of Edinburgh
MRes, University of Glasgow

Department of Biological Sciences, Lancaster University, UK

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Declaration

This thesis is my own work and the result of my own investigations. Any work not my own is indicated by reference to the original authors. This thesis has not been submitted for the award of a higher degree elsewhere.

Megan Dickens

27th of February 2006

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Abstract

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Megan Dickens, BSc (Hons) University of Edinburgh.
Department of Biological Sciences,
Lancaster University, UK.

Current research into parental investment has focused on the influence of conflicts of interest between family members. This thesis examines how these conflicts affect parental investment into individual offspring within broods of blue tits, *Cyanistes caeruleus*. Experimental work mid-way through the nestling period investigates how nestlings solicit parental care through begging, and the food allocation rules of male and female parents. Nestling begging was found to relate to short-term hunger, but contrary to expectation, small nestlings did not beg more than their larger siblings (*Chapter 3*). Begging behaviour was also context dependent, as it was influenced by the sex of the provisioning adult and the reliability of the stimulus to beg (*Chapters 3 & 4*). *Chapter 5* shows that parents allocate food to offspring in response to a composite of nestling begging and nestling position, and although this resulted in them allocating more food to hungry offspring, they also gave more food items to the largest nestlings in the brood. However, female parents allocated food in a more complex way than males, controlling for nestling size when responding to the position of nestlings in the nest cup. This may help to prevent the largest nestlings from

completely controlling food distribution. Parents did not appear to be flexible in their provisioning rules, as even when they were provided with extra food they continued to allocate more food to larger offspring (*Chapter 6*). This may be to the parent's advantage, however, as it maintains size differences between offspring, allowing adaptive brood reduction should environmental conditions decline during the breeding attempt.

Chapter 1: General introduction

Conflicts of interest within families over parental investment

By providing parental care, parents can invest heavily in their offspring (Clutton-Brock 1991). This investment, by the definition of Trivers (1972), increases an offspring's chance of surviving at the cost of the parent's ability to invest in other offspring. Thus parental investment in the current reproductive attempt may decrease the parent's future reproductive success through reductions in future fecundity or survival rates (Williams 1966; Lessells 1991). There is good empirical evidence for this cost of reproduction, although causal relationships may be unclear in some cases (Clutton-Brock 1991; Dhondt 2001) and mechanisms unestablished (Stjernman et al. 2004). For instance, experiments increasing the number of offspring that parents raise have demonstrated reduced parental survival (Golet et al. 2004) as well as reduced future reproductive success (Gustafsson & Sutherland 1988; Hanssen et al. 2005). This assumption of reproductive costs has been used to establish one of the main arguments in life-history theory, that parents must trade-off investing in current and future reproductive attempts, where behaviour that ensures survival to the next breeding attempt conflicts with providing parental care to the current offspring. This life-history trade-off has the potential to create conflicts of interest between family members over the supply and division of parental care, when parents attempt to withhold investment from demanding offspring, fuelling parent-offspring conflict. As Figure 1.1 shows, conflict is generated between all parties who have the potential to influence parental investment. Parent-offspring conflict is generated, when parents and offspring disagree over the division of parental investment between each offspring and its current and future siblings (Trivers 1974, see Box 1). It is generated between parents, termed sexual conflict, as each parent would prefer the other to pay higher costs of reproduction and also because the benefit gained from providing parental care may differ between parents, most importantly when relatedness asymmetries occur within the family. Sibling conflict occurs as siblings are in competition with each other over the division of investment, each would prefer a larger share than that going to current and future siblings. These conflicts must be resolved in evolutionarily stable strategies of demand and supply between family members in which no actor gains by a unilateral change in behaviour (Parker et al. 2002a).

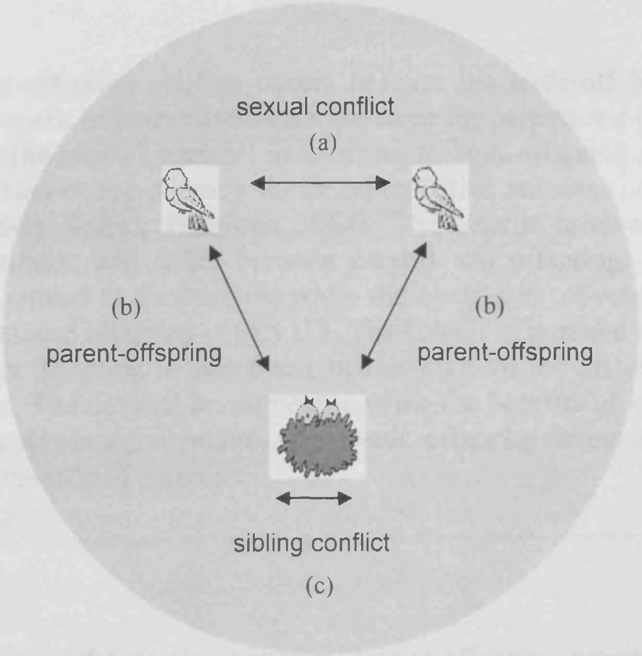


Figure 1.1. Conflicts of interest within the family over parental investment take the form of (a) sexual conflict between parents over how much each parent should invest in current offspring and over the division of investment between individual offspring, (b) parent-offspring conflict over the amount of investment that each offspring obtains from each parent and (c) sibling conflict over the proportion of parental investment that each offspring obtains (note that sibling conflict can occur within the current reproductive attempt and between offspring from current and future reproductive attempts).

BOX 1.1

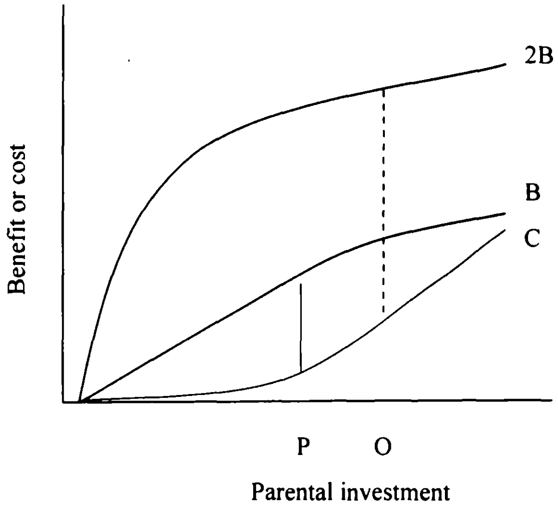


Figure 1.2 Difference in the trade-off of the cost and benefit of parental investment between parent and offspring. The benefit of parental investment to parents (B) and offspring (2B) and the cost of the same investment to both (C). P = the optimal trade-off for parents, O = the optimal trade-off for the offspring (from Lazarus & Inglis 1986).

Parent-offspring conflict occurs because the trade-off between the cost and benefit of investment is not the same for parents and offspring (Figure 1.2). The cost of parental investment, to both offspring and parents, is a reduction in the parent's future reproductive success (i.e. a reduction in inclusive fitness, Hamilton 1964). The benefit received from parental investment, will differ between parents and offspring, as offspring are fully related to themselves, while the coefficient of relatedness between parents and offspring is only 0.5. The benefit of parental investment to the current offspring is therefore twice as high for the offspring than for the parent. The optimal investment is when the benefits of investment minus the costs are a maximum. As a result, offspring favour a higher level of investment than parents.

In many species, the supply of parental care to offspring is mediated through offspring begging behaviour. Research in this area has been centred on parental care in birds, although there has recently been several studies on begging and family conflicts over parental investment in taxa as diverse as grey seals, *Halichoerus grypus*, (Smiseth & Lorentsen 2001), burying beetles, *Nicrophorus vespilloides*, (Smiseth et al. 2003a) and ponerine ants *Gnamptogenys striatula,* (Kaptein et al. 2005). In altricial birds, nestlings beg to provisioning parents to gain indivisible food items. Begging behaviour in birds consists of gaping, stretching upwards towards parents and vocalising. It also includes movement in the nest relative to the provisioning adult. Parents are confronted with a brood of gaping nestlings and must decide who to feed. In recent years begging behaviour has become the focus of intensive research into how family conflicts affect parental investment (Kilner & Johnstone 1997; Parker et al. 2002b). Conflicts between family members have been viewed as the driving force behind the exaggerated begging signals seen in many species (Kilner & Johnstone 1997). The first models of parent-offspring conflict viewed begging behaviour as purely manipulative in intention, with the outcome of parent-offspring conflict being in favour of either parents or offspring (Parker & Macnair 1978; Parker & Macnair 1979; Parker 1985). In this scenario, begging is an opportunity for offspring to ask for more resources than it is optimal for parents to give. However, more recent models have viewed begging behaviour as a means for offspring to reliably inform parents about otherwise cryptic levels of need (Godfray 1991; Godfray 1995). Honesty in communication has been shown to be viable due to signal handicaps (i.e. costs) (Zahavi 1975; Grafen 1990). This application of the handicap principle proposes that the cost of signalling insures intense begging signals are produced by those offspring with greatest need. In the context of parent-offspring and sibling conflict, this signalling cost ensures that potentially demanding offspring only signal when the benefit they gain from doing so outweighs the cost, which under simplified conditions is when they are in need. Thus, conflict within the family drives the production of costly communication between parents and offspring (Kilner & Johnstone 1997). Demonstrating that these costs occur, however, has not been straightforward. Early work looked for metabolic costs, but recorded low energy expenditure from begging (Leech & Leonard 1996; McCarty 1996; Weathers et al. 1997; Bachman & Chappell 1998). Later work took a different approach and converted the proposed energetic cost into changes in offspring growth rate. Growth rate is a currency that is likely to be directly linked to offspring fitness (reviewed in Lindstrom 1999). Attempts to measure this have yielded equivocal results. While work on canaries, *Serinus canaria*, and magpies, *Pica pica*, found effects of begging on growth rate (Kilner 2001; Rodriguez-Girones et al. 2001) in a third species, ring doves, *Streptopelia risoria*, there was no effect (Rodriguez-Girones et al. 2001). Begging vocalisations may also attract predators and so a predation cost may help to explain the maintenance of honest begging signals. Experimental and comparative work has suggested a role for predation in selection on begging calls (Redondo & Castro 1992b; Haskell 1994; Leech & Leonard 1997; Briskie et al. 1999; Haskell 1999). However, demonstrating that predation costs currently act to retain the honesty of calls will require more experimental work (Haskell 2002; Wells 2003). Reductions in sibling fitness, through decreased allocation of food, may represent a third cost of begging to offspring (Wells 2003). In a comparative study, Briskie *et al.* (1994) showed that when sibling relatedness was lower, begging calls were louder, which is consistent with this cost. Taken together, these three potential costs of begging may be enough to maintain the reliability of begging signals in communicating information on nestling need, however the issue is unresolved at present (Chappell & Bachman 2002; Haskell 2002) and more evidence is required for its conclusion.

Recently, attention has turned away from honest signalling models back to models that view nestling begging as scramble competition among siblings (Parker et al. 2002b). As before (e.g. Macnair & Parker 1979) these models predicts that parents respond passively to the outcome of sibling competition. Parker *et al.* (2002b) show that when the allocation of resources is determined by sibling competition, begging behaviour reflects an interaction between offspring competitive ability and need. Predictions from this model about the behaviour of parents and offspring largely match those from honest signalling models, making the interpretation of empirical data difficult (Royle et al. 2002). In some circumstances parents may wish to allocate food in response to offspring competitive scrambles, as scrambles also provide parents with useful information, namely as to offspring competitive ability, which is likely to relate to offspring quality (Parker et al. 2002b). In which case, judging the outcome of parent-offspring conflict (i.e. which party has control over allocation patterns) will be extremely hard.

Offspring demand

Empirical work has been used to support the idea that begging signals offspring need (Kilner & Johnstone 1997). Both the visual and vocal begging of nestling birds contains information on offspring hunger, thermal need and condition. Begging posture relates to nestling hunger in many species (Smith & Montgomerie 1991; Redondo & Castro 1992a; Leonard & Horn 1998; Lotem 1998; Saino et al. 2000). Call rate is also correlated with nutritional state (Iacovides & Evans 1998; Kilner et al. 1999; Leonard & Horn 2001a) and individual components of calls can be related to different aspects of need (Sacchi et al. 2002). In addition, one study has related call variables to the need for brooding by the parent (Leonard & Horn 2001a). Correlations between the visual and vocal components of begging signals and nestling condition have been found by several experimental studies. These studies have used feeding rate, brood-size manipulation and artificial parasite infection to alter chick condition. They have shown that nestlings in poor condition beg at significantly higher rates and at higher volumes than nestlings in good condition (Christe et al. 1996; Price et al. 1996; Iacovides & Evans 1998; Lotem 1998; Sacchi et al. 2002; Wright et al. 2002). However, empirical work has also revealed that there are other factors influencing begging behaviour, such as nestling competitive ability, competitive environment and parental response (Stamps et al. 1985; Price et al. 1996; Kolliker et al. 1998; Leonard & Horn 1998; Leonard et al. 2000; Rodriguez-Girones et al. 2002). This strongly suggests that begging is context dependant and may only partially represent offspring need to parents, making it harder for parents to assess true need (Kilner & Johnstone 1997).

The original models of Godfray (1995) and subsequent theoretical work leading on from this (Johnstone 2004) predicted that signalling offspring should be sensitive to the begging signals of their competitive nestmates. Thus, when offspring have to compete with siblings whose need is greater, they should elevate their own begging signals. Conclusions of empirical work have been equivocal in response to this prediction. Some studies have shown that begging intensity increases as a result of an experimental increase in the need of nestmates (Smith & Montgomerie 1991; Price & Ydenberg 1995; Leonard & Horn 1998), when the number of competitors is experimentally increased (Leonard et al. 2000) and when nestlings are paired with superior competitors (Price et al. 1996). In contrast, others have found no affect of competitor state (Kacelnik et al. 1995; Cotton et al. 1996). Johnstone (2004) suggests that these discrepancies are due to differences in the function of the components within begging signals. Certain components of begging signals may influence allocation of food items and are the result of competition between nestlings, while other aspects are more cooperative as they influence provisioning to the whole brood. Escalation of begging in response to rivals as predicted by Godfray (1995) should apply only to the competitive aspects of begging. These may differ between species, potentially explaining why different studies make different conclusions, and this is further complicated by variation in the indices of begging used in each study (Johnstone 2004). Furthermore, whether nestlings respond to rivals is predicted to depend on nestling competitive ability. While competitive aspects of begging influence food allocation and can be dominated by larger nestlings, cooperative begging that influences parental provisioning rate may be subject to exploitation by competitive nestlings, who cash in on the efforts of their weaker siblings (Johnstone 2004).

Many altricial birds hatch nestlings asynchronously so that there is a size hierarchy within the brood and this is often maintained throughout the nestling period with consequences for the survival, condition and subsequent reproductive success of individual nestlings (reviewed in Magrath 1990). Thus nestling long-term need can differ within broods, with younger nestlings having greater need, while at the same time the competitive ability to obtain food from parents can vary in the opposite direction. There is substantial evidence that, due to these competitive asymmetries, the smallest nestlings in a brood have to work harder to receive equivalent amounts of parental care to their siblings (Lotem 1998; Cotton et al. 1999; Smiseth & Amundsen 2002). For example, larger nestlings can dominate positions close to provisioning parents (Kilner 1995; Cotton et al. 1999) where they are more likely to be fed (Bengtsson & Ryden 1983; McRae et al. 1993; Kilner 1995; Leonard & Horn 1996). Larger nestlings may also find it easier to produce intense begging signals, for instance louder begging vocalisations or greater postural height, which is supported by the common observation that begging signals become more intense with brood age (Kilner & Johnstone 1997). Thus the costs and benefits of signalling are not thought to be equal across nestling size ranks and consequently nestling begging strategies may differ with nestling size (Glassey & Forbes 2002b). In support of this, empirical work has demonstrated that smaller nestlings often beg at greater intensities than their older nestmates (Price et al. 1996; Cotton et al. 1999; Krebs 2001).

The response of provisioning adults may also influence nestling begging. Experimental work on begging in house sparrows, *Passer domesticus*, (Kedar et al. 2000) has revealed that nestlings can learn to beg at the intensity that brings them greatest reward, so that nestlings with equal need can beg at very different levels. A follow-up study on hand-reared magpies supported this and also showed that large nestlings escalated their begging intensity when it was easier for small nestlings to obtain food (Rodriguez-Girones et al. 2002). Further experimental work on learning in southern grey shrikes, *Lanius meridionalis*, has shown that nestlings can learn to beg in the most profitable position in the nest (Budden & Wright 2005). Thus begging strategies appear to be modified by past experience. Under biparental care, this leads to the prediction that if there is a difference in the provisioning of the two parents, offspring may alter solicitation according to the sex of the provisioning adult. Male and female parents may follow different provisioning rules (Bengtsson & Ryden 1983; Stamps et al. 1985), feed at different rates (Bengtsson & Ryden 1983) and bring food items of different type or quality (Cowie & Hinsley 1988; Banbura et al. 2001). This could make one parent more profitable than the other, and as a result there may be increased competition for 'begging patches' near to the more profitable parent (Kolliker et al. 1998) and more competitive offspring may dominate these positions (Slagsvold 1997). Furthermore, there is evidence from several species that, within nests, male and female parents may differ in how they allocate resources to different types of offspring (reviewed in Slagsvold 1997; reviewed in Lessells 2002). This may result in nestlings of particular types soliciting the parent who is most likely to respond. For example in great tits, *Parus major*, hungry nestlings move closer and beg more intensely to female parents, who are more likely than male parents to feed them (Kolliker et al. 1998).

How do parents respond to nestling begging?

Empirical work supports the idea that parents respond to the information contained in nestling begging behaviour, with begging intensity positively influencing both provisioning rate (Muller & Smith 1978; Bengtsson & Ryden 1983; Christe et al. 1996; Burford et al. 1998; Price 1998) and food allocation to individual nestlings (Kilner 1995; Mondloch 1995; Leonard & Horn 1996; Saino et al. 2000; Leonard & Horn 2001a). For example, in an experimental paired choice test in tree swallows, *Tachycineta bicolor*, Leonard & Horn (2001a) showed that parents directed significantly more feeding attempts to model nestlings near speakers playing deprived calls than to those near speakers playing fed calls.

How do parents respond to the different types of begging behaviour? Parents may combine information from vocal and visual signals, in order to gain a more accurate representation of offspring need. A study by Kilner *et al.* (1999) demonstrated that reed warbler, *Acrocephalus scripaceus*, parents integrate signal components to adjust their provisioning rates in response to nestling need. Parents use the total gape area displayed in the nest as a crude estimate of how often to bring food. This signal will reflect chick age and brood size. Parents then use the vocal signal, begging call rate, to fine tune provisioning rules, as this signal will contain more complex information regarding nestling hunger. In a recent review, Kilner (2002b) suggests that multicomponent displays function in the resolution of parent-offspring conflict, providing more reliable information on offspring state than single signals would alone. This could be especially important as offspring age and certain aspects of begging, for instance posture, become less reliable signals of need. Conversely, there is some evidence that the different components of begging signals elicit different aspects of parental provisioning response. By temporarily muting individual nestling red-winged blackbirds, *Agelaius phoeniceus*, Glassey & Forbes (2002a) showed that begging vocalisations influence parental provisioning rate but not allocation to individual offspring, which is presumably influenced by other aspects of begging. However in a third alternative, as stated by Kilner (2002b), these components could also function to increase parental response to the begging display as a whole, as the response of the receiver is often greater to a multicomponent display than to the sum of the individual components (Rowe 1999). In which case, the multiple components of begging behaviour would indicate that offspring are manipulating parents to invest more.

In order to assess whether begging behaviour is involved in parent-offspring communication as opposed to parental manipulation, studies must demonstrate that parents respond to the signalling content rather than the competitive aspects of begging (Kilner & Johnstone 1997). Many studies have assumed that demonstrating a parental response to begging signals is evidence for honest signalling models (e.g. Leonard & Horn 1996). However, Parker *et al.* (2002a) challenge this, stating that parental allocation rules must be shown to be an active response to begging for honest signalling models to be supported. However, in some cases parents may be choosing to respond to aspects of competitive begging, for instance if the outcome of interactions between siblings indicates offspring quality. In many cases, parents appear to provision larger offspring more than their smaller siblings, even though they are not begging more intensely (Price & Ydenberg 1995; Cotton et al. 1999; Smiseth & Amundsen 2002). This could be because parents are responding passively to sibling competition, for instance by feeding nestlings that are positioned close to the provisioning adult. Parents may be constrained by provisioning efficiency, unable to pay the time cost of discriminating smaller more needy offspring. Alternatively, parents could prefer to invest in high quality offspring that are more likely to survive and have higher reproductive success (Clutton-Brock 1991). In many species, offspring size during development is a good indication of offspring future reproductive success (reviewed in Lindstrom 1999). However, even if parents choose to invest in high quality offspring, at some point the benefit of investing more in low quality offspring will be greater, and at this point parents should switch allocation patterns. This behaviour may still be compatible with a scenario of parents responding passively to scramble competition, for instance if low quality nestlings are fed only when their larger siblings are satiated. Therefore, distinguishing parental control in allocation from offspring manipulation will be difficult. Few studies have been conclusive when addressing this problem. By controlling nestling positions, Kilner (1995) showed that canary parents can override competition between offspring when allocating food within the brood. Parents are capable of feeding according to begging signals and not position in the nest, which certainly suggests that parents have some control over allocation. Work on parrots in two studies has also shown that in this group parents actively control food allocation (Stamps et al. 1985; Krebs 2002). For instance, in crimson rosellas, *Platycercus elegans*, there does not appear to be scramble competition to get close to the provisioning parent (Krebs & Magrath 2000) and parents may be able to control allocation in this species because the cost of selectively feeding small offspring is low (due to large size differences between nestlings, asynchronous fledging within the brood and a long nestling period with low provisioning rates) (Krebs 2002).

To further complicate matters in the debate over parental control, there may be an effect of offspring age on the degree to which parents can assess offspring need without sibling competition as a confounding factor. For example, in hole-nesting birds physical sibling competition is often increased over the nestling period. When nestlings are close to fledging they will compete for access to the nest entrance, where they will remain until a parent arrives with food. Parents usually have little choice over allocation at this stage, simply feeding the nestling that meets them at the hole (Kacelnik et al. 1995). By contrast, shortly after hatching there is very little physical competition in most species, and here honest signalling models are much more likely to apply. In between these two extremes, direct parental control may steadily decrease from hatching to fledging.

Variation in parental response to offspring demand

Between parents

If parents have control over how food is allocated between offspring, then they should invest in individual offspring according to the benefits of that investment for offspring survival and quality (i.e. offspring fitness, Parker et al. 2002a). Parents should give each unit of investment to the offspring whose increase in quality is largest on receiving the investment. As Figure 1.3 shows, offspring quality rapidly increases with parental investment, until a point at which additional investment brings only small increases in quality, beyond which point additional investment brings no further benefit. If all offspring are of equal reproductive value to both parents, then investment into different offspring should be egalitarian by both parents (where resource availability permits this, see below) (Smith & Fretwell 1974), with each parent investing to optimize the fitness of each offspring, trading-off these benefits with the cost of reproduction. With relatedness asymmetries within the family however, the benefits of investment to the male and female parent will vary with offspring parentage. In many socially monogamous species of bird, females engage in

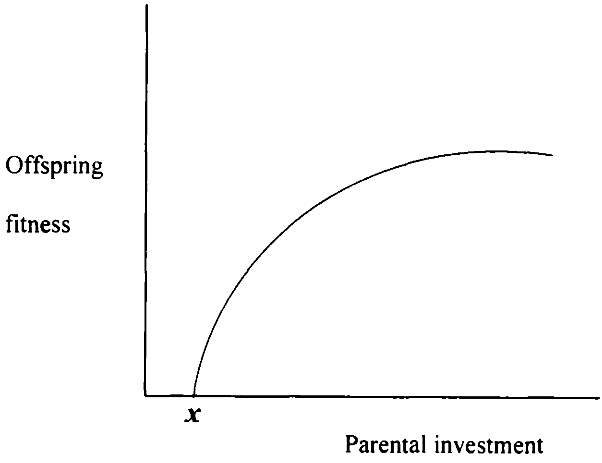


Figure 1.3. The relationship between the amount of parental investment that an offspring receives and its fitness (the function of offspring survival and future reproductive success). At x parental investment ensures offspring survival. From Parker *et al.* (2002).

extra-pair copulations, with the result that some of the nestlings are not related to the provisioning male. Fathers risk wasting investment in offspring that they are not genetically related to (Westneat & Sherman 1993) but it does not appear that males can identify extra-pair young directly (Keller 1997; Whittingham & Dunn 2001). Slagsvold (1997) suggested that extra-pair young are more likely to occur later in the clutch, and could therefore be identified by size. Paternity does appear to vary predictably with laying order in house martins, *Delichon urbica* (Riley et al. 1995), snow geese, *Chen caerulescens* (Dunn et al. 1999), collared flycatchers, *Ficedula albicollis* (Krist et al., 2005) and house sparrows (Cordero et al. 1999), but the direction of the effect differs between species and in at least two species no pattern occurs: tree swallows (Whittingham et al. 2003) and red-winged blackbirds (Westneat et al. 1995). Even if males cannot identify extra-pair young, they may still alter patterns of allocation to different types of offspring. The presence of extra-pair young in the nest causes males to have lower relatedness on average to all offspring and potentially this could cause males to decrease investment into low quality offspring, especially if low quality offspring have high mortality rates (Lessells 2002).

Slagsvold et al. (1994; 1995) have suggested that if male and female parents invest differently in different individual offspring or different types of offspring (known as parentally biased favouritism, Lessells 2002) it could be due to a sexual difference in the priority of current and future reproductive attempts. In many species of birds, females have higher mortality rates than males, possibly due to factors outside the breeding season, for example higher over-winter mortality due to smaller body size (reviewed in Breitwisch 1989). Slagsvold *et al.* (1994; 1995) suggest that this would lead to females investing more in the current brood and thus being more willing than males to invest in small, low quality offspring. However, it is hard to establish the direction of causation in patterns of parental investment and survival rates (Dhondt 2001) and in many species provisioning rates at least are relatively equal between the two parents (Ligon 1999). Therefore, there is currently some debate over when the allocation patterns of the two parents should differ. In a review of parentally biased favouritism, Lessells (2002) presents several models examining whether differences in life-history trade-offs (cost of reproduction) and relatedness asymmetries within families could cause parentally biased favouritism. The models predict extreme bias between parents, with each parent caring for only one type of offspring when there are differences between the parents in the costs or benefits of care given to different types of offspring. However, contrary to the expectations of these models, studies of various species of bird have revealed that parents can differ in their preference of feeding different types of offspring, a more moderate form of parentally biased favouritism. For instance, in budgerigars, *Melopsittacus undulatus*, crimson rosellas and tree swallows female parents preferentially feed smaller nestlings whereas males do not, but the bias is not extreme and both parents allocate food to all sizes of nestling (Stamps et al. 1985; Leonard & Horn 1996; Krebs et al. 1999). Why does the parentally biased favouritism seen in these studies not match that predicted by the theoretical models? Lessells (2002) suggests that this is due to the cost of active parental discrimination. Provisioning parents are usually working under strong time constraints and discriminating between offspring types is likely to be time-consuming. The observed pattern of food allocation may represent the optimal trade-off between discrimination for preferred offspring and provisioning efficiency.

Variation in parental response with resource availability

When parents are making investment decisions and trading off the costs and benefits of investment, the availability of resources in the environment will have a crucial impact, especially when parental care involves the direct transfer of those resources to offspring. Parents making reproductive decisions often have to make predictions about future resource availability. However, resources in the environment are subject to short-term fluctuations and parents often produce more offspring than they can support (Mock & Parker 1997). In many species of passerine bird, food shortages during breeding cause a proportion of the brood to starve. In 1947, Lack linked hatching asynchrony with adaptive brood reduction, a connection which has been extremely influential ever since (e.g. Boland et al. 1997). As hatching asynchrony produces competitive asymmetries within the brood it will promote adaptive brood reduction when there is not enough food being delivered to the nest to support the whole brood and smaller young are outcompeted by their older siblings. Work on red-winged blackbirds has explained in detail the adaptive value of this process. In this species there is usually one nestling that is younger and smaller than the rest of the brood. When competition for food within the nest was experimentally increased by manipulating brood size it was this nestling that suffered, whereas larger offspring were unaffected (Forbes et al. 1997). The survival of the smaller, 'marginal' offspring depends on both the number of competitors and the food supply provided by parents (Forbes & Glassey 2000). Hatching asynchrony provides a means for parents to optimistically overproduce, while protecting the core of their brood from the effects of food shortage when resources are not available to support the extra marginal offspring (Mock & Forbes 1995). In an experiment to test this, Magrath (1989) manipulated both the hatching asynchrony and the food supply available in broods of nestling blackbirds, *Turdus merula*. Food supply had a larger effect on synchronous broods, they produced less young in bad conditions than asynchronous broods. Brood reduction was more efficient in asynchronous nests, occurring earlier, whereas in synchronous broods parents wasted part of their food supply, giving it to nestlings that did not survive, with consequences for the quality of the whole brood.

A fundamental question arises from this work on brood reduction. In circumstances where resource availability varies, do parents alter their feeding strategies or are competitive interactions between siblings enough to explain adaptive brood reduction and conversely the survival of marginal offspring in good breeding conditions? Theoretical work supports both scenarios. Bonabeau *et al.* (1998) present a model that maximizes parental fitness in unpredictable food conditions when there is initial brood overproduction. Their model shows that competition between siblings can be enough to permit optimal partioning of resources in an unpredictable environment. Certainly when breeding conditions are poor, scramble competition between offspring for parental resources is a cheap way for parents to ensure that high quality offspring get enough food (Royle et al. 2002). Conversely the models of Davis *et al.* (1999) show that parents should vary provisioning decisions based on environmental conditions, although they assumed that parents have full control over food allocation. Their results suggest that as food supply increases parents should switch from a more biased strategy of feeding the largest offspring to a more egalitarian strategy, eventually feeding all offspring equally. Whether parents or offspring have control over food allocation appears to be crucial. Providing some evidence for flexibility in parental provisioning Smiseth *et al.* (2003b) experimentally manipulated the food available to broods of bluethroat, *Luscinia svecica*, nestlings by temporarily removing the male parent. After male removal, food allocation became more biased in favour of large nestlings. As there was no difference in the change in begging behaviour of large and small nestlings in response to the experiment, this result suggests that females altered their allocation rules in response to the pressure of being the sole provider for the brood. In contrast to scramble competition models (Parker et al. 2002b) there was no evidence that large offspring controlled parental behaviour by out-competing siblings, for example for positions close to parents. However, the authors caution that a fixed parental allocation rule could still alter allocation patterns in response to changes in nestling behaviour with brood hunger. Thus parents could interpret begging signals by including an interaction with nestling size, so that they are more likely to feed large nestlings. Small nestlings are then fed under good conditions, when large nestlings are less likely to beg, but less under bad conditions as they would often be competing against a larger nestmate (Smiseth et al. 2003b). A second study directly controlled food availability through supplementation and measured the effect on parental allocation decisions in white-winged choughs, *Corcorax melanorhamphos* (Boland et al. 1997). They showed that when food was plentiful, provisioning adults favoured smaller chicks, while in control broods large chicks were favoured. However, this study did not measure offspring behaviour, so it is hard to assess whether parents are actively altering provisioning decision making with food availability, although the authors state that chicks in the supplemented broods did not appear to be satiated, which suggests that parents were actively allocating food to smaller chicks. It is clear that more empirical studies are needed to determine whether environmental conditions affect how parents distribute food between offspring and that this will have implications for the debate on whether honest signaling or scramble competition models apply to parent-offspring interactions over parental care.

This project

Whether begging behaviour contains information on offspring need is dependent on how competitive interactions between siblings influence begging strategies. For example, need may interact with competitive ability on nestling position in the nest relative to provisioning adults. If less competitive nestlings are either out competed (e.g. Cotton et al. 1999) or are strategic ‘prudent beggars’(Glassey & Forbes 2002b) then information on nestling need will be withheld from parents unless parents can assess offspring competitive ability through a visual measure such as size and integrate this with information from begging signals. Variation in sibling competition and parental response between species may have confused this issue still further. Detailed work in this area on more species would be useful. An issue that has received much less attention is whether biparental care influences begging strategies. Given that begging reflects an offspring's past experience as well as current level of need (Kedar et al. 2000; Budden & Wright 2005) and that parents may differ in how they allocate food to different types of offspring (Kolliker et al. 1998), strategic begging behaviour might be expected to incorporate the sex of the provisioning adult (Kolliker et al. 1998). This has been shown to occur in great tits (see above), however that study did not involve competitive asymmetries between offspring, although these do occur within great tit broods, and so may not be representative of what actually happens in the nest. This project aims to address how competitive interactions and biparental care influence begging strategies in nestling blue tits, *Cyanistes caeruleus*.

A second major issue in the study of parent-offspring conflict is whether parents or offspring have control over patterns of food allocation (Kilner & Johnstone 1997; Parker et al. 2002b). If parents respond passively to nestling competitive interactions then this will limit their ability to respond to changing breeding conditions or for the two parents to have different allocation rules (see above for reasons why this might occur). For instance, in good breeding conditions, parents should prefer a more equitable distribution of resources, so that overall nestling condition is maximised. However, if parents respond passively and there is hatching asynchrony in the brood, then the most competitive offspring will take more than their share. One way to examine this is to compare how parents respond to changing conditions when allocating food within the brood. If parents change allocation rules, this suggests that they have some degree of flexibility and thus control over allocation. Few studies have used this approach (but see Boland et al. 1997). Likewise, by comparing male and female allocation patterns in response to nestling begging and cues of quality there is the opportunity of demonstrating parental control where rules differ.

This project attempts to address these issues through experimental work on parent and offspring behaviour during the nestling period. An experimental approach allows control over variables of interest that are likely to differ between nests within the study population, in this case, nestling hunger and resource availability, both of which are normally highly variable within populations. This approach, together with statistical control of variation between broods allows us to determine why the behaviours of interest occur, against a background of considerable variation in both environmental conditions and individual responses to those conditions (e.g. Both et al. 2005).

Study species

Blue tits make an excellent study species, as they are both extremely common and nest readily in accessible nest boxes. They are also tolerant of human disturbance, making them a good candidate for research that involves manipulation of breeding conditions and as a consequence they have been previously studied in great detail, so that much is already known about their ecology and behaviour (for reviews see Perrins 1979; Cramp & Perrins 1993). In relation to the present study, their socially monogamous breeding system with biparental care and large brood sizes forms a useful model system within which to test ideas about intrafamilial conflicts over parental investment. During the breeding season both parents invest heavily in offspring and have similar parental roles during the nestling period, although only females carry out brooding and nest sanitation duties (Perrins 1979; Cramp & Perrins 1993; Banbura et al. 2001). The breeding season is very short, usually most birds in a particular area will start to lay eggs within a two week period (Perrins 1979). This is because breeding success is tightly constrained by timing and is dependent on the peak in nestling demand for food falling within the annual peak for caterpillars (*Lepidoptera* larvae) (Perrins 1979; Perrins 1991) which is the main food item for nestlings (Cramp & Perrins 1993). Thus during the breeding attempt there will be intense selective pressure on the behaviours that affect seasonal reproductive success.

There are indications of intrafamilial conflict over parental care in the blue tit from: (1) evidence for the costs of reproduction (Nur 1984b; Nur 1988; but see Pettifor 1993; Merila & Andersson 1999; Richner & Tripet 1999; Kullberg et al. 2002; Stjernman et al. 2004), (2) strong sibling competition, due to large brood sizes and dependence on a seasonal food supply, so that if the food supply is not sufficient nestlings may starve (Nur 1984a), furthermore competition between siblings is asymmetric due to hatching asynchrony, and (3) high rates of extra pair paternity (extra pair young occur in 40 % of broods, Leech et al. 2001). Previous work has shown that there appears to be sexual conflict over investment in different types of offspring within broods. Female parents tend to feed smaller fledglings than male parents and suffer from decreased survival rates when nestling size differences within broods are larger, presumably as males invest less in smaller nestlings in these broods (Slagsvold et al. 1994; Slagsvold et al. 1995). Slagsvold (Slagsvold & Lifjeld 1989;

Slagsvold et al. 1994; Slagsvold et al. 1995) suggests that the male bias towards feeding larger offspring causes a sexual conflict between parents over hatching asynchrony, with females hatching nestlings synchronously in order to obtain higher male investment in the brood. This thesis will investigate further the potential for conflicts of interest within the family over the flow of parental investment from parents to offspring during the nestling period.

Outline of the thesis

Chapter 2 introduces the approaches and methods used in this study. This will form a background for the following chapters, which describe the experimental work. The following four chapters form the experimental core of the thesis. *Chapter 3* investigates the dual effects of offspring size and hunger on offspring begging behaviour in a breeding system with biparental care. Whether begging strategies are context dependent is investigated further in *Chapter 4*, which examines how nestlings respond to different stimuli that elicit begging behaviour. *Chapters 5 & 6* examine parental responses to nestling begging. First, *Chapter 5* looks at patterns of allocation in individual nestlings by male and female parents and discusses whether parents take into account offspring competitive ability when responding to nestling solicitation. *Chapter 6* examines whether resource availability affects parental allocation rules. Resource availability is influenced experimentally by supplementing the food supply to certain broods and comparing parental allocation rules in these broods to those in control broods in two different paired designs: (1) control broods without food supplementation and (2) periods of parental provisioning in the same broods with the supplementary food removed. Finally, all experimental chapters are reviewed in

Chapter 7 and discussed in the light of the issues presented in *Chapter 1*, setting the conclusions of each chapter in a wider setting.

Chapter 2: General methods

Fieldwork

Study species

This project studied parental care in a wild population of blue tits in Lancashire, England. Blue tits are frequently used in behavioural studies, as they are both extremely common and nest readily in accessible nest boxes. As a result, much is already known about their ecology and behaviour (see Perrins 1979; Cramp & Perrins 1993). The breeding season is short; most birds will start to lay eggs within a two-week period (Perrins 1979). This is because breeding success is dependent on the peak in nestling demand for food falling within the annual peak for caterpillars (*Lepidoptera* larvae) (Perrins 1979; Perrins 1991) which is the main food item for nestlings (Cramp & Perrins 1993).

Blue tits have a socially monogamous breeding system with biparental care. However, even in a socially monogamous breeding system there can be variation in the reproductive success among breeding males due to extrapair fertilizations, which are common in the blue tit (e.g. Kempenaers et al. 1992; e.g. Kempenaers et al. 1997). For example, a previous study on this population revealed that extrapair young occurred in 39.8% of broods and accounted for 11.7% of all offspring (Leech et al. 2001). Therefore, in many broods male parents provide parental care for offspring that they are not related to. During the breeding season, both parents provision nestlings with food and defend the nest. The relative contributions of the male and female parent to provisioning the brood may differ between individual pairs and populations.

Several studies have found a difference in provisioning rate between the sexes (males provision at a higher rate than females: Greico 1999; females provision at a higher rate than males: Banbura et al. 2001). Parents can also differ in the quality of food items that they bring to the nest, with males more likely to bring larger food items (Cowie & Hinsley 1988; Blondel et al. 1991; Banbura et al. 2001). However, other studies, including one on this population, have found no difference in either provisioning rate or prey size between the sexes (Przybylo & Merila 2000; Leech 2002). Both parents remove faecal sacs from the nest but females alone also incubate eggs, brood nestlings and clean the nest (Perrins 1979; Cramp & Perrins 1993; Banbura et al. 2001).

Blue tits are notable for their extremely large brood sizes (up to 16). Young often hatch over several days, as females can commence incubation while still completing the clutch. Where there is hatching asynchrony, size differences between offspring of different ages are often retained through much of the nestling period and later hatched young are likely to have lower survival rates (Merila & Wiggins 1995; Descamps et al. 2002; Brommer 2004). Breeding success can be low in years where breeding conditions are poor and brood reduction is common (Perrins 1979; Slagsvold et al. 1995). Post-fledging survival is also usually low, for instance offspring post-fledging recapture rates after the first three months can be as low as 9% (Nur 1986), and is probably influenced by fledging body mass (Perrins 1979; Nur 1984a). Table 2.1 provides information on brood size, hatching spread and brood reduction in the focal broods used for this thesis, from each of the three study years 2003-2005.

Table 2.1. Information on focal broods: Brood size (at hatching), hatching spread (the number of days over which nestlings hatch) and brood reduction (the % of nests where brood reduction takes place, and in those nests the average % of mortality within the brood), over the three study years. Parameters represent averages across nests (mean, followed by the range), except for brood reduction measures (1) & (3). Sample sizes are as follows: 2003, N = 22, except for hatching spread, where N = 18; 2004, N = 20; 2005, N = 23.

Breeding parameters	*2003*	*2004*	*2005*
Brood size	8.6 (7-11)	9.9 (7-14)	9.4 (5-12)
Hatching spread (days)	2.6 (2-3)	3.0 (2-4)	2.8 (1-4)
Brood reduction:			
(1) % of nests with brood reduction	27.3	20.0	52.2
(2) % of brood lost	27.8 (9.1-55.5)	22.9 (12.5-37.5)	37.5 (8.3-90.9)
(3) Timing of brood reduction:			
% of brood reduction occurring before 10 days post-hatching	33.3	100.0	50.0
% of brood reduction occurring after 10 days post-hatching	66.6	0.0	50.0

Study area

The study area consisted of two small deciduous woodlands, Lancaster University campus (grid reference SD4857) and Hazelrigg wood (SD4857 and SD4957). The dominant tree species in these woodlands are oak, *Quercus robur*, birch, *Betula pendula* and beech, *Fagus sylvatica*. All birds in the study nested in wooden nest boxes of a standard size and designed to be used by blue tits only; a 26mm diameter entrance hole prevented larger species from entering. The study site has a total of 67 nest boxes, with 45 boxes at Lancaster University and 22 boxes at Hazelrigg wood, although not all are used every year.

General procedures

Fieldwork was carried out over the breeding seasons (late March to mid-June) of three years: 2003-2005. All nest boxes were regularly monitored from the start of each breeding season to establish laying date of the first egg, clutch size, hatch date and hatching success, and boxes were checked at the end of the breeding season to establish fledging success.

Nestlings were ringed with numbered metal British Trust for Ornithology (BTO) rings at day six (day 0 is hatching day). Pairs of breeding blue tits were monitored in the field for the presence of unique colour ring combinations, placed on the birds as part of a previous study (Leech 2002). Any unmarked adults were caught at the nest during the second half of the nestling period and fitted with a BTO and colour ring combination.

On days 10 and 13 post-hatching in 2003, and on days 10 and 14 in 2004 and 2005, the following biometrics were taken from all nestlings; mass (to the nearest 0.1g), head and bill length, tarsus length, gape width and gape length (all measured to the nearest 0.1mm with dial calipers). Final measurements of nestling biometrics prior to fledging were taken on day 14 as visiting the nest after this age may cause nestlings to fledge prematurely.

Experimental procedure

During the field season in 2003, an experiment was carried out controlling nestling hunger across size ranks within broods (Chapters 3, 4 & 5). Ten days after hatching, nestlings in experimental nests were marked individually with small head patterns using white Tippex, to allow identification on the video recordings. The two largest and two smallest nestlings (according to mass) in each nest were chosen as focal nestlings. The average mass of focal nestlings was 9.7g (SD = 0.72) for 'large' chicks, and 8.0g (SD = 0.95) for 'small' chicks. As nestlings at this age gain, on average, under 1g per day (Perrins 1979), the mass difference between large and small nestling categories represents between one and two days growth. Focal nestling hunger was manipulated by either hand feeding or by depriving nestlings of food. The four focal nestlings were randomly allocated to either a fed or deprived experimental treatment so that each of the two treatments was carried out on both a large and small nestling. After removal from the nest, focal nestlings were kept warm in dummy nests for one hour while the treatment proceeded. At the start of the procedure all of the focal nestlings were fed until satiation with Nectarblend chick rearing softfood (Haiths, Cleethorpes UK). Nestlings were fed until they would no longer gape in response to a standardised stimulus of a tap on the bill and the sound of a 'squeak' made by the experimenter (which mimicked the parental feeding call). The amount of food that each nestling consumed was recorded as wet mass (to the nearest 0.1g). Nestlings in the deprived treatment were not fed again during the hour they were kept away from the nest. Fed nestlings were kept warm in a separate dummy nest and were offered food every 10 minutes for one hour, each time feeding them until they did not gape to the stimulus. The amount of food consumed was recorded as before. At 60 minutes, after feeding the nestlings in the fed treatment, nestling mass was recorded for all four focal nestlings and they were then returned to the nest. The nest was then recorded for one hour using a nest box camera linked to a Sony digital camera (DCR-TRV330E) and an outside video camera (Sony Handycam, CCD-TR913E). The nest box camera is attached to a nest box lid, which replaces the actual lid at each nest box and allows recording of parental provisioning behaviour from vertically above the nest cup. At 10 days old nestlings are rarely brooded, and both parents are working at approximately their maximum provisioning rate for the nestling period (Perrins 1979). Video recording took place between 07:30h and 18:00h. Outside video cameras were placed on tripods approximately 5-10m from the nest box and used to identify adults (using colour rings) during provisioning visits, when this was not possible from inside cameras. Dummy cameras were placed at the nest one day before recording, to allow adult birds to become used to their presence. After one hour of recording, nestling mass was recorded again and the cameras removed.

Ethical considerations

All procedures were carried out under license from English Nature, The British Trust for Ornithology and the Home Office as appropriate. The experimental treatment did not appear to have a detrimental effect on focal nestlings. In particular, nestlings in the deprived treatment were kept under close observation during the treatment hour and did not show any signs of physical stress, such as hypothermia, listlessness or excessive panting. Previous studies have carried out longer periods of deprivation (e.g. Kolliker et al. 1998) without harmful effects in the short or long term. Treatment had no long-term affect on nestling mass. At 13 days old (three days after the experimental treatment) there was no significant difference between the mass of nestlings in each of the treatment groups (ANOVA: $F_{1,173} = 0.141$, $P = 0.708$). Nestlings classed as 'small', 'medium' or 'large' during the experiment, at 10 days post-hatching, were still significantly different in mass from each other, on 13 days post-hatching (ANOVA: $F_{1,173} = 13.08$, $P < 0.001$), but there was no interaction between nestling size class and the experimental treatment, on mass at day 13 (ANOVA: $F_{1,173} = 0.274$, $P = 0.601$). Most nestlings fledged and the probability of fledging did not differ between treatment groups: deprived 92%, fed 90% and untreated 91% (chi-square test; $\chi^2 = 0.157$, DF = 2, $P = 0.924$).

Data collection from videotapes

Nestlings were successfully identified on the screen using head patterns. Each time that at least one nestling gaped was termed a beg event (i.e. the event was recorded whether or not an adult was present). During each beg event the behaviours of nestlings and adults, if present, were recorded as described below. Beg events were considered to be over when all nestlings had stopped gaping and the adult, if present, had fed at least one of the nestlings. All time variables were recorded to a 25th of a second (one frame on the video).

Nestling and adult location in the nest

To record the positioning of parents and offspring in the present study, the nest area was divided into nine equal areas on the screen (following McRae et al. 1993) with one central area and eight areas in a circle adjacent to the centre (Fig. 2.1). Nestling and adult location were then assigned to one of the nine areas, at each beg event, immediately before a feed occurred (adults could not occupy area 1, in the middle of the nest). The distance between each nestling and the provisioning adult was quantified by transforming the two locations into a position score, ranging from one (nestling and parent were in the same area of the nest) and six (nestling and parent were opposite each other). When the nestling was in area 1 (Fig. 2.1), they had a position score of 3, regardless of where the adult fed from around the nest cup.

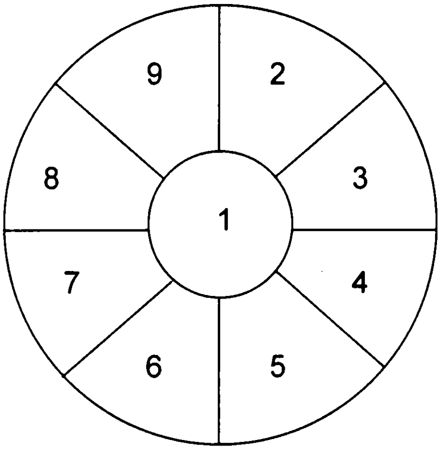


Figure 2.1. The divisions of the nest on the video screen, used to record nestling position (all sections used) and adult position (only the outer segments 2-9).

Nestling begging variables

In altricial birds, begging behaviour consists of gaping, stretching towards the parent and vocalising. For each nestling, observations were made of visual begging signals at each beg event. Beg posture was coded as shown in Figure 2.2, with postural begging intensity categorised into six levels (adapted from Redondo & Castro 1992a) where zero represents not begging and five represents begging at full intensity (the nestling is stretching upwards towards the parent with the whole body raised). Begging posture was measured directly before a feed and every second for six seconds from the time of the adult's arrival at the nest. Latency to beg (the time taken from the arrival of the adult and the nestling first opening its gape) and begging duration were measured in seconds.

Adult behaviour

Where an adult bird was present at a beg event, observations were made of provisioning and nest maintenance behaviour. The duration of time that an adult spent in the nest box and the time that the adult spent before feeding: 'assessment time' (Kolliker et al. 1998), were measured in seconds. The identity of fed nestlings was recorded at all feeds. In all nests, adults occasionally offered food to one nestling and then immediately removed the prey item from the nestling gape and offered it to another nestling. This behaviour was termed a 'rejection'. The size of prey items were recorded on a scale 1-3 (1= small, 2 = intermediate, 3 = large, where an intermediate prey length is between 80-100% of adult bill length). Prey items were classified as insect larvae, winged insects, and spiders/harvestmen, or as unidentified.

Data analysis

The analysis of nestling begging behaviour and parental response is complicated by interactions between nestlings within broods, by potentially large differences between broods due to food availability and by small sample sizes (Forbes 2002). Controlling for this statistically is difficult. Where possible, the analyses presented in this thesis were carried out on brood means, or means for individual focal nestlings within broods. Mixed models were used to account for variation between nests. Furthermore, where it was necessary to analyse data from individual interactions, models included a term for each interaction (i.e. each parental feed) to account for the non-independence of data from each individual.

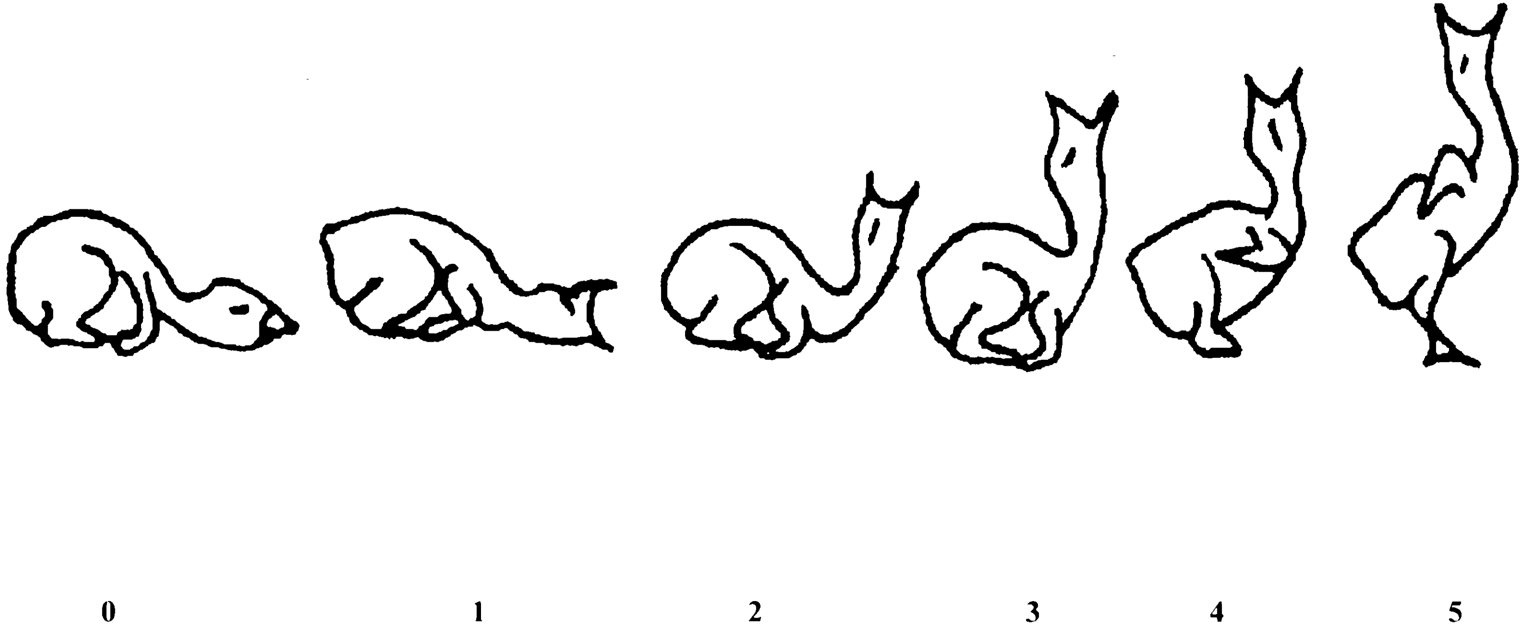


Figure 2.2. Postural begging intensity categorised into six levels (adapted from Redondo & Castro 1992): (0) no begging, (1) gape open, head flat (2) gape open, head raised, (3) gape open, head raised, neck fully stretched, (4) gape open, head raised, front of body raised, (5) gape open, head raised, whole body raised

Chapter 3: Begging strategies and biparental care

Introduction

Both the visual and vocal components of begging behaviour in nestling birds have been shown to contain information on nestling hunger, thermal need and condition (Smith & Montgomerie 1991; Redondo & Castro 1992a; Leonard & Horn 1998; Lotem 1998; Saino et al. 2000; Leonard & Horn 2001b). However, as well as communicating offspring need to parents, begging signals also reflect the competitive environment in which they are performed (Price et al. 1996; Leonard & Horn 1998; Leonard et al. 2000; Rodriguez-Girones et al. 2002) and as such can be viewed as an adaptive strategy reflecting nestling need, relative competitive ability and parental response (Godfray 1995; Johnstone 2004).

Where nestlings hatch asynchronously, later hatched nestlings often remain smaller and in worse condition than their older siblings for the whole of the nestling period (reviewed in Magrath 1990). As a consequence, they may have greater short and long-term need than older siblings. However, they may also be inferior competitors, for example large nestlings can dominate positions close to parents (Kilner 1995; Cotton et al. 1999) and parents often preferentially feed nestlings that are closer to them (Bengtsson & Ryden 1983; McRae et al. 1993; Kilner 1995; Leonard & Horn 1996). Parents may also bias their provisioning towards large, high quality offspring regardless of their begging intensity (Kilner 1995; Price & Ydenberg 1995; Cotton et al. 1999; Smiseth & Amundsen 2002). As a result, nestlings of different sizes may experience very different costs and benefits in relation to begging tactics (Godfray

1995; Glassey & Forbes 2002b). In support of this, studies have generally shown that younger, smaller nestlings beg at greater intensities and for longer periods than their older nestmates (Price et al. 1996; Cotton et al. 1999; Krebs 2001). Theoretical models also predict differences in the begging strategies of different sized nestlings within the brood in response to competitors (Godfray 1995; Johnstone 2004) and several empirical studies support this (Smith & Montgomerie 1991; Price et al. 1996; Leonard & Horn 1998; Leonard et al. 2000) although others do not (Kacelnik et al. 1995; Cotton et al. 1996).

Where there is biparental care, the benefit nestlings receive from solicitation may also depend on the sex of the parent that they solicit, as there is evidence that within nests male and female parents can differ in how they allocate resources to different types of offspring (for reviews see Slagsvold 1997; for reviews see Lessells 2002). Several studies have shown that nestling sex, size and need can differently affect how much male and female parents invest in individual offspring (e.g. Stamps et al. 1987; e.g. Kolliker et al. 1998; Krebs et al. 1999). Even if parents follow the same provisioning rules, they may still differ in their potential value to offspring if they provision at different rates or bring food items of different quality (Slagsvold 1997). If this is the case, then competition for 'begging patches' (Kolliker et al. 1998) near to the two parents will not be equal and the more competitive offspring will dominate positions next to the more profitable parent (Slagsvold 1997). In either case it should pay nestlings to adjust their demand to the sex of the provisioning adult, subject to the profitability of begging to that parent. This would make begging more efficient as it would reduce begging costs and increase the benefits. It would be especially relevant where brood division takes place and each parent only allocates food to certain offspring, as occurs in common coots, *Fulica atra*, where chicks can suffer physical punishment if they beg to the 'wrong' parent, (Horsfall 1984). Even where the brood is not divided, differential demand to parents could still be advantageous. It would be particularly profitable where there are simple cues that allow offspring to discriminate between parents, for instance if parents feed from different locations at the nest (as shown in the great tit, Kolliker et al. 1998). Great tit nestlings orientate themselves so that they are close to where the provisioning adult typically feeds (Kolliker & Richner 2004) and they move closer to parents when they become more hungry (Kolliker et al. 1998). Studies on other species have shown that nestlings often change positions in hungry broods (McRae et al. 1993) and can learn to beg in the most profitable locations in the nest (Budden & Wright 2005). Therefore, there is potential for offspring to adaptively alter levels of solicitation to the male and female parent where there is the opportunity to do so. Kolliker *et al.* (1998) showed that great tit nestlings move closer to, and beg more intensely towards, the parent that is most likely to feed them. Parents may favour influencing begging tactics in this way, as it may both reduce competition within the brood, by forcing offspring to choose between parents, and reduce the time cost of parental allocation to preferred offspring (Kolliker et al. 1998).

This study looked at the begging behaviour of nestling blue tits, *Cyanistes caeruleus*, according to their hunger, size and the sex of the provisioning adult. Specifically, the study aimed to determine whether: (1) Nestling begging behaviour relates to nestling hunger level, (2) the smallest nestlings are inferior competitors within broods and therefore beg more intensely than large nestlings, given equivalent levels of hunger, and (3) nestling begging behaviour differs according to whether nestlings are soliciting parental care from the male or the female parent.

Methods

General fieldwork followed the methods described in Chapter 2 and was carried out between March and June in 2003. Twenty-five pairs of breeding blue tits were used in the experimental procedure, however, due to technical problems with videotaping, data from three of these nests could not be used.

Experimental procedure

The experimental procedure is described fully in Chapter 2; using hand feeding and periods of food deprivation to control nestling hunger across size ranks and filming parental provisioning visits for one hour to record allocation rules by both parents, when nestlings were 10 days old.

Data collection from videotapes

Nestlings were successfully identified on the screen using head patterns. Information on nestling begging behaviour was recorded as described in Chapter 2.

Data analysis

The four measures of nestling begging behaviour; begging posture, latency to beg, begging duration and the position of nestlings relative to the provisioning adult were significantly correlated although in five out of six cases the correlation was not strong (Spearman's correlation coefficient ranges from –0.454 - 0.837, N ranges from 2336-5031). Furthermore, principal component analysis indicated that at least three components would be needed to explain 86.9% of the variance in the data. Therefore, the different measures of begging were analysed separately.

As information on individual begging bouts within nests was not independent, the analysis used average values of begging variables for each focal nestling within nests (except in the analysis of nestling position, see below). Differences between nests were accounted for by using mixed models with nest as a random factor. The models examined the importance of the following factors on the begging behaviour of focal nestlings: experimental treatment (whether the nestling was deprived or satiated), nestling size and sex of the provisioning adult, together with interactions between the terms. Three-way interactions between terms were examined but were not significant in any model. Model terms were fitted by examining the significance of each term when they were the last term in the model within main effects and interactions. Final models contained only significant factors. Data on begging posture were not suitable for mixed models due to significant deviations from normality and so were analysed using non-parametric statistics. Mixed models were performed using PROC MIXED in SAS 9.1 and non-parametric tests were carried out in SPSS11.5.

Nestling position changes over time as nestlings move around the nest cup, competing to be near to the provisioning adult. The analysis of these movements was carried out on the relative positions of nestlings to adults over the observation hour. For ease of interpretation the observation hour was divided into four 15-minute periods. A longitudinal multilevel model (Goldstein 2003) for ordinal data was then used to assess how hunger, size and the sex of the provisioning adult influence nestling position, including interactions between the explanatory terms. This model uses a generalisation of standard binary logistic regression to handle ordinal data. The ordinal response is partitioned in five separate models so that only adjacent categories are combined, thus retaining the original ordinal relationships. For example, the first model partitions the positions into nestlings that were closest to the adult (a distance score of one) and all other positions. All five possible partitions are then fitted simultaneously using a proportional odds model (McCullagh 1980). Models were carried out using the GLLAMM program (Rabe-Hesketh et al. 2001a; Rabe-Hesketh et al. 2001b) in STATA release 9 (StataCorp. 2003). Random effects (nestling and nest) were 'nested' to take into account multiple observations from individual nestlings in each nest (Rabe-Hesketh et al. 2005). Terms were added sequentially into the model and then assessed for significance using changes in deviance (-2 log likelihood).

Results

The experimental treatment affected the begging behaviour of focal nestlings. Food-deprived nestlings begged with more intense postures (Wilcoxon signed ranks test: Z = -3.95, N = 22, P <0.001, Figure 3.1), for longer durations and were quicker to beg than satiated nestlings (Table 3.1). However, nestling size did not influence begging behaviour (begging posture: Wilcoxon signed ranks test: Z = -1.19, N = 22, P = 0.236, latency to beg and begging duration: Table 3.1, *size* effect and *treatment*size* interaction).

Deprived and satiated nestlings did not beg at significantly different postural intensities towards the male and female parents (Wilcoxon signed ranks test, deprived nestlings: Z = -0.052, N = 21, P = 0.96, satiated: Z = -0.639, N = 21, P = 0.52). Similarly neither latency to beg nor duration of begging was influenced by the sex of the provisioning adult and neither nestling size nor nestling hunger altered this pattern (Table 3.1: *parent* main effect and *parent*size* interaction).

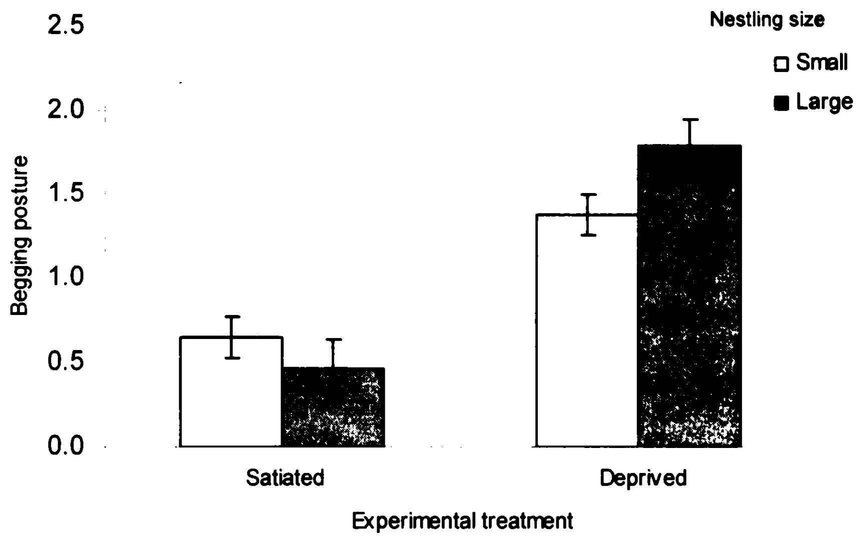


Figure 3.1. The postural begging intensity (see Fig. 2.2) of focal nestlings over the one-hour observation period following the experimental treatment of either feeding until satiation or one hour of food deprivation. Bars represent means ± SE for small (unshaded bars) and large (shaded bars) nestlings.

Table 3.1. Variation in begging latency and duration amongst deprived nestlings according to nestling size and the sex of the provisioning parent. Nest was included as a random effect in the mixed model (latency to beg: Z = 1.61, P = 0.0537, duration to beg: Z = 1.50, P = 0.0667). Explanatory variables were assessed for significance when they were the last terms in the model, within three-way, two-way and main effects, to control for any influence of the order of terms. Non-significant terms were removed from the final model.

Begging behaviour	*Effect*	*df*	*F-value*	*P*
Latency to beg	Treatment	1,121	18.64	<0.0001
	Size	1,118	0.29	0.5911
	Parent	1,118	3.32	0.0711
	Treatment*size	1,117	1.13	0.2900
	Treatment*parent	1,114	0.17	0.6832
	Size*parent	1,113	0.50	0.4801
Duration of begging	Treatment	1,147	35.48	<0.0001
	Size	1,147	0.00	0.9830
	Parent	1,150	0.10	0.7494
	Treatment*size	1,144	1.68	0.1968
	Treatment*parent	1,144	0.68	0.4105
	Size*parent	1,144	0.05	0.8153

Nestling position

During the observation hour almost all focal nestlings moved across positions in the nest cup (median number of positions used = 4, range 1-9, Figure 3.2). Hunger affected the number of positions that nestlings moved into, with hungry nestlings moving into more positions than satiated nestlings (median number of positions used; deprived nestlings = 4.5, range 2-9; satiated nestlings = 3.5, range 1-8, Wilcoxon signed-ranks test: *Z* = -2.756, N = 22, P = 0.006, Figure 3.2).

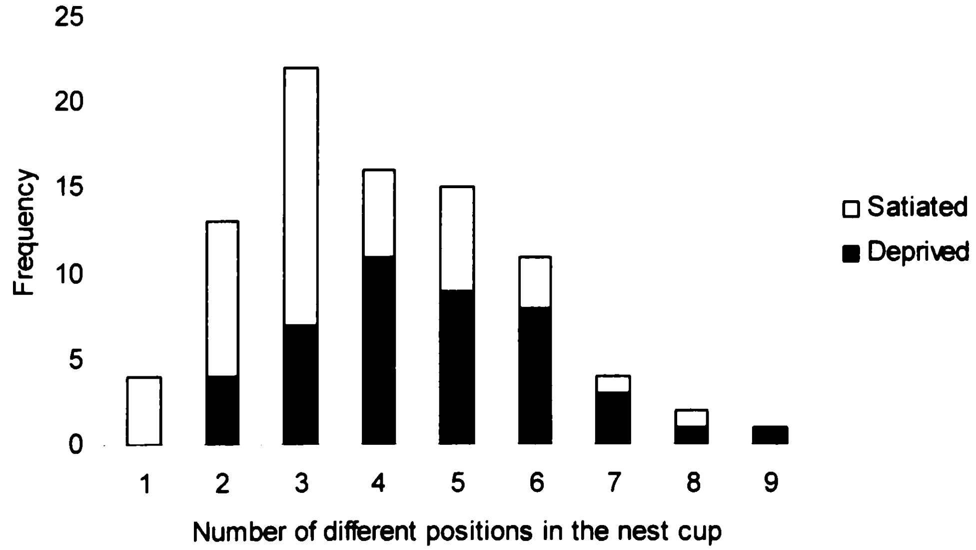


Figure 3.2. The number of different positions (after the nest cup was divided up on the video screen into nine sections; see Methods section) used by satiated (unshaded bars) and deprived (shaded bars) focal nestlings over the one hour observation period.

Nestling position in the nest was significantly affected by the experimental treatment, nestling size, the sex of the provisioning parent and time (Table 3.2). However, the effect of size involved an interaction with the sex of the provisioning adult and the experimental treatment. Both large nestlings and small deprived nestlings were closer to the male parent, while small satiated nestlings were closer to the female (Figure 3.3). Focal nestlings were closer to the male parent than to the female parent and they also moved further away from the female parent over the observation hour (Figure 3.4). Over the observation period, nestlings changed positions relative to the provisioning male parent according to their hunger and size, with large deprived nestlings obtaining positions close to the male at the start of the observation period and small deprived nestlings obtaining these positions in the latter half of the observation period (Figure 3.5). Over time, presumably as they became hungrier, large satiated nestlings moved closer to the male parent, however small satiated nestlings showed the opposite pattern (Figure 3.5).

Table 3.2. Final model examining the importance of focal nestling size, experimental treatment (deprived and satiated nestlings), parental sex and time on the position of nestlings relative to the provisioning parent. Time refers to time from the start of the experiment, when focal nestlings are placed back in the nest (positions are recorded within 15-minute time intervals: 15, 30, 45 and 60 minutes). Only significant terms are included in the final model.

Term	*Change in deviance*	*df*	*P*
Null model	7235.38		
Treatment	3.98	1	0.0460
Nestling size	0.01	1	0.9203
Parent	43.63	1	<0.0001
Time	16.65	3	0.0008
Treatment*time	7.88	3	0.0486
Treatment*parent	52.25	1	<0.0001
Nestling size*parent	9.64	1	0.0019
Parent*time	26.41	3	<0.0001
Nestling size*treatment*parent	20.64	1	<0.0001

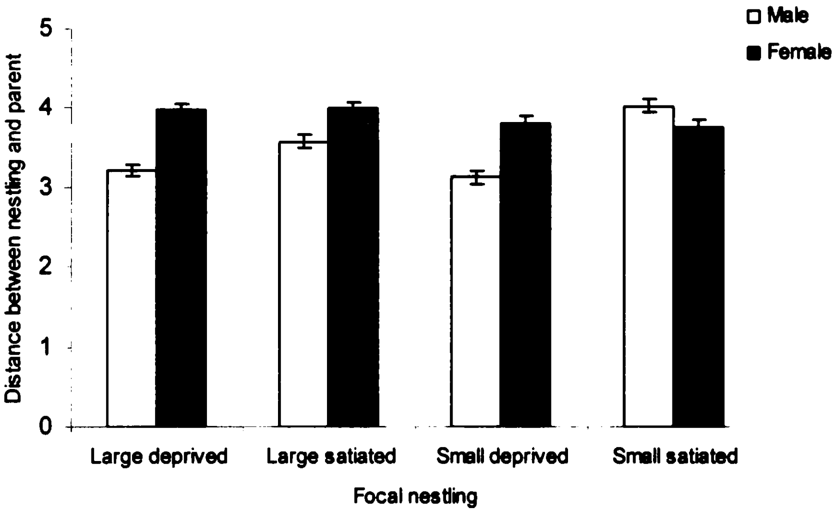


Figure 3.3. The distance (mean ±SE) between focal nestlings (nestling size and experimental treatment) and the provisioning adult (male = unshaded bars, female = shaded bars).

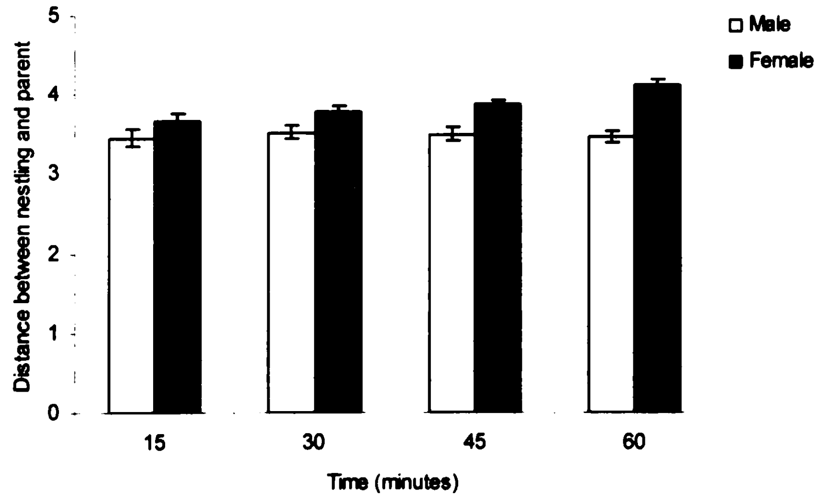
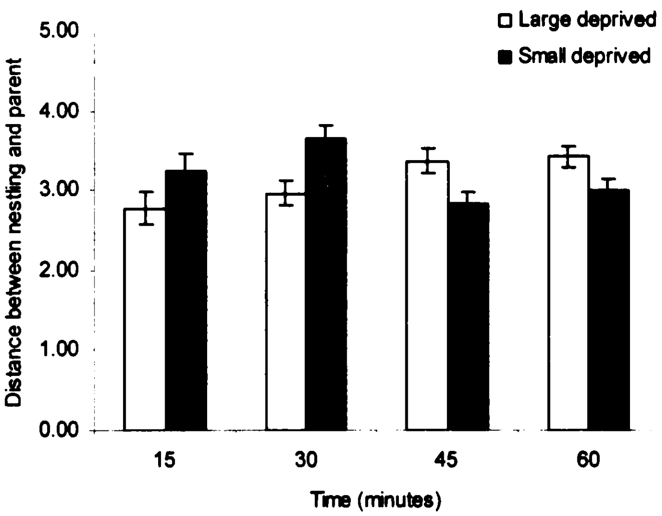
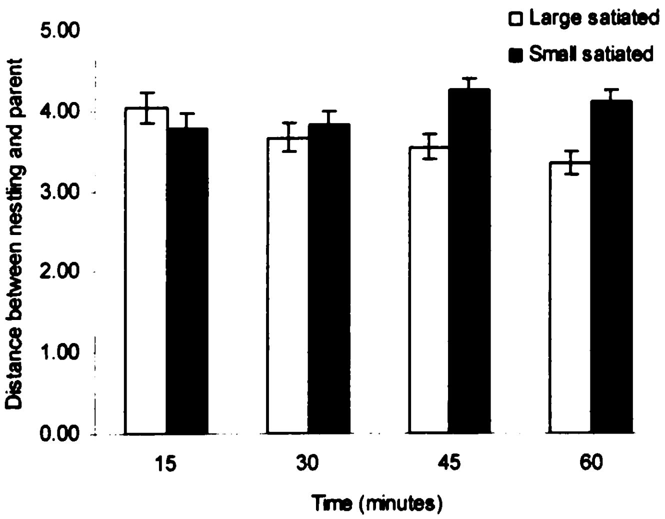


Figure 3.4. The position of focal nestlings (mean ±SE) over time relative to the provisioning male and female parent (male = unshaded bars, female = shaded bars).



(a)



(b)

Figure 3.5. The distance (mean ±SE) between large and small focal nestlings and the provisioning male parent: (a) Deprived nestlings and (b) Satiated nestlings.

Discussion

Begging and nestling need

Food deprived nestlings increased the intensity of their begging signals. This is consistent with the theory that begging is an honest signal of nestling need (reviewed in Kilner & Johnstone 1997) and corresponds with empirical work carried out on other species (Smith & Montgomerie 1991; Redondo & Castro 1992a; Leonard & Horn 1998; Lotem 1998; Saino et al. 2000; Leonard & Horn 2001b). However, expectations that smaller nestlings with greater long-term need would beg more than larger siblings were not fulfilled. This suggests that the influence that long-term need has over begging strategies is more complex, and may involve differences in both the cost and effectiveness of begging with nestling size, as proposed by recent theoretical work (Parker et al. 1989; Godfray 1995; Lotem 1998; Parker et al. 2002b; Royle et al. 2002).

There is substantial evidence from other studies that due to competitive asymmetries, the smallest nestlings in a brood have to work harder to receive equivalent amounts of parental care to their siblings (Lotem 1998; Cotton et al. 1999; Smiseth & Amundsen 2002). These studies have generally shown that small nestlings beg more than older nestmates, both in a natural setting and when experimentally paired with larger nestlings when hunger is controlled (Price et al. 1996). Furthermore, small nestlings have greater long term need, as in order to fledge successfully they must achieve a higher rate of growth than older siblings. In contrast to these expectations, in blue tits small nestlings did not have higher begging rates than their larger siblings after a period of deprivation, despite having between one and three days of growing time to catch up on. This may in part be due to the stage of nestling development at which the experiment was carried out. At day ten in the nestling period, smaller nestlings are still in the period of high daily growth rate, while the growth rate of the larger nestlings has begun to decline (Gibb 1950). As a result, the potential marginal costs of begging are not equal for large and small nestlings. Performing begging signals may carry significant metabolic costs (Leech & Leonard 1996; but see Bachman & Chappell 1998) and there is evidence that these costs can equate to a decrease in nestling growth rate (Kilner 2001). Furthermore, Kilner (2001) shows that the marginal cost of begging, in terms of impaired growth, declines with nestling age. As small nestlings are attempting to catch up with their larger siblings they may be strategically selecting not to escalate begging in order to avoid these costs. Lotem (1998) also found that at later stages in the nestling period, small nestlings (barn swallow, *Hirundo rustica*) begged less than expected from their long-term need, while Gottlander (1987) found that in the middle of the nestling period pied flycatcher, *Ficedula hypoleuca*, nestling mass did not influence begging intensity. The efficiency of begging with nestling size may also influence begging strategies. Parents may either preferentially feed large nestlings (Smiseth & Amundsen 2002) or may passively accept the outcome of sibling competition, for example large nestlings can obtain positions near to the provisioning adult (Kilner 1995; Cotton et al. 1999). In either case, small nestlings find that their begging signals are less efficient. Glassey & Forbes (2002b) suggest that marginal (smaller) offspring may be 'prudent beggars' in certain circumstances, for instance when their older siblings are hungry. If this is the case, smaller nestlings might wait until older siblings are satiated before performing costly begging signals even though they have higher levels of long-term need.

Alternatively, although small nestlings may have greater long-term need, body size may dictate that larger nestlings need more food in the short-term or there may be physiological constraints acting on the ability of smaller nestlings to utilise food resources for growth (Lotem 1998; Karasov & Wright 2002), and as a result, larger nestlings may become hungry faster.

Dynamic begging strategies as a consequence of biparental care

Biparental care has the potential to influence begging strategies, especially if nestling characteristics affect how parents allocate food items (Kolliker et al. 1998). Although nestling begging behaviour has been viewed as strategic and thus dependent on the signaller's state, relative competitive ability and probability of success (e.g. Cotton et al. 1999) few studies have looked for evidence that nestling begging behaviour is affected by the sex of the provisioning adult. In a study on biparental care in the great tit, Kolliker *et al.* (1998) manipulated the hunger of nestlings and recorded their begging behaviour towards the male and female parent. Interestingly, the study showed that hungry nestlings moved closer and begged more intensely towards the female than to the male parent. These differences were then explained by the observation that female parents were feeding hungry nestlings more often than male parents. Great tit nestlings therefore appear to adjust their demand to the male and female parent depending on their need and in doing so increase the profitability of their begging signals. Presumably this adaptive behaviour is the result of nestlings learning the profitability of begging strategies in different areas of the nest. A study on crimson rosellas, *Platycercus elegans*, (Krebs 2001) found that chick size affected how close chicks were to the male and female parent. Irrespective of hunger, larger chicks tended to be closer to the male parent and smaller chicks closer to the female parent. Again, the positioning of nestlings relates to the provisioning rules of the parents, male parents preferentially feeding large chicks and females small chicks (Krebs & Magrath 2000). However, unlike great tit nestlings, in parrots there is no difference in the begging intensity of small and large chicks to the two parents and chick hunger did not cause chicks to be positioned closer to parents (Krebs 2001), strongly suggesting that chicks do not alter their solicitation with the sex of the parent. In fact, it appears most likely that in crimson rosellas parents control the allocation of food to individual chicks.

These two studies suggest that differences in how parents integrate begging signals with other cues (nestling size and position), both between the sexes within species and between different species, can produce different nestling begging strategies. One of the main factors determining these differences may be how much control parents versus offspring have over the allocation of food. Parental assessment of offspring state may be constrained by limits on provisioning efficiency and by competitive interactions between siblings, leading to begging 'scrambles' where parents are passive (Parker et al. 2002b). By feeding from different locations and assessing offspring need through relative size, parents may be able to regain a measure of control over allocation. In highly asynchronous parrots, large size differences mean that parents can easily assess nestling need and therefore respond less to begging intensity and offspring positioning (Krebs 2002).

The present study provides some evidence that dynamic patterns of offspring solicitation can occur as a result of biparental care. While offspring appear to move closer to parents when hungry, they also show complex patterns of movement that relate to nestling size, hunger and the sex of the provisioning adult. Large nestlings and those that have been deprived of food obtain positions closer to the male parent, changing positions with time according to motivation and competitive ability. This suggests that the differences in provisioning rules between the parents with respect to nestling position (Chapter 5) have driven competition between offspring to get closer to the male parent. Thus nestlings bias one aspect of their begging behaviour to address the differences in male and female allocation. By dominating positions close to the male parent, large nestlings can capitalise on male provisioning rules.

Alternatively, nestlings could be biasing their solicitation behaviour towards the male parent because of the profitability of doing so. Slagsvold (1997) suggested, in his sibling rivalry hypothesis, that offspring solicitation is influenced by the relative provisioning rate of the parent. This theory predicts that competitive offspring are able to obtain positions close to the parent that is provisioning at the highest rate and that parents respond passively to sibling competition, feeding the nestlings that are closest. In the present study there was no difference in the provisioning rates of the two parents, however more detailed work on provisioning in blue tits has had mixed results. Several studies found that male parents provision at a higher rate than females (Greico 1999; but see Banbura et al. 2001 for the reverse pattern) or bring larger food items (Cowie & Hinsley 1988; Blondel et al. 1991; Banbura et al. 2001), while others found no difference in provisioning (Leech 2002). It is possible that the relative contributions of the two parents to provisioning may differ with individuals and environmental conditions and that begging strategies could be flexible in response to this. There is some evidence from studies on other species that nestlings compete for access to the parent provisioning most frequently, for example Leedman & Magrath (2003) suggest that in fledgling white-browed scrubwrens, *Sericornis frontalis*, the most dominant fledging obtains parental care from the best feeder.

In conclusion, the present study has shown that blue tit nestlings alter begging signals with short-term need, however long-term need with respect to body size does not appear to relate to begging intensity. Nestlings do not alter begging signals according to the sex of the provisioning adult but there is differential competition for positions close to the male and female parent. Nestlings appear to compete for positions close to the male parent, with large nestlings primarily obtaining closer positions but with nestling hunger also motivating all nestlings to move closer to the male.

Chapter 4: Begging strategies and the reliability of the begging stimulus

Introduction

In altricial birds, nestlings must beg towards the provisioning adult to have a chance of receiving food. In order to do so, they have to perceive when a feed is imminent. Nestlings usually beg when an adult arrives at the nest, and seem to respond to the sound of the adult's arrival on the nestbox (Leonard & Horn 2001c) or to the appearance of the parent at the nest (Budden & Wright 2001). They can also, however, respond to apparently irrelevant stimuli, such as noises in the environment, the sound of the parent leaving the nest and to parental vocalisations that are not related to provisioning (Clemmons 1995a; Price & Ydenberg 1995; Leonard & Horn 2001c; Maurer et al. 2003), and sometimes fail to beg to an adult arriving with food (Leonard et al. 1997; Grieco 2001a). Therefore, nestling discrimination between correct and incorrect stimuli is error prone. Signal detection theory states that when a receiver cannot perfectly distinguish signals, it is not possible for the receiver to both maximise correct responses as well as minimise errors (Koops 2004). Receiver error is expected to vary with the costs and benefits of correct detection to the receiver (Koops 2004) and in addition will be constrained by perceptual ability, i.e. when the ability to distinguish correct from false stimuli is low, receivers will be forced to either commit errors or to refrain from responding. Examining nestling begging response to a variety of stimuli that differ in their reliability should give valuable insights into nestling begging behaviour and help to clarify constraints and strategies involved in the evolution of parent-offspring communication.

The ability to respond correctly to the sound of a parent arriving at the nest has obvious consequences for nestlings in terms of getting access to food. Nestlings are in competition with each other and being the first to beg increases a nestling's chances of being fed (e.g. Teather 1992; e.g. Leonard & Horn 1996). Failure to respond to the correct stimuli, or responding too slowly, means losing out on a feed, a cost that would have severe implications in the long term for nestling growth and survival. Conversely, as begging may be costly to nestlings (Kilner 2001; Chappell & Bachman 2002), discrimination against responding to irrelevant stimuli is adaptive, as it decreases the likelihood of a nestling begging without reward. In addition, if begging vocalisations increase the risk of nest predation this will also select for discrimination against false alarms (Haskell 2002). Indeed, when parents perceive a threat close to the nest they may give an alarm call, to which nestlings will respond by instantly ceasing to beg (Flanagan & Morris 1975; but see Maurer et al. 2003; Davies et al. 2004; Platzen & Magrath 2004). The ability of nestlings to respond to species-specific alarm calls appears to be innate, with learning fine-tuning the ability to correctly discriminate these calls (Davies et al. 2004). The ability of nestlings to beg in the correct context might be expected to be influenced by the level of predation risk, so selection should act to improve the ability of nestlings to correctly discriminate between stimuli when deciding whether to beg, and to respond appropriately. Thus, nestling begging in the absence of parents has largely been thought to represent a costly error in perception (e.g. Leonard & Horn 2005) with a resultant cost to the individual.

The ability of nestlings to correctly discriminate between stimuli, and therefore reduce the frequency of errors, will be constrained by perceptual ability, which alters with age. Nidicolous young are born blind, remaining so for a period after hatching. Sensory development continues while the young are in the nest and therefore perceptual ability increases with nestling age (Khayutin 1985). This being the case, the ability of nestling birds to discriminate between the arrival of a parent at the nest and random noise from the environment will be influenced by nestling age. Where nestlings hatch asynchronously age differences between siblings, especially early on in the nestling period, may also represent differences in sensory ability. As a result, younger siblings may be more prone to beg to irrelevant stimuli and more likely to fail to beg to the sound of a parent arriving with food (Budden & Wright 2001; Leonard & Horn 2001c).

The individual need of nestlings within nests may also affect how much they discriminate between different stimuli. Receiver error is expected to vary with receiver motivation (Koops 2004). For instance, hungry nestlings might be expected to be more willing to risk begging to any stimuli, while satiated nestlings respond to a narrower range of stimuli; those that are least likely to lead to errors. Thus there is the potential for an interaction between a receiver's perceptual ability and its motivation when discriminating between correct and incorrect stimuli.

Parents can influence the interaction between receiver motivation and ability on discrimination, through unambiguously announcing their arrival and intention to feed their offspring. Many altrical birds appear to do so by giving a distinct 'feed call' on arrival at the nest. This call stimulates nestlings to beg (Flanagan & Morris 1975; Khayutin 1985; Clemmons 1995a; Clemmons 1995b; Leonard et al. 2005). Observations in blue tits, *Cyanistes caeruleus*, (Grieco 2001a) show that this call is given less frequently as nestlings age, presumably because older nestlings are more likely to respond correctly to the arrival of the parent.

This chapter asks whether nestling begging strategies are influenced by the reliability of the stimulus to beg and examines how nestling motivation affects the response to stimuli that differ in reliability. Specifically the following predictions are tested: (1) nestlings with greater motivation to beg, are more likely to beg to unreliable stimuli, and (2) less motivated (satiated) nestlings respond mainly to the most reliable stimulus type. By controlling nestling hunger across size-ranks within broods, the analysis also examines whether nestling begging responses are constrained by potentially size-related perceptual ability halfway through the nestling period. If this is the case, smaller nestlings may either be more likely than large nestlings to commit errors, begging when the adult is not present, or their begging response may depend on the adult's feed call, if they are unable to detect the more subtle stimulus of the provisioning parent arriving at the nest.

Methods

General fieldwork followed the methods described in Chapter 2 and was carried out between March and June in 2003. Twenty-five pairs of breeding blue tits were used in the experimental procedure, however, due to technical problems with videotaping, data from three of these nests could not be used.

Experimental procedure

The experimental procedure is described fully in Chapter 2; using hand feeding and periods of food deprivation to control nestling hunger across size ranks and filming parental provisioning visits for one hour to record allocation rules by both parents, when nestlings were 10 days old.

Data collection from videotapes

Nestlings were successfully identified on the screen using head patterns. Information on nestling begging behaviour was recorded as described in Chapter 2. Both male and female adult blue tits occasionally gave a short call at the nest cup after they arrived with food for the nestlings. This call has been previously described in blue tits by Grieco (2001a) and other species appear to have an equivalent call (e.g. tree swallows Leonard et al. 1997). It has been termed a feeding call, as it appears to have a function in the provisioning of nestlings. This feed call was noted when it occurred and the precise time recorded to allow the call to be linked to the begging behaviour of nestlings. In all nests, nestlings occasionally begged when both parents were absent from the nest, responding to a noise from the environment, or to the sound of the parent leaving the nest box. The begging behaviour of nestlings during these occasions was recorded as for a parental visit and these begging bouts were termed false alarms, following Leonard & Horn (2005).

Data analysis

The analysis aimed to compare the begging responses to three different types of stimuli: (1) The adult arriving at the nest, (2) The adult arriving at the nest and giving a feed call, and (3) Random sounds from the environment causing a false alarm. As the feed call was not used in all nests (see results section) the analysis was carried out on two separate datasets: (1) nests where the feed call was given (N = 13), and (2) nests where more than one false alarms took place (N = 20 nests). In each of these separate analyses, the response to the stimulus of interest was compared to the response to the parent arriving at the nest, firstly for all nestlings in the brood and secondly for focal nestlings (comparing responses with focal size and experimental treatment). Although the different measures of begging were significantly correlated (Spearman's correlation coefficient ranges from –0.332-0.835, N ranges from 2688-5845, in all cases P < 0.0001), they were tested separately as stimulus type may affect particular components of begging displays differently.

Feed calls and nestling begging

To test whether nestlings respond differently to the feed call and the arrival of the adult, the proportion of begging nestling in the brood that begged to each type of stimulus, was compared, together with the following measures of nestling begging: begging posture, the latency to beg and begging duration. Begging postures were compared directly before the adult provided a feed, i.e. after the feed call during a feed call visit. Latency to beg was measured either as the time from the sound of the parent arriving at the nest or from the feed call, depending on whether it was a feed call visit or not. Mean values for each stimulus type within nests were compared with paired t-tests or Wilcoxon signed ranks test where appropriate. Data on the proportion of nestlings gaping were arcsine square root transformed.

False alarms and nestling begging

To test whether nestlings respond differently to the arrival of the adult and stimuli that elicit a false alarm, the proportion of nestlings begging in the brood begging to each type of stimulus (arcsine transformed) was compared, together with nestling begging posture and begging duration. For each stimulus type, nestling begging posture was taken as the mean of the begging posture, each second, for the first three seconds after either the sound of the parent arriving or after the first nestling began to beg when there was no adult. Again, mean values for each stimulus type within nests were compared with paired t-tests or Wilcoxon signed ranks test where appropriate.

Focal nestling begging and stimulus type

Mixed models were used to test for the effects of nestling size and hunger on the mean begging response of each focal nestling to each of the stimulus types. The begging response was examined in terms of (1) Begging frequency, the proportion of feeding visits during which a nestling begged, (2) latency to beg and (3) duration of begging. Latency to beg was not analysed in the case of nestling response being a false alarm, as the timing of the stimulus (i.e. a noise from the environment) was not recorded. Data on begging frequency were arcsine square root transformed. Models incorporated both fixed effects (nestling size and hunger) and random effects (nest). The model considered all two and three-way interactions between explanatory variables. Explanatory variables were assessed for significance when they were the last terms in the model, within three-way, two-way and main effects, to control for any influence of the order of terms. Non-significant terms were removed from the final model.

Paired t-tests and Wilcoxon signed ranks tests were carried out in SPSS11.5 and mixed models were performed using PROC MIXED in SAS 9.1.

Results

Feed calls

Parents used feed calls in 13 of the 22 nests filmed. At those nests, feed calls were given infrequently, the median feed call rate being 0.048 calls/parental feed (quartiles 0.038 – 0.071). Over all nests there were a total of 494 provisioning visits and 43 feed calls. Males gave more feed calls than females at the same nest (Wilcoxon signed ranks: Z = -2.223, p = 0.026, N = 11 nests, median call rate: females = 0.030, quartiles: 0.000, 0.120, males = 0.110, quartiles: 0.055 – 0.475). Male and female call rate was not correlated within nests (Spearman's correlation coefficient = -0.105, p = 0.759, Figure 4.1).

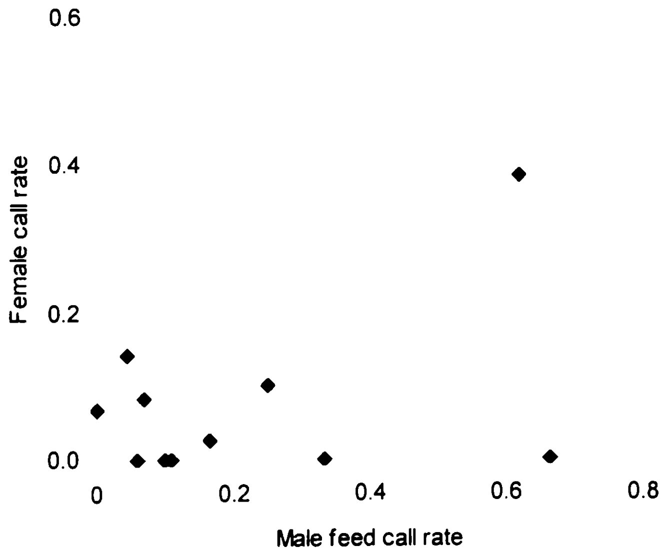


Figure 4.1. The feed call rate (the number of calls/parental feed) for males and females from each nest.

Feed calls and nestling begging

The feed call was always given prior to a feed and was always followed by at least one nestling begging to the provisioning adult. Comparing within nests and across feeds showed that a feed call visit evoked a greater proportion of nestlings to beg than the presence of the adult alone (Table 4.1). Therefore, the feed call effectively solicits nestlings to beg to the provisioning adult. Nestlings were also quicker to respond to the feed call than to the arrival of the provisioning adult (beg latency, Table 4.1). This suggests that nestlings recognise the stimulus of the feed call as specific to a provisioning event, in contrast to the sound of the adult's arrival, which might not necessarily signify an imminent feed and which is more likely to be confused with sounds in the environment. Indeed, when there is no feed call given, nestlings appear to stimulate each other to beg (i.e. the first nestling to beg acts as a stimulus to the others, pers.obs.). Nestlings appear to beg to the feed call for a shorter length of time than to a normal adult visit, although the trend is not statistically significant (Table 4.1). However, begging to the feed call is at the same level of postural intensity as begging to an adult visit alone (Table 4.1).

Table 4.1. Nestling begging response to the arrival of the provisioning adult without a feed call and the arrival of the adult with a feed call (mean & SE). Responses were tested using paired t-tests (df = 12) except where indicated with * where a Wilcoxon signed ranks test was used.

Begging response	*Arrival of adult*	*Feed call*	*Test statistic*	*P*
Proportion of nestlings gaping	0.441 (0.032)	0.571 (0.045)	3.425	0.005
Begging posture	3.062 (0.082)	3.138 (0.126)	0.909*	0.363
Latency to beg (seconds)	1.079 (0.088)	0.418 (0.049)	5.908	< 0.001
Begging duration (seconds)	5.986 (0.401)	5.032 (0.407)	2.023	0.066

Response to feed calls with nestling size and hunger

Only the experimental treatment affected nestling begging rate, with deprived nestlings begging more often than satiated nestlings (Table 4.2, Figure 4.2). There was a trend for all focal nestlings to beg more frequently to the feed call than to a silent adult (Figure 4.2), but this effect was not statistically significant (Table 4.2). Both large and small nestlings responded to the stimulus type in the same way, i.e. there was no interaction between nestling size and whether nestlings were responding to the feed call or to the adult alone. Similarly, nestling hunger did not interact with the stimulus type. As expected focal nestlings were quicker to respond to the feed call than to the arrival of the adult alone (latency to beg, Table 4.2, Figure 4.3). The experimental treatment did, however, interact with the type of stimulus. Satiated nestlings decreased their latency to respond dramatically in response to the feed call, while in deprived nestlings, who were already responding rapidly to the adult, there was a much smaller decrease (Figure 4.3). Duration of begging was influenced only by treatment, the stimulus to beg had no effect (Table 4.2).

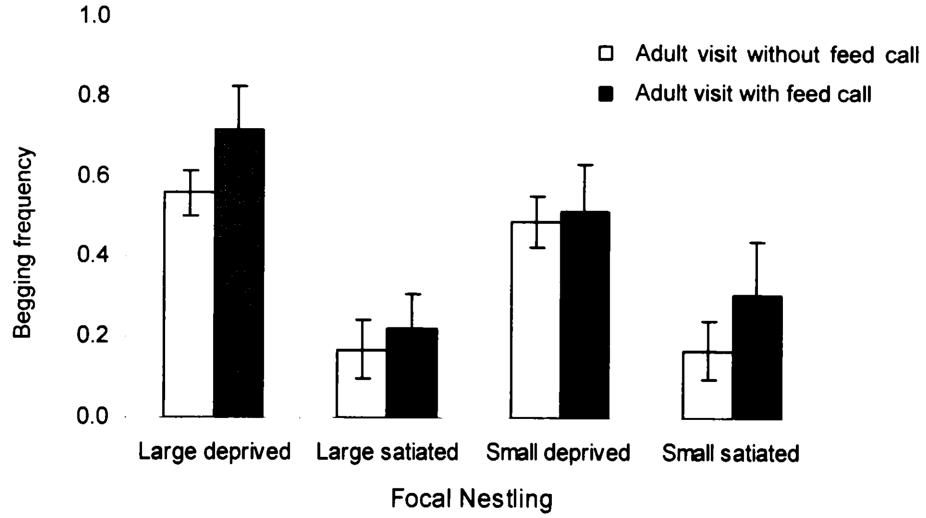


Figure 4.2. Mean begging frequency (± SE) in response to the arrival of a silent adult at the nest (white bars) and the arrival of an adult with a feed call (shaded bars) for focal nestlings (experimental treatment manipulating nestling hunger across large and small nestlings).

Table 4.2. The effect of the parent's feed call on nestling begging behaviour. Begging variables are examined in a mixed model, with nest as a random effect, to determine the influence of nestling size, the experimental treatment (whether nestlings are deprived or satiated), when the stimulus to beg is either the arrival of the provisioning adult with a feed call or the arrival of a silent adult alone. Explanatory variables were assessed for significance when they were the last terms in the model, within three-way, two-way and main effects, to control for any influence of the order of terms. Non-significant terms were removed from the final model.

Begging behaviour	*Effect*	*DF*	*F-value*	*P*
Begging frequency	Treatment	1,88	30.48	<0.0001
	Size	1,88	0.59	0.4459
	Feed call	1,88	2.20	0.1420
	Treatment*size	1,85	2.25	0.1372
	Treatment*feed call	1,85	0.10	0.7582
	Size*feed call	1,85	0.07	0.7977
Latency to beg	Treatment	1,64.4	9.78	0.0026
	Size	1,60.8	0.02	0.8791
	Feed call	1,64.5	27.39	<0.0001
	Treatment*size	1,57.4	0.87	0.3538
	Treatment*feed call	1,58.8	5.90	0.0182
	Size*feed call	1,59	1.06	0.3078
Duration of begging	Treatment	1,66.5	24.74	<0.0001
	Size	1,64.1	2.72	0.1039
	Feed call	1,64.9	2.14	0.1483
	Treatment*size	1,62.5	0.77	0.3850
	Treatment*feed call	1,61.5	1.26	0.2651
	Size*feed call	1,60.7	0.06	0.8098

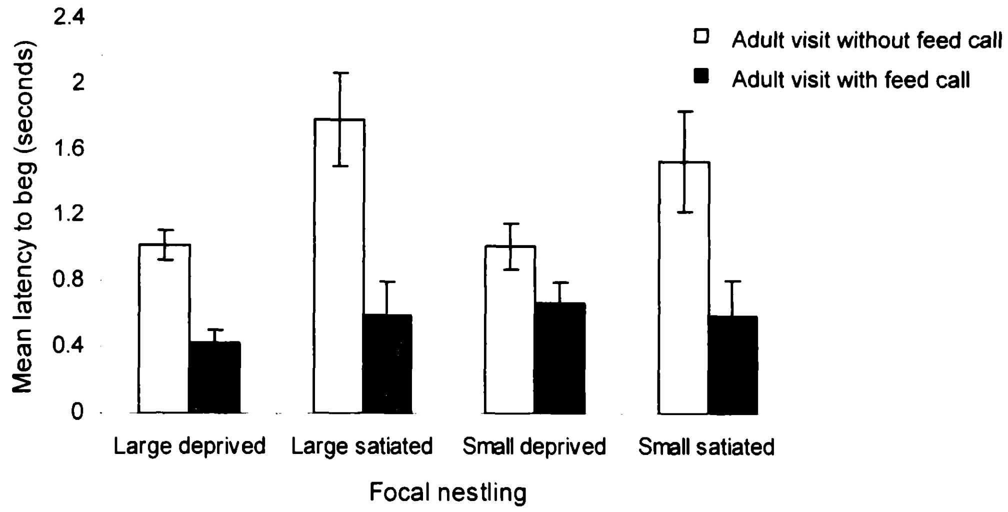


Figure 4.3. The mean latency to beg (± SE) in response to the arrival of an adult without a feed call (white bars) and arrival with a feed call (shaded bars) in focal nestlings (experimental treatment manipulating nestling hunger across large and small nestlings).

False alarms

At nests where they occurred, the median number of false alarms was 9.5, (quartiles 6.5-16.0) over the one hour observation period. Although relative to provisioning rate false alarm rate was low, it did account for a substantial proportion of begging bouts (begging due to false alarms accounted for 26.3% of all begging bouts). Data from a total of 213 false alarms from 20 nests were used in the analysis.

False alarms and nestling begging

Mean values for nestling begging parameters were calculated for false alarms and for adult visits at each nest. Nestlings were less likely to beg to false alarms than to a normal provisioning visit (Table 4.3). When nestlings did beg to a false alarm, the stimulus had an effect on how they begged. Nestlings begging to a false alarm begged for a shorter period than they did to the provisioning adult and begged at a lower postural intensity (Table 4.3).

Table 4.3. Nestling begging response to the provisioning adult and to a false alarm (mean & SE). Responses were tested using paired t-tests (df = 19) except where indicated with * where a Wilcoxon signed ranks test was used.

Begging response	*Arrival of adult*	*False alarm*	*Test statistic*	*P*
Proportion of nestlings gaping	0.454 (0.023)	0.244 (0.016)	9.534	< 0.001
Begging posture	2.741 (0.081)	2.458 (0.093)	-2.670*	0.008
Begging duration (seconds)	3.023 (0.310)	0.845 (0.078)	7.195	< 0.001

False alarms and nestling size and hunger

In focal nestlings, begging rate was influenced by whether the response was a false alarm or not, with nestlings begging less frequently to false alarms (Table 4.4, Figure 4.4). Nestling size however did not affect the begging response either to the parent or during a false alarm (Table 4.4, Figure 4.4). Hunger did affect how nestlings responded, with deprived nestlings responding more frequently to both the adult and to stimuli that elicited false alarms (Table 4.4, Figure 4.4). All focal nestlings begged for a shorter period during a false alarm, and there was no additional effect of nestling size on begging duration while hunger caused nestlings to beg for longer to all stimuli (Table 4.4).

Table 4.4. The effect of false alarms on nestling begging behaviour. Begging variables are examined in a mixed model with nest as a random effect to determine the influence of nestling size, the experimental treatment (whether nestlings are deprived or satiated), when the stimulus to beg is a false alarm versus a visit by the provisioning adult. Explanatory variables were assessed for significance when they were the last terms in the model, within three-way, two-way and main effects, to control for any influence of the order of terms. Non-significant terms were removed from the final model.

Begging behaviour	Effect	DF	F-value	P
Begging frequency	Treatment	1,136	84.25	<0.0001
	Size	1,136	0.02	0.8872
	False alarm/adult visit	1,136	21.86	<0.0001
	Size*treatment	1,133	3.80	0.0534
	Treatment*false alarm/adult visit	1,133	1.41	0.2365
	Size*false alarm/adult visit	1,133	0.06	0.8142
Begging duration	Treatment	1,137	52.48	<0.0001
	Size	1,137	0.03	0.8542
	False alarm/adult visit	1,137	53.65	<0.0001
	Size*treatment	1,134	0.83	0.3630
	Treatment*false alarm/adult visit	1,134	2.48	0.1175
	Size*false alarm/adult visit	1,134	0.00	0.9591

As nestlings may react to each other when begging, only the first nestling to respond to a false alarm can be considered to be responding to the false alarm stimulus alone. If errors were due to differences in perceptual ability, we might expect smaller nestlings to be more prone to begging first during a false alarm. However, nestling size did not have an effect on which nestling was the first to respond to a false alarm, (Wilcoxon signed rank test, $Z = -0.446$, $p = 0.655$, $n = 20$ nests) giving further evidence for there being no variation in perceptual ability between large and small nestlings at day 10.

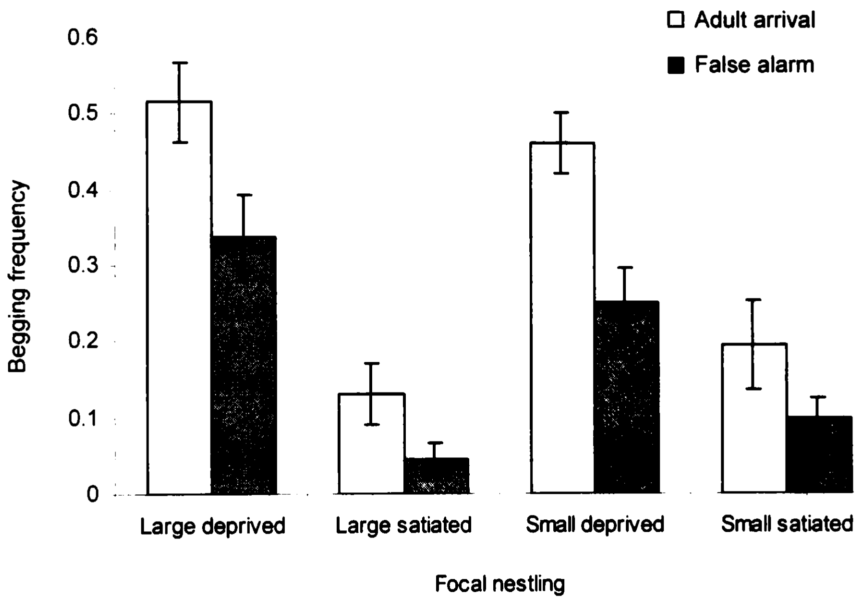


Figure 4.4. Mean begging frequency (± SE) in response to the arrival of an adult at the nest (white bars) and to a false alarm (shaded bars), for focal nestlings (experimental treatment manipulating nestling hunger across large and small nestlings).

Discussion

Nestling begging response to the feed call

The feed call was more effective at eliciting nestling begging than the arrival of the adult alone. This concurs with previous studies that have examined nestling responses to the feed call in black-capped chickadees, *Parus atricapillus*, (Clemmons 1995b) and in tree swallows, *Tachycineta bicolor* (Leonard et al. 1997). There is evidence that shortly after hatching the feed call acts to reinforce the signal of the parents arrival with food, at this stage the perceptual ability of nestlings is low (Khayutin 1985) and they might otherwise fail to beg at the correct time (Clemmons 1995a; Clemmons 1995b; Leonard et al. 1997). After this learning period (Clemmons 1997), nestlings presumably associate the feed call with a provisioning event. By learning to beg when the reliability of the stimulus is high, nestlings can reduce errors and minimise the costs of begging.

Short latencies to beg after the feed call demonstrate that nestlings are responding to the call alone, whereas with other stimuli there is the possibility that they are responding to sibling begging, as latencies are longer and more variable. With the arrival of the adult, it is also possible that nestlings are responding to different aspects of the stimulus, for instance one may be responding to the sound of the adult entering the box while another responds to the visual signal of the adult at the nest. Other aspects of begging do not change in response to the feed call, for instance begging posture is not altered. This appears counterintuitive, as nestlings might be expected to beg at a greater intensity when the certainty of a feed is high. In addition, as the feed call elicits more nestlings to beg, competition for a feed after a feed call is higher than when there is no call. Elevated competition might be expected to increase begging intensity (Leonard et al. 2000). However, the higher costs of more intense begging postures may be enough to keep begging levels constant over both different levels of competition and with different begging stimuli that vary in reliability. Although not statistically significant, there is a trend for the feed call to decrease the duration of nestling begging. As the feed call signifies an imminent feed, it would not benefit nestlings to beg for long periods after the call. When there is no call, the relationship between the sounds of adult arrival and feed time is longer and more variable, so it might benefit nestlings to continue begging for longer.

Response to the feed call with nestling hunger and size

Small nestlings did not elevate their begging rate in response to the feed call more than large nestlings. Similarly, small nestlings did not differ from large nestlings in their latency to beg, either in response to the adult or to the feed call. This implies that the feed call does not release small nestlings from any disadvantage caused by size-related differences in perceptual ability. However it is equally possible that by this point in the nestling period (ten days after hatching), the perceptual abilities of younger nestlings have caught up with their older nestmates. For instance, this is around the time that both large and small nestlings will have their eyes fully open for the first time (pers. obs). It is certainly likely that earlier in the nestling period differences in nestling perceptual ability within nests will have consequences for size-related nestling begging strategies, and at this point the feed call may be more influential. For instance, Khayutin (1985) shows that great tit, *Parus major*, nestlings open their eyes gradually between six and ten days after hatching and the visual stimulus of the parent entering the nest box is effective in eliciting begging only between eight and twelve days after hatching. Clearly there will be a point at which more developed nestlings are able to respond to visual stimuli while their younger siblings must rely on hearing alone.

Both hungry and satiated nestlings responded quickly to the feed call. Normally, without the feed call, latency to beg is influenced by nestling motivation, with hungry nestlings responding quicker than satiated nestlings. However, the feed call removes this difference, with all nestlings responding quickly. There are several possible reasons for this effect. First, nestling motivation may change how nestlings respond according to the reliability of the stimulus. Hungry, more motivated nestlings are willing to respond to less reliable stimuli (see false alarm section below) and thus they respond rapidly to the sound of the parent arriving at the nest box, which could be easily confused with background noise. The parent arriving at the nest cup is a much more reliable visual signal. Provisioning parents land at the nest box entrance and take on average 1.31 seconds (SD = 1.53, N = 708) from arrival to appearing actually in the nest cup ready to feed offspring. If less motivated nestlings are responding to seeing the parent at the nest rather than the sound of the parent landing on the nest box, this could explain their slower response time. Alternatively, less motivated nestlings could be more responsive to the begging of nestmates, which again may represent a more reliable stimulus, especially for those nestlings further from the nest entrance. Second, in order to respond swiftly, nestlings may have to remain alert between feeds which may be metabolically costly, which has been termed the cost of vigilance (Roulin 2000). Hungry nestlings may be more willing to pay this cost if the chances of being fed on the next feed are increased, and thus they respond quicker than less motivated siblings. The intensity and reliability of the feed call would remove the influence of vigilance on the speed of the begging response.

Nestling begging and false alarms

False alarms account for a significant proportion of each nestling's overall begging costs. Twenty six percent of all begging bouts are due to false alarms, which is comparable to that found in tree swallows at a similar age, (30% of all begging bouts, Leonard & Horn 2001c) but notably more than found in both southern grey shrikes, *Lanius meridionalis* (around 10% of all begging bouts at 10 days old, Budden & Wright 2001) and in black-capped chickadees (an average of 11% of all begging bouts at 6 and 12 days old, Clemmons 1995a). Interspecific differences in the costs of begging may account for nonconformity in the frequency of false alarms, for instance, as suggested by Budden & Wright (2001), predation risk, potentially increased by begging vocalisations, will have a stronger influence on begging strategies in open nesting species than in cavity-nesters.

Nestlings begging to a false alarm did so for a shorter period than they did to the provisioning adult and they begged at a lower postural intensity. This implies that although the false alarm stimulus elicits begging, it does not elicit as strong a response as the correct stimulus. The strategy of varying responsiveness with the strength of the stimulus will reduce nestling begging costs. Leonard *et al.* (2005) also found that tree swallow nestlings begged at lower intensities to a false alarm.

Response to false alarms with nestling hunger and size

As fewer nestlings beg to a false alarm than to the arrival of the adult, it is clear that it is possible for (at least some) nestlings to distinguish the stimulus causing the false alarm. In other words, some nestlings are either unable to distinguish false alarms or are risking responding to a less reliable stimulus. Small nestlings were not more likely to respond to false alarms, which indicates that the difference does not result from disparities in perceptual ability. Leonard *et al.* (2005) found that nestling age had no effect on the proportion of false alarms, comparing nestling begging in six and eight day-old tree swallow nestlings and Roulin (2000) also found that younger barn owl, *Tyto alba*, chicks were not more likely to be the first to beg when the adult was absent. In blue tits halfway through the nestling period, there appears to be no influence of age-related perceptual constraints on false alarms, although this may be a factor earlier in the nestling period. Instead, false alarms may occur when increased motivation causes nestlings to alter the threshold above which they respond. This corresponds with the finding that experimentally deprived nestlings had higher begging rates both in response to the adult and during false alarms. When nestlings are hungry, the gain from a feed is more important, so the increased begging cost due to mistakes is more readily traded-off against the benefit gained. This has parallels with other risk-taking behaviour, for example when animals are foraging they will expose themselves to a higher predation risk (Milinski & Heller 1978; Godin & Crossman 1994; Soto et al.

2005), and also favour more variable food rewards (Caraco et al. 1980), as their hunger increases. In support, both Leonard & Horn (2001c) and Budden & Wright (2001) find correlational evidence that hunger affects the rate of false alarms and Leonard *et al.* (2005) demonstrate this experimentally using playback of correct and irrelevant stimuli. Variation in risk sensitivity with motivational state would be a useful concept to apply to future studies of nestling begging strategies.

Competitive begging strategies and begging stimulus

How nestlings choose to beg appears to depend on an interaction between the reliability of the stimulus and nestling motivation. As pointed out by Leonard et al. (2005) this has relevance for the findings of the numerous studies of nestling begging that have used different stimuli to elicit begging. It also has implications for the study of parental investment and communication between parents and offspring (discussed further in Chapter 7). More experiments are needed, controlling nestling hunger and manipulating the begging stimulus across nestling ages to explore how the reliability of the begging stimulus affects nestling begging during the development of perceptual ability. For example, early in the nestling period, differences in perceptual ability between large and small nestlings within the same nest may have a strong effect on sibling competition and the reliability of the begging stimulus may strongly influence the outcome of this competition. This may explain why parents influence the reliability of the stimulus more, by giving more feeding calls, in the first week after hatching (Clemmons 1995a; Leonard et al. 1997). Variation in nestling begging with respect to the begging stimulus has consequences for the information transfer that is thought to occur between parents and offspring, whereby begging honestly signals offspring need to parents. It appears that while some elements of the begging signal remain constant, whether or not the parent gives a feed call (begging posture, and begging duration to a lesser extent), other elements are altered (begging rate and latency to beg). This suggests that the relationship between offspring need and the begging signal changes with the begging stimulus. As variability in some aspects of the begging signal is reduced in response to the feed call, overall begging to the feed call may be less honest.

In conclusion, this chapter has found no evidence that age-related perceptual constraints affect begging responses halfway through the nestling period in blue tits. Instead, nestling motivation in terms of immediate hunger appears to strongly influence the response to begging stimuli that vary in their reliability. Hunger causes nestlings to respond to less reliable stimuli, thus allowing them to maximise the number of correct responses, and to respond quickly which increases the chance of being fed. This strategy however, also causes them to commit more errors, as predicted by signalling theory (Koops 2004).

Chapter 5: Parental food allocation decisions by male and female parents

Introduction

Where two parents simultaneously provide parental care for their offspring, each parent should prefer the other to invest more than themselves, so that conflict arises between parents over levels of investment (Trivers 1972). Potentially there is also conflict between parents over how parental care is divided up between offspring. Each parent must decide how much to invest in individual offspring according to the costs and benefits of doing so (Clutton-Brock 1991). If these costs and benefits differ between parents, their patterns of investment in individual offspring may also differ. This is a potential area of conflict between parents, if one is biasing investment towards the non-preferred offspring of the other (Lessells 2002) or withholding investment from particular offspring and thus investing less overall (Slagsvold et al. 1994).

Why should the costs and benefits of investing in individual offspring differ between parents? Explanations for parentally biased favouritism (when the two parents invest differently in different offspring or different kinds of offspring) have centred around two themes: (1) that male and female parents may differ in the priority of current and future reproductive attempts and (2) that male and female parents may differ in the benefits they receive from investment into different offspring, (Slagsvold et al. 1994; Slagsvold 1997; Lessells 2002). Parents have to trade-off investing in current and future offspring, optimising their levels of investment in the current brood (Lessells 1991). In many species of birds, females have higher mortality rates than males, possibly due to factors outside the breeding season, for example higher over-winter mortality due to smaller body size (reviewed in Breitwisch 1989). Slagsvold *et al.* (1994; 1995) suggest that this would lead to females investing more in the current brood and being more willing than males to invest in small, low quality offspring. However, it is hard to establish the direction of causation in patterns of parental investment and survival rates (Dhondt 2001) and in many species, provisioning rates at least are relatively equal between the two parents (Ligon 1999). Aside from costs, parents may differ in the benefits that they receive from investment in individual offspring. Extra-pair offspring cause relatedness asymmetries within avian families. While mothers know that they are related to all their offspring and will benefit from investing in them, fathers risk wasting investing in offspring that they are not genetically related to (Westneat & Sherman 1993). The presence of extra-pair young may have several consequences for the division of paternal care between offspring. First, if the male can identify extra-pair young, he should choose not to invest in them. However, it is apparent that males can not do so (Keller 1997) and although it has been suggested that the proportion of extra-pair paternities may increase through the laying period and that males invest less in younger offspring as a result (Slagsvold 1997) there has been no evidence to support this theory so far (e.g. Westneat et al. 1995; Whittingham et al. 2003). Second, as the presence of extra-pair young in the nest cause males to have lower average relatedness to all offspring, this might select for males to decrease investment in low quality offspring, especially if they have high mortality rates (Lessells 2002). Although several studies have found evidence for parentally biased favouritism (see below), there has been no consensus on the reason for its occurrence. Theoretical models have been able to explain parentally biased favouritism only in the case of brood division, where each parent cares for a subset of the brood and then only if parents differ in the benefits of caring for particular types of offspring (Lessells 2002). Several authors have presented verbal hypotheses predicting that males and females should not differ in how they invest in individual offspring (Smiseth et al. 1998). Furthermore, even when parentally biased favouritism does occur, its overall result may be an equal division of resources between offspring, which may in fact be its purpose (Leonard & Horn 1996).

In altricial birds, parents respond to nestling begging signals when they bring food items to the nest, both in terms of provisioning rate and when allocating food to individual nestlings (reviewed in Kilner & Johnstone 1997). The mechanism for parentally biased favouritism may be a difference in how males and females respond to nestling begging behaviour when they are allocating food items (Kolliker et al. 1998). Kilner (2002a) showed that in canaries, *Serinus canaria*, male and female parents differ in their provisioning rules, males being more responsive to competitive aspects of begging (nestling height) while females respond to both nestling height and begging intensity. Kolliker (1998) found that, in great tits, male parents fed nestlings begging at a higher level than female parents, and Porkert & Spinka (2004) showed that male common redstarts (*Phoenicurus phoenicurus*) have a stronger preference than females for feeding nestlings close to the provisioning adult. There are additional cues, however, that parents could be using when making investment decisions. Where offspring hatch asynchronously, offspring size may be a reliable indicator of quality, as later hatched offspring are often relatively small and have lower survival rates and reproductive potential (Magrath 1990). Evidence for parentally biased favouritism in relation to offspring size has been found from studies on several species (reviews in

Slagsvold 1997; Lessells 2002). In eight of the 15 species tested, female parents were found to preferentially feed smaller nestlings, with the male parent showing this pattern in only one study (Table 1 in Lessells 2002). In the remaining six studies, neither parent showed a preference to feed smaller nestlings. In addition, several studies have also found evidence for parentally biased favouritism in relation to offspring size after fledging, and in all but one of these studies the female parent was investing more in smaller offspring (Table 1 in Lessells 2002). Parents may also respond differently to a combination of nestling size and begging behaviour. For instance, in an experiment on provisioning in crimson rosellas, *Platycercus elegans*, male parents allocated food in response to begging intensity in small but not in large chicks (although they biased provisioning towards large chicks overall), whereas females did not adjust their food allocation in response to begging intensity at all (Krebs 2001). This pattern was reversed in a second experiment where brood hunger was increased, when females responded to begging intensity in large chicks and males responded only to chick size.

This study aims to establish whether parentally biased favouritism is occurring in broods of blue tits. Slagsvold (1994) showed that during post-fledging care male blue tits are more likely to feed large offspring than females. As a result females have to provide more care for smaller fledglings. This appears to have an adverse affect on female survival post-breeding, and this sexual conflict between parents may drive females to produce broods that hatch more synchronously, thus manipulating males to provide more care to the brood (Slagsvold et al. 1994; Slagsvold et al. 1995). In the present study, the investment decisions of male and female parents are examined in the nestling period with respect to nestling begging signals and also to nestling size, which is a potential indicator of nestling quality, in order to determine whether male and female parents differ in how they invest in large and small nestlings.

Methods

General fieldwork followed the methods described in Chapter 2 and was carried out between March and June in 2003. Twenty-five pairs of breeding blue tits were used in the experimental procedure, however, due to technical problems with videotaping, data from three of these nests could not be used. One of the nests had only a single parent provisioning during the filming period.

Experimental procedure

The experimental procedure is described fully in Chapter 2; using hand feeding and periods of food deprivation to control nestling hunger across size ranks and filming parental provisioning visits for one hour to record allocation rules by both parents, when nestlings are 10 days old.

Data collection from videotapes

Both parents and nestlings were successfully identified on the screen using individual combinations of color rings and head patterns respectively. Information on nestling begging behaviour and parental allocation of food items was recorded as described in Chapter 2.

Data analysis

As parents may have been disturbed at the start of the filming period, when focal nestlings were placed back into the nest, analysis was carried out on the last 45 minutes of data only.

Parental feeding location

Parental feeding locations were analysed using circular statistics (Mardia & Jupp 2000). Feeding locations in each of the eight divisions around the circumference of the nest cup were converted to the mid-point in degrees covered by that segment (with the nest entrance taken as 0°). As data on feeding location did not follow the von Mises distribution (which may be thought of as a circular version of the normal distribution), parametric tests were not appropriate and the non-parametric Watson's two-sample U^2 test, which can be regarded as analogous to the Mann-Whitney test on linear data, was used to compare male and female feeding locations within nests. The test ranks data according to the combined data set, therefore ties in the data set were broken in favour of the null hypothesis that there was no difference between male and female feeding locations (following Mardia & Jupp 2000). Tests were carried out using the CircStat package (Agostinelli 2005) in R 2.1.1. (R Development Team, 2005).

Parental allocation rules

For those nests where both parents provisioned nestlings (N = 21) the provisioning behaviour of male and female parents was compared within nests using appropriate parametric or non-parametric paired tests. Parents may combine information from nestling begging behaviour with other cues that indicate nestling quality and need, such as nestling size and position in the nest relative to the provisioning adult. A model was created to examine how parents integrate different cues, with the following explanatory factors assessed for their ability to predict the allocation of food items to individual nestlings; nestling begging posture (used to represent begging intensity, as separate measures of begging behaviour are usually correlated, e.g. begging posture and latency to beg: Spearman's correlation coefficient = -0.454, $P < 0.001$, $N = 3278$), nestling position (which is only weakly correlated with nestling begging behaviour, e.g. correlation for nestling position and begging posture: Spearman's correlation coefficient = 0.058, $P < 0.001$, $N = 6342$), nestling size and the sex of the provisioning adult. A multilevel model (Goldstein 2003) with binomial errors and a logit link was used to retain information from individual feeds while guarding against pseudoreplication due to multiple observations occurring for each individual nestling. Therefore, the model was structured to contain random effects from both the nest and the particular feed from which observations on individual nestlings originated. The dependent variable was whether each individual nestling was fed at a particular feeding event (0/1) to identify nestlings that received (1) or did not receive (0) food during a provisioning event. Only the first nestling to be offered a food item was considered to be allocated food by the adult, whether or not the adult then went on to give the food item to another nestling. The model considered all two and three-way interactions between explanatory variables. Explanatory variables were assessed for significance when they were the last terms in the model, within three-way, two-way and main effects, to control for any influence of the order of terms. Non-significant terms were removed from the final model. Mixed models were created in S-plus 7.0.6 and all other tests carried out using SPSS 11.5.

Results

Parental feeding positions

Parents usually chose to feed between 45-90 degrees from the entrance hole (Figure 5.1) either moving to the right or to the left of the hole (17 individuals consistently going to the right and 26 going to the left). This pattern held for both male and female parents (Rayleigh test of uniformity: Females, $r = 0.96$, $N = 22$, $P < 0.001$. Males, $r = 0.97$, $N = 21$, $P < 0.001$). Males and females did not differ in their feeding locations across nests (Figure 5.2). However, the feeding locations of the two parents did differ within 52.4% of nests (11 of 21 nests: Watson U^2 test, in all $P < 0.05$). Where there was a significant difference between the positions of parents, this was either because they fed from different sides of the nest ($n = 6$ nests, mean angular distance between parents = 137.8°, ± SD = 13.1°) or because, although on the same side, the female fed from further back in the nest than the male ($n = 5$ nests, mean angular distance between parents = 25.5°, ± SD = 12.9°, Figure 5.3(a) nests 1-5). In three nests the male and female parent consistently fed from the same location (Figure 5.3(a)). Where parents fed from opposite sides of the nest there was no consistent trend for either parent to feed from further back in the nest (Figure 5.3(b)).

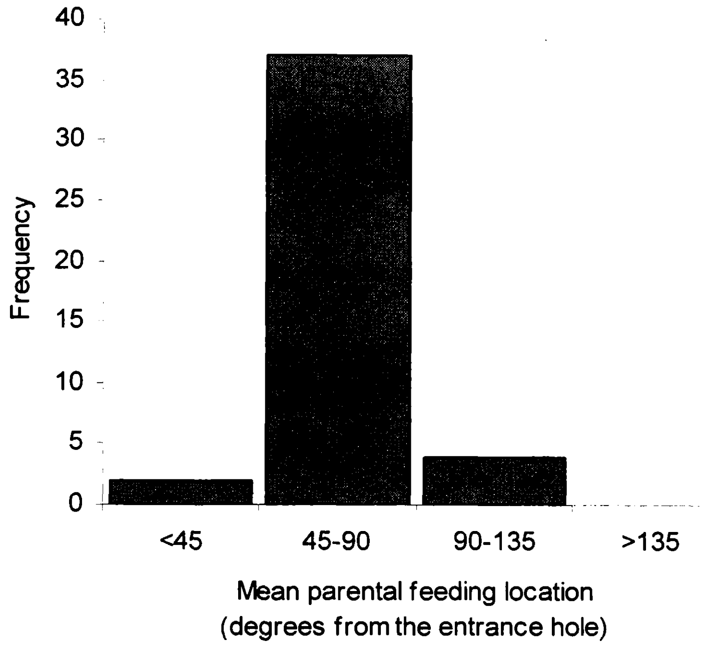


Figure 5.1. The frequencies of parental feeding location falling within each 45-degree section between 0 and 180 degrees from the entrance hole.

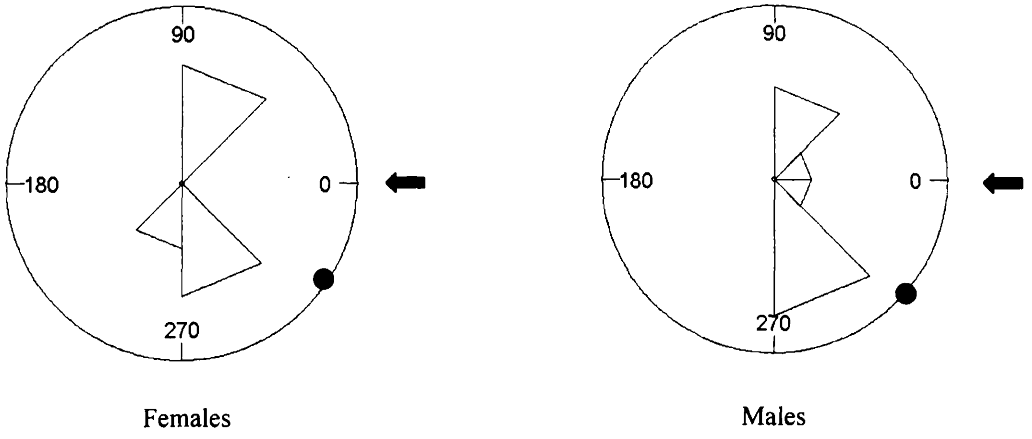
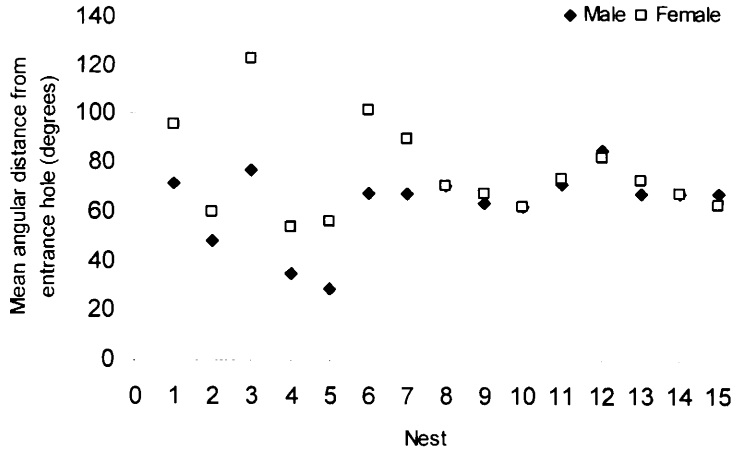
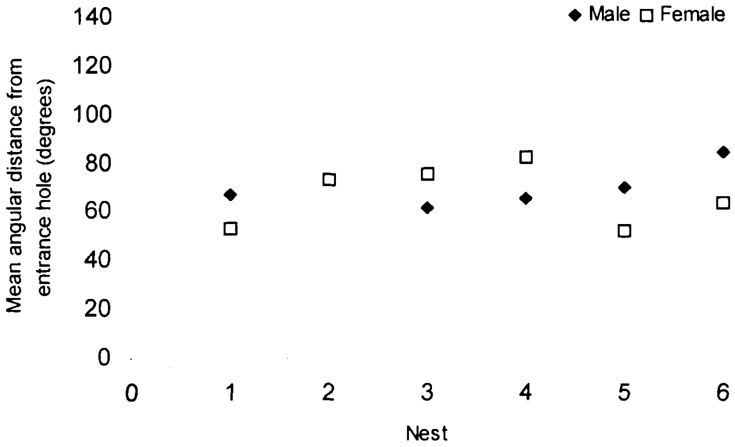


Figure 5.2. The feeding locations of female and male parents at the nest. Bars inside the circles represent histograms of the circular distribution of feeding locations around the nestcup; data are the mean feeding locations of each parent (in degrees). Filled circles represent the mean feeding location across nests. The entrance hole is indicated with an arrow.



(a)



(b)

Figure 5.3. The mean angular distance of male and female parents from the entrance hole in nests where (a) the parents feed on the same side of the nest cup and (b) parents feed from opposite sides of the nest cup.

Within individuals of both sexes there was little variation in feeding location, shown by the strong preference parents had for feeding from a fixed position at the nest (on average parents fed from their most frequently used position in 85.7% of feeds, Figure 5.4). Out of 43 parents, 10 used only a single position. Where parents used more than one position, their second-most preferred position was usually adjacent to the preferred position (32 individuals had an adjacent second position, while only 1 did not). Parental feeding locations appear to be very predictable, at least within the time scale of the experiment. Only females used a third or fourth feeding position, suggesting that their feeding locations are less predictable than male parents, however, they were still very predictable, as an average of 80.3% of their feeds were allocated from only one position.

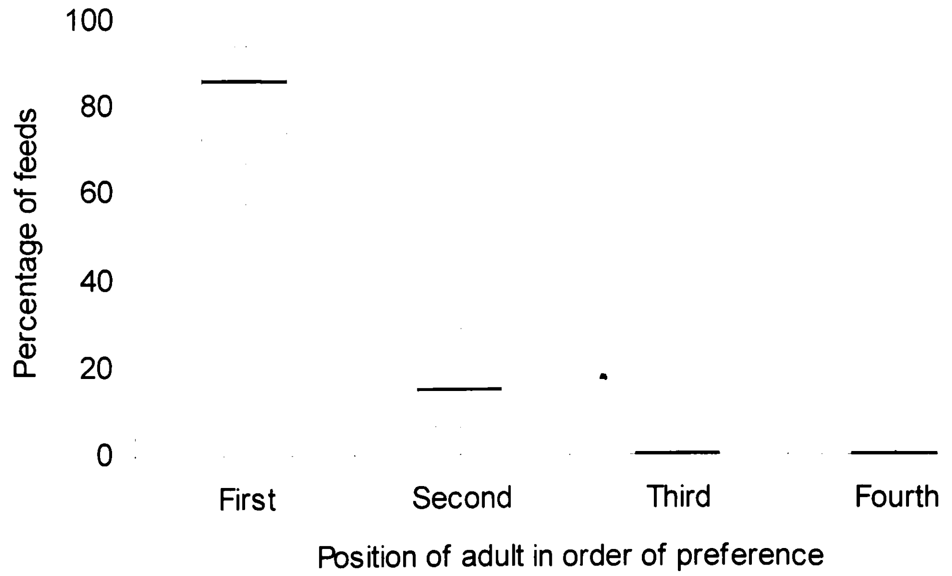


Figure 5.4. The percentage of parental feeds in the first to fourth most frequently used feeding position by each adult. Note that no adults fed from more than four different positions and that most adults fed from only two positions. In 97.0% of individuals that fed from two positions, the second most preferred position was adjacent to the most preferred position (with no more than 45 degrees between the two).

Provisioning behaviour

Parents fed at the same rate, and brought food items of similar size and type (Table 5.1). They did not differ in how long they assessed nestling begging behaviour before allocating food items, nor in how likely they were to alter their original provisioning decision and offer the same food item to another nestling (Table 5.1). Female parents spent longer in the nest during provisioning visits, due to carrying out brooding and nest maintenance activities.

Table 5.1. Parental provisioning behaviour by the male and female parent over the 45-minute observation period (mean ± SE) and statistical tests of potential differences between the parents. Tests are paired: Wilcoxon signed ranks test or paired t-test* (N = 21 nests)

Variable	*Female*	*Male*	*Test value*	*P*
Provisioning rate/nestling	2.03 (0.19)	2.05 (0.27)	t_{20} = 0.23*	0.823
Size of food item	2.07 (0.07)	2.09 (0.07)	Z = -0.22	0.825
Assessment time (seconds)	1.41 (0.21)	1.32 (0.21)	Z = -0.30	0.768
Time spent at nest (seconds)	26.63 (5.49)	8.60 (0.43)	Z = -3.46	< 0.001
Rate of altering a provisioning decision	0.23 (0.04)	0.24 (0.05)	Z = -0.21	0.835

Does nestling hunger influence food allocation?

Both parents fed deprived nestlings more than satiated nestlings (Wilcoxon signed ranks, Female: n = 22, Z = -3.74, P < 0.001, Males: n = 21, Z = -3.62, P < 0.001, Figure 5.5). However, there was a non-significant trend for deprived nestlings to gain a higher proportion of male than female feeds (t-test: t = -1.979, df = 20, P = 0.06) whereas satiated nestlings gained an equal proportion of feeds from each parent (Wilcoxon signed ranks: n = 21, Z = -0.420, P = 0.675).

Does nestling size influence food allocation?

When food deprived, large nestlings received more food than small nestlings (Wilcoxon signed ranks: n = 22, Z = -2.34, P = 0.019). Both parents appeared to feed large deprived nestlings more than small deprived nestlings (Figure 5.5). However, this trend was not statistically significant for either parent individually (Wilcoxon signed ranks, Females: n = 22, Z = -1.02, P = 0.306, Males: n = 21, Z = -1.53, P = 0.127). Furthermore, despite a trend in that direction (Figure 5.5) large deprived nestlings did not gain a significantly higher proportion of male than female feeds (Wilcoxon signed ranks: n = 21, Z = -1.53, P = 0.125).

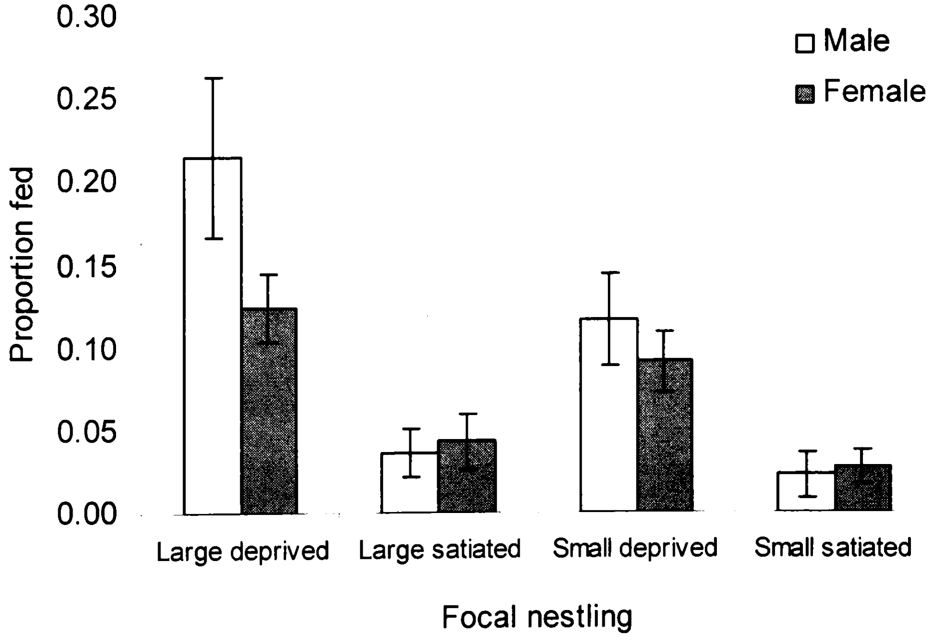


Figure 5.5. The proportion of food (mean ± SE) allocated to focal nestlings by the male and female parent.

Does nestling begging behaviour influence food allocation?

Parents fed nestlings that begged more intensely (median, range, postural begging score: fed nestlings = 3.0, 3.0-5.0, unfed nestlings = 0.0, 0.0-4.0, Wilcoxon signed ranks: n = 22, Z = -4.08, P < 0.001) and there was no difference between the parents in the begging level of fed nestlings (median begging posture, range: females = 3.0, 3.0-5.0, males = 3.5, 3.0-5.0, Wilcoxon signed ranks: n = 21, Z = 0.00, P = 1.000). Parents also fed according to nestling position in the nest, preferentially feeding those nestlings that were closest to them (distance score: fed nestlings = 2.91, 0.13, unfed nestlings = 3.75, 0.09, Wilcoxon signed ranks: n = 22, Z = -3.75, P < 0.001, Figure 5.6). The male parent had a stronger preference to feed nestlings that were close to the provisioning adult than the did female (mean distance of adult from fed nestling: male = 2.76 (0.14), female = 3.17 (0.17), paired t-test: t = -3.50, df = 20, P = 0.021, Figure 5.6).

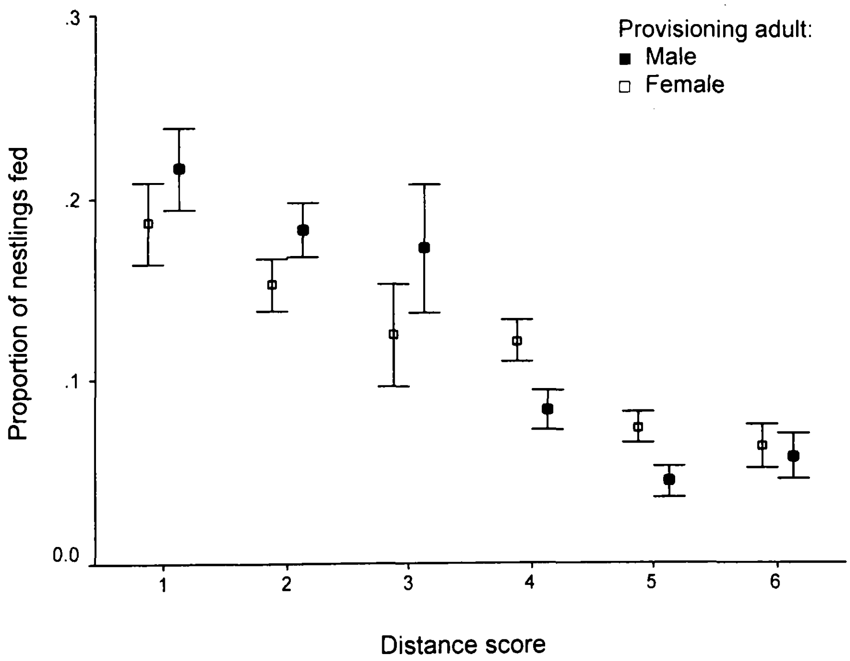


Figure 5.6. The proportion of nestlings fed (mean ± SE) by the provisioning male and female parent with distance of the nestling from the adult. As the distance score increases, nestlings are further away from the provisioning adult. Closed circles indicate the male parent and open squares the female parent.

How do parents integrate begging and non-begging cues?

Nestling begging intensity was the most important factor influencing parents in the allocation of food items to individual nestlings (Table 5.2). However, the influence of begging intensity depended on how close nestlings were to the provisioning adult (begging posture*nestling position interaction, Table 5.2). In contrast to nestlings that were close to the provisioning adult, when nestlings were further away from the adult, begging posture did not strongly influence the allocation of food (Figure 5.7). This meant that for a similar level of begging intensity a nestling begging close to the provisioning adult was more likely to receive food than one begging further away.

Table 5.2. Summary of mixed effects model examining how begging (begging posture and nestling position) and non-begging cues (nestling size) influence how the male and female parent allocate food to individual focal nestlings. The dependent variable is 'fed' (0/1) to identify nestlings which received (1) or which did not receive (0) food at each provisioning event. Each provisioning event is 'nested' within brood as a random effect and the model has binomial errors with a logit link. Explanatory variables were assessed for significance when they were the last terms in the model, within three-way, two-way and main effects, to control for any influence of the order of terms. Non-significant terms were removed from the final model.

Model term	*df*	*F*	*P*
Nestling begging posture	1,2179	549.25	<0.0001
Nestling position	1,2179	130.16	<0.0001
Parental sex	1,708	0.44	0.5061
Nestling size	1,2179	10.51	0.0012
Begging posture*nestling position	1,2173	27.22	<0.0001
Begging posture*parental sex	1,2173	0.01	0.9324
Begging posture*nestling size	1,2173	15.21	0.0001
Nestling position*parental sex	1,2173	9.27	0.0024
Nestling position*nestling size	1,2173	7.13	0.0077
Provisioning adult*nestling size	1,2173	0.15	0.7009
Begging posture*nestling position*parental sex	1,2169	0.002	0.9685
Begging posture*nestling position*nestling size	1,2169	0.85	0.3555
Nestling position*parental sex*nestling size	1,2169	6.00	0.0144
Begging posture*parental sex*nestling size	1,2169	0.07	0.7898

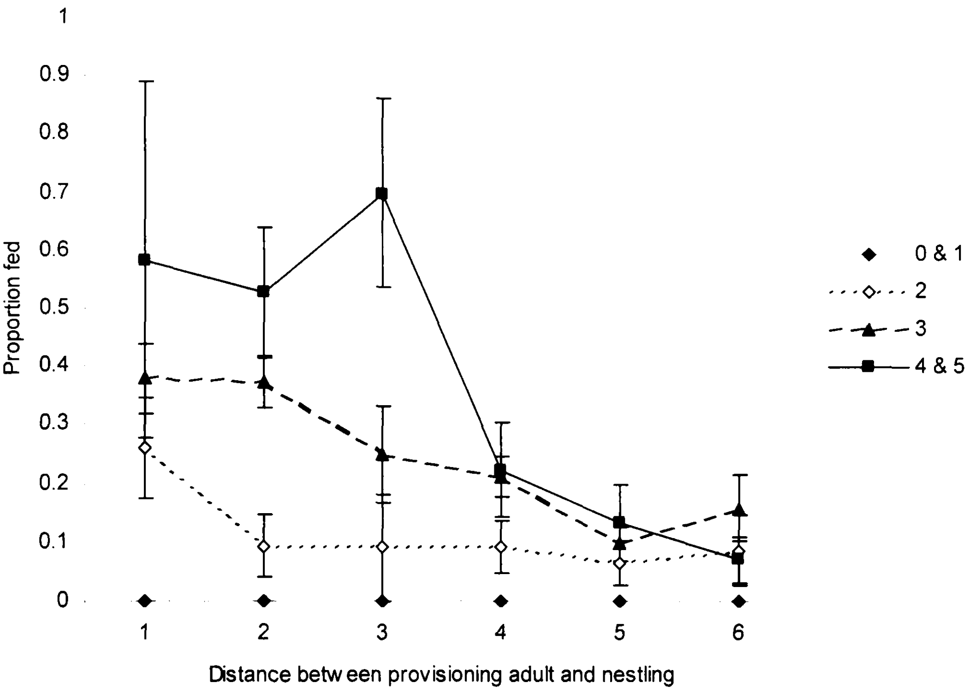


Figure 5.7. The proportion of nestlings fed (mean ± SE) at each postural begging intensity (begging categories: 0 = no begging, 1= gape open, 2 = gape open and head raised, 3 = gape open, necked fully stretched upwards, 4 = gape open and front of body raised, 5 = gape open and standing up on legs) and distance between the nestling and the provisioning adult (see methods).

Nestling size also influenced the response of parents to begging intensity (begging posture*nestling size interaction, Table 5.2). At high begging intensities small nestlings were fed considerably less than large nestlings while at low begging intensities the difference was less marked (Figure 5.8). Therefore, large nestlings gained relatively more from begging at higher intensities than small nestlings.

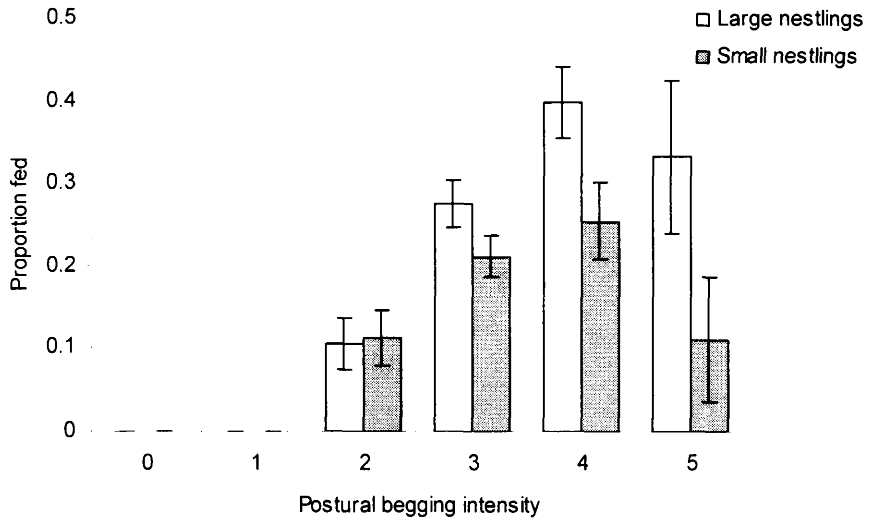
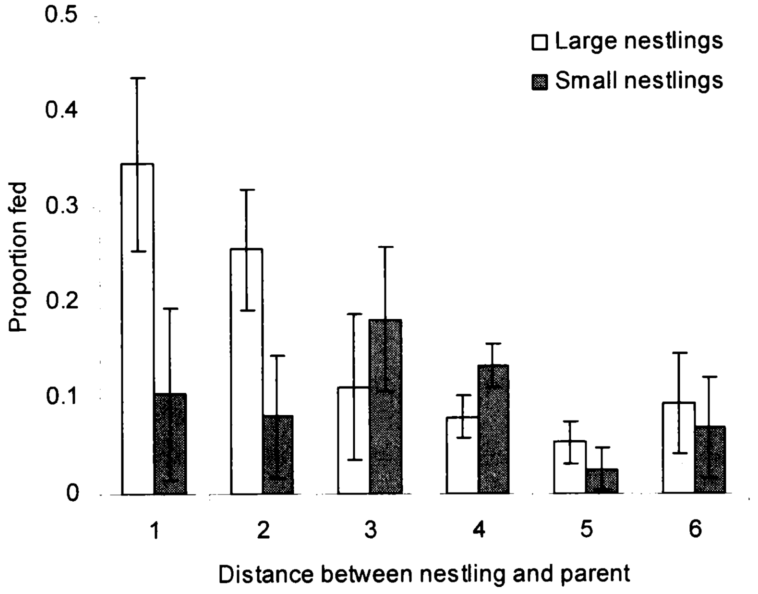
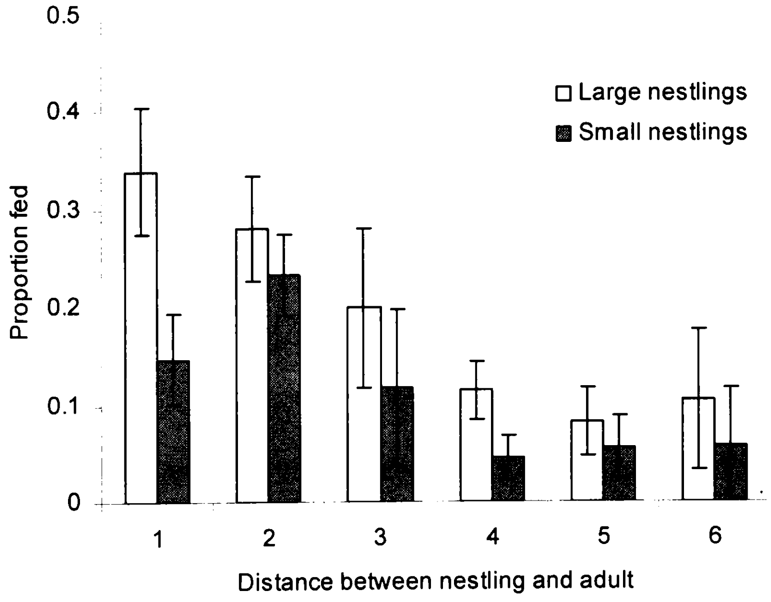


Figure 5.8. The proportion of large and small nestlings fed (mean ± SE) at each postural begging intensity (0 = no begging, 1= gape open, 2 = gape open and head raised, 3 = gape open, necked fully stretched, 4 = gape open and front of body raised, 5 = gape open and standing up on legs).

Male and female parents differed in how they responded to the combination of nestling position and nestling size (*nestling position*parental sex*nestling size* interaction, Table 5.2). Male parents allocated less food to both small and large nestlings that were further away (Figure 5.9). Female parents also allocated less food to large nestlings as they were further away, but showed a different pattern of allocation towards small nestlings (Figure 5.9). Small nestlings that were close to the adult were fed less than those at intermediate distances and at intermediate distances the female fed small nestlings more than large nestlings. As small nestlings were generally fed less than large nestlings over all other positions and over all positions by the male parent, this pattern of allocation by the female represents a distinct difference, with the response integrating both nestling size and position.



(a)



(b)

Figure 5.9. The proportion of large and small deprived focal nestlings fed (mean ± SE) and the distance between the nestling and the provisioning adult (see methods) for (a) the female parent and (b) the male parent.

Discussion

In concordance with earlier studies on other species (e.g. Teather 1992; e.g. Kilner 1995; Leonard & Horn 1996), in blue tits, provisioning parents fed individual nestlings in relation to their begging behaviour. Nestlings that begged more intensely, and which were positioned closer to the parent, were most likely to be fed. Parents integrated information on nestling begging and position in the nest, so that while begging strongly influenced the allocation of food, this response decreased as nestlings were further from the provisioning adult. As both nestling begging behaviour and position in the nest relate to nestling hunger (Chapter 3), this response by parents resulted in them allocating more food to hungry nestlings. Almost all studies on other species have shown that nestling proximity influences the probability that a nestling is fed (Bengtsson & Ryden 1983; Gottlander 1987; Smith & Montgomerie 1991; but see Teather 1992; McRae et al. 1993; Leonard et al. 1994; Kacelnik et al. 1995; Kilner 1995; Leonard & Horn 1996; Whittingham et al. 2003; Porkert & Spinka 2004). That parents integrate proximity with begging cues, i.e. the intensity of the postural display, has also been shown in experiments on canaries, *Serinus canaria,* where nestling position was controlled in the nest cup (Kilner 1995).

Does nestling size influence food allocation?

Large nestlings obtained more food from parents than small nestlings, despite there being no difference in begging intensity with nestling size (Chapter 3). There is a general consensus that begging efficiency is greater for the largest nestlings in a brood (Lotem 1998; Cotton et al. 1999; Smiseth & Amundsen 2002), for instance they can obtain positions close to provisioning adults where they are more likely to be fed (Bengtsson & Ryden 1983; Kilner 1995; Leonard & Horn 1996). Ostreiher (1997) showed experimentally that older Arabian babbler, *Turdoides squamiceps*, nestlings obtained more food through being positioned closer to the provisioning adult. When this advantage was eliminated by restricting nestling movement in the nest, food was distributed equally. Similarly in tree swallows, *Tachycineta bicolor*, large nestlings obtained more food through begging first and obtaining positions closer to the nest entrance (but see Leonard & Horn 1996 for evidence showing equal investment in large and small offspring in the same species; Whittingham et al. 2003). In blue tits, large nestlings were certainly closer to the male parent than small nestlings but the same pattern did not apply to the female parent (Chapter 3). The success of large nestlings may therefore be partly due to the outcome of sibling competition for positions near to the adult, however it also depended on them being much more effective than small nestlings at eliciting food at higher begging intensities. The begging level of an individual nestling will often reflect the general begging level of the whole brood, as provisioning rate to the nest affects the hunger level of the whole brood in the long term. Studies often find that there is a large amount of variation between broods in a study population in the average begging intensity of each brood, probably due to the long-term need of the brood and the amount of sibling competition (Redondo & Castro 1992b; Christe et al. 1996; Leonard & Horn 1998; Leonard et al. 2000; Neuenschwander et al. 2003). Thus, when one nestling is begging at high intensities it is likely that broodmates will also be doing so as well, so that competition for food is increased. Under these conditions small nestlings are most likely to be outcompeted by their larger nestmates who can stretch higher and get closer to the provisioning adult. Teather (1992) showed that large nestlings out compete smaller nestlings in red-winged blackbird, *Agelaius phoeniceus*, broods due to reaching higher in the nest regardless of proximity to the parent.

Do parents differ in how they allocate food?

Male and female parents responded similarly to begging intensity, allocating more food to nestlings begging at higher intensities, but they differed in how they responded to non-begging cues. By feeding nestlings that are further away, female parents may be ensuring that allocation patterns are more egalitarian, while the male parent, with a stronger preference based on nestling proximity, allows sibling competition to wholly dictate his investment. This result concurs with that found in several other studies comparing male and female allocation rules. Porkert & Spinka (2004) found that male common redstart, *Phoenicurus phoenicurus*, parents had a stronger preference for feeding nestlings that are in the front positions in the nest than did the female parent. In a study on parental allocation rules in tree swallows, Whittingham & Dunn (2003) also found that males had a stronger preference than females to feed the nestling that was closest to the entrance of the nest.

Parents appeared to respond in the same general way to nestling size, however their responses differed in a complex way that related to both nestling size and position in the nest. Male parents followed the general rule of feeding nestlings less as they get further away, regardless of nestling size. Females, however, preferentially fed smaller nestlings when they were at intermediate distances from the parent. This difference in how the female allocated food with respect to nestling size may ensure that sibling competition does not eliminate feeds to the most needy offspring; those that can not obtain positions close to the provisioning adult.

Despite these differences in parental allocation rules, however, there was no evidence for differential investment by the male and female in individual nestlings over the observation period. There may be several reasons for this. First, as part of the experimental treatment all focal nestlings were satiated prior to the treatment hour. This meant that at the end of the experimental treatment the hunger level of deprived nestlings could be relatively low compared to that found under natural conditions in some of the more hungry broods (for example in broods occurring late in the breeding season when food availability is low). Thus, despite the difference between sexes in their allocation rules, focal nestlings were not fed at high rates compared to the rest of the brood, which might explain why no overall difference in investment between the sexes was observed. Second, when breeding conditions are poor, or late in the breeding season, when hatching asynchrony increases, size differences between siblings will be larger and under these conditions the allocation rules of females might become more significant, leading them to invest more than the male parent in small offspring.

Why do the male and female parents differ in their allocation rules? If these rules led to the female parent investing more than the male in small offspring this might be due to conflict between parents over levels of investment in different types of offspring. Small nestlings may be more valuable to the female parent because (1) lower annual survival rates cause females to value the current reproductive attempt more than males and/or (2) small nestlings are more likely to be extra-pair offspring (but it is not yet known if this is true) or the presence of extra-pair offspring make offspring less valuable to the male and thus he is less interested than the female in investing in low quality offspring (reviewed in Lessells 2002). A previous study on this population of blue tits has shown that extra-pair young occur in 39.8% of broods, accordingly, males in this population will often find themselves providing parental care for nestlings that they are not related to. Alternatively, these differences in provisioning rules might lead to parents optimising investment in each individual offspring in the face of sibling competition. Parents are constrained when making allocation decisions, by high provisioning rates, which means that they must make the assessment of nestling need as efficient as possible. Under these circumstances, it may be possible for competitive offspring to dominate positions close to the provisioning adult, especially where the two adults feed from the same location, which occurred in around half of the blue tit nests in this study. If the parents differ in their allocation rules, it would enable them to each feed a different subset of the brood, thus ensuring that all nestlings get fed (Kolliker et al. 1998; Kilner 2002a). This would not explain however, why parents do not feed from separate locations in all nests.

Do parents or offspring control food allocation?

As both parents fed from fixed positions in the nest and used allocation rules that depended on nestling position, the allocation of food was strongly influenced by interactions between nestlings over positioning in the nest relative to the provisioning adult. Presumably as a consequence of this, the largest nestlings were able to obtain more food from parents without begging more intensely. However, as nestling position was partly influenced by nestling hunger, parents may be actively responding to this cue of nestling need. The complexity of female allocation rules suggests a degree of control over investment in different types of offspring, whereas the male parent appears to respond more passively to offspring demand, and this difference in itself suggests that parents may often choose to respond passively to sibling competition, because this represents the best investment strategy (Kilner 2002a).

Chapter 6: Food availability and parental allocation rules

Introduction

As in many bird species, the breeding season of blue tits, *Cyanistes caeruleus*, is timed to coincide with the peak in food availability that occurs in the spring. However, in a normal breeding season, many breeding pairs will fall either side of this peak and then the availability of food suitable for provisioning nestlings becomes a limiting factor on parental reproductive success. In addition, both the quality of food items available in the environment and their diversity will vary with time. Nestlings have different nutritional requirements as they grow, which is reflected in the types of prey items given to them by provisioning adults, as well as the overall amount of food brought to the nest (Gibb & Betts 1963; Banbura et al. 1999). Periods of bad weather can also restrict parental foraging success, with consequences for nestling growth (Keller & Vannoordwijk 1994). In addition to these extrinsic factors, parental trade-offs between reproductive effort and survival can also limit food supply to the brood (Lessells 1991). Parents may compensate for poor breeding conditions by increasing foraging effort (Stauss et al. 2005; Tremblay et al. 2005), but in doing so are likely to incur higher post-breeding mortality rates (Nur 1984b; Nur 1988). As studies on other species have shown, at the level of the individual, environmental conditions will interact with parental decision making to dictate reproductive effort at each breeding attempt (e.g. Erikstad et al. 1998; e.g. Festa-Bianchet & Jorgenson 1998). As a result of these constraints, in many species there can be periods of food limitation when offspring are not receiving the diet that would allow them to grow optimally. Thus, experiments that increase the food available to provisioning parents report increases in offspring growth and/or survival (e.g. Magrath 1989; e.g. Simons & Martin 1990;

Richner 1992). In addition to influencing offspring survival, conditions during growth can also influence offspring subsequent lifetime reproductive success (Lindstrom 1999; Metcalfe & Monaghan 2001).

While periods of food limitation in altricial birds act on the whole brood through the parents' provisioning behaviour, the detrimental effects of such periods may not be equally shared out amongst nestlings within the brood. Hatching asynchrony and subsequent competitive asymmetries appear to ensure that poor environmental conditions have a differential effect on offspring within the brood (Mock & Forbes 1995). Typically, the growth and survival of smaller nestlings is more strongly affected by environmental conditions and provisioning effort than that of their larger siblings (Magrath 1989; Magrath 1990). This can occur to the extent that while small fluctuations in food availability may leave most of the brood largely unaffected, the diet of less competitive siblings reflects these conditions perfectly, as shown by recent work on red-winged blackbirds, *Agelaius phoeniceus* (Forbes et al. 1997; Forbes & Glassey 2000).

Linking food availability to parental investment within broods

In some species of bird, for example great white egrets, *Egretta alba*, competition for food amongst siblings involves direct fighting over food items and can even result in aggression outside feeding bouts and in siblicide (Mock & Parker 1997). More commonly in passerine species, nestlings compete by performing begging behaviour directed at the provisioning adult and it is this that protects dominant offspring from fluctuations in food availability. Larger siblings may be superior competitors mainly because some of the cues parents use when allocating food are related to offspring size. For example, parents may preferentially feed nestlings that are reaching highest in the nest when begging (Leonard & Horn 1996), which larger nestlings may find easier to achieve (Kilner & Johnstone 1997). Similarly, parents often feed the nestlings that are closest to them (Bengtsson & Ryden 1983; McRae et al. 1993; Kilner 1995; Leonard & Horn 1996) and large nestlings are able to dominate these positions in the nest cup (Kilner 1995; Cotton et al. 1999).

When allocating food items within broods, parents either respond passively to competitive interactions between offspring (Parker et al. 2002b) or actively to information on offspring need, gained through observing nestling begging behaviour (Kilner & Johnstone 1997). In bad conditions, the best parental investment patterns may fit with responding passively to scramble competition, or parents may actively choose to invest more in offspring of high reproductive value at these times (e.g. Smiseth et al. 2003b). In good breeding conditions, however, when food availability is increased, theoretical models suggest that parents would benefit from actively increasing investment into offspring with greater need (Davis et al. 1999) and at least one empirical study supports this (Boland et al. 1997).

This chapter looks at whether food allocation rules in provisioning blue tits are affected by food availability. By experimentally altering breeding conditions through food supplementation, this study asks if parents can alter their response to nestling begging signals and non-begging cues such as size and position in the nest, which are potential indicators of nestling quality. Specifically, the study aims to determine whether parents provisioning offspring under increased food availability alter allocation patterns, in order to invest more in low quality, less competitive offspring.

Methods

General fieldwork followed the methods described in Chapter 2 and was carried out between March and June in 2004 and 2005. Each year, focal broods were randomly assigned to be either a 'food supplemented' or 'control' group, controlling for seasonal effects by alternating the groups between consecutive days. In 2004, 11 broods were supplied with supplementary food (see below), however, two of these nests failed in the early part of the nestling period. In 2005, 15 broods were supplied with supplementary food, however one brood failed early in the nestling period and the parents in one further brood did not use the food provided. In addition to taking standard nestling biometrics from control and food supplemented nests, as previously described in Chapter 2, on both day 10 and day 14 of the nestling period the length of both the left and right tarsi were measured, each three times, for every nestling in each brood. This was to provide a measure of tarsus asymmetry, which a previous study had found to be related to food availability (Grieco 2003). Bilateral traits are subject to fluctuating asymmetry, when traits are not perfectly symmetrical (van Valen 1962; Aparicio 2001), and these may be a result of environmental or genetic stress during development (Parsons 1992). In 2004, nestling biometrics were compared from 11 control and 9 food supplemented nests. In 2005, nestling biometrics were compared from 10 control and 13 food supplemented nests. Measurements for all nestling biometrics could not be blind as to whether the nest was receiving extra food.

Supplementary food

Supplementary food was provided each morning, starting from the day that the first nestlings in the brood hatched. It was not provided after day 14, as visiting the nest after this age may cause nestlings to fledge prematurely. Every morning the amount of food remaining from the previous day was measured (wet mass, to the nearest 0.1g) to provide an indication of the consumption of supplementary food items at the nest. Food items were placed on a small plastic tray (6 × 6 × 2.5 cm) inside the nest box, to prevent other birds from taking food items (following Grieco 2001b). Control nests were given empty trays. Supplementary food consisted of two sizes of live mealworm, *Tenebrio molitor* (purchased from Global live foods, UK). 'Mini' mealworms (10-15mm) were offered at supplementary nests until day seven of the nestling period, while after day seven only fully grown mealworms (20-30mm) were offered. The size of natural prey items brought to the nest increases with nestling age (Gibb & Betts 1963), presumably as younger nestlings are unable to process larger items (Banbura et al. 1999). Offering different sized supplementary food items over the nestling period should therefore allow parents to feed supplementary food items to nestlings, as they would do natural prey items. The amount of supplementary food offered followed Grieco (2001b), in giving approximately half the daily requirements of the brood according to Gibb & Betts (1963). The amount of food offered was calculated to account for brood size and nestling age. Nestling food intake is thought to increase linearly with age until half way through the nestling period at which point it remains constant (van Balen 1973). Supplementary food was supplied to follow this linear increase (as in Grieco 2001b). The mealworms were contained within the trays until consumed by adults or removed the following day (pers. obs.).

Recording parental provisioning visits

Parental nest visits were recorded with a video camera at six food supplemented nests and six control nests in 2004, and at twelve food supplemented nests in 2005. However, due to technical problems with videotaping, data from three of the nests in 2005 could not be used. Each nest was recorded for between 1 and 1.5 hours when nestlings were ten days old, following methods described in Chapter 2.

In 2004, brood sizes in four supplemented nests and five control nests were temporarily halved prior to recording, as part of a separate experiment. During recording, half the brood was placed in a nearby nest of similar age, nestlings were replaced back in their original nests immediately after recording had finished. As part of this separate experiment, broods were divided according to nestling mass, and middle-ranked nestlings were removed.

During 2005, nine food supplemented nests were recorded twice; once immediately after supplementary food had been placed in the tray, and again when supplementary food was temporarily removed (for the recording period only). The two recording periods took place on the same day with a 30 minute gap between them. The order of recording was rotated between nests so that any effect of order could be controlled.

On transcription of behaviour from the videotapes, the observer could not be blind as to whether each nest was in the supplemented or control category. Nestling begging behaviour and parental provisioning decisions were documented as described in Chapter 2. In 2004, nests were observed from a hide, and recording began when parents were observed to be provisioning normally again after the initial disturbance of setting up the cameras at the nest. This meant that details of the provisioning behaviour of parents for the full observation period could be used in data analysis. In 2005, the hide was not used and the first 20 minutes of data were discarded from the transcription from the videotapes. Due to time constraints on transcription, only the first 15 feeds were transcribed from videotapes in 2005.

Observations of fledging dates and fledging success

In 2005, focal nests were visited once daily from day 14 after hatching, to measure fledging date. Nests were observed from a distance, to ascertain whether parents were still provisioning nestlings. In both 2004 and 2005 the nest was visited after each brood had fledged, and fledging success was recorded as the number of nestlings fledged.

Data analysis

Food supplementation and nestling growth

The effect of food supplementation on nestling growth was tested using doubly multivariate repeated measures ANOVA on nestling body mass, gape width, tarsus length and tarsus asymmetry, measured at 10 and 14 days after the hatching of the first nestling in the brood. Food supplementation and year of measurement were the between subject effects of interest in the ANOVA, while brood size and hatch date (difference, in days, from the median hatch date for the breeding population) were treated as covariates in the analyses. First, the effect of food supplementation on variation in nestling growth between broods was tested using brood means for each of the measures. Tarsus asymmetry was calculated for each nestling, at day 10 and 14, by taking the average of the three measurements for each tarsi and then taking the unsigned difference between the average for the left and right side, (following Grieco 2003). Second, the effect of food supplementation on within-brood variation in nestling body mass was tested, by calculating the difference in mass between the largest and smallest nestling in each nest and expressing this variable as a proportion of the mass of the largest nestling in the brood (to allow for differences between broods in mass). Proportional within-brood variation in nestling body mass was arcsine transformed. All other dependent variables were normally distributed, thus meeting the assumption for the repeated measures ANOVA.

Food supplementation and parental allocation rules

A model was created to examine how parents respond to nestling begging behaviour under food supplemented and control conditions, with the following explanatory factors assessed for their ability to predict the allocation of food items to individual nestlings; nestling begging posture (used to represent begging intensity, as separate measures of begging behaviour are usually correlated, e.g. begging posture and latency to beg: Spearman's correlation coefficient = -0.454, $P < 0.001$, $N = 3278$)

and nestling position (which is not strongly correlated with nestling begging behaviour, e.g. correlation for nestling position and begging posture: Spearman's correlation coefficient = 0.058, $P < 0.001$, $N = 6342$) and the interactions between these begging behaviours and whether nests received food supplementation. A multilevel model (Goldstein 2003) with binomial errors and a logit link was used to retain information from individual feeds while guarding against pseudoreplication due to multiple observations occurring for each individual nestling. Therefore, the model was structured to contain random effects from both the nest and the particular feed from which observations on individual nestlings originated. The dependant variable was whether each individual nestling was fed at a particular feeding event (0/1) to identify nestlings that received (1) or did not receive (0) food during a provisioning event. Only the first nestling to be offered a food item was considered to be allocated food by the adult. The model considered all two and three-way interactions between explanatory variables. Explanatory variables were assessed for significance when they were the last terms in the model, within three-way, two-way and main effects, to control for any influence of the order of terms. Non-significant terms were removed from the final model.

Food supplementation and parental allocation according to nestling mass

Food supplemented and control nests from 2004 were examined for the effect of nestling size on how much food each nestling obtained during the observation period. Nestling mass was related to the competitive ranking of the nestling within each nest by dividing the weight of the nestling by the mean weight of the nestlings in the brood; giving the variable 'relative weight' (following Boland et al. 1997). For each nestling the number of feeds obtained per hour (square root transformed) was the dependent variable in a mixed model with nestling relative mass, food supplementation, brood size and hatch date (in days from the 1st of April) and all interactions as explanatory terms. Nest was entered as a random effect in the model. Three-way interactions between terms were examined but were not significant in any model. Model terms were fitted by examining the significance of each term when they were the last term in the model within main effects and interactions. Final models contained only significant factors.

Post-hoc power analysis (Cohen 1977) was conducted on non-significant results. Minimum detectable differences were calculated, at a power of 0.8, for the main questions addressed in non-significant t-tests, given the sample sizes and sample variances obtained. Mixed models were performed using PROC MIXED in SAS 9.1 (food supplementation and allocation with nestling mass) or S-plus 7.0.6 (parental allocation rules) and repeated measures ANOVA, together with all other tests, were carried out using SPSS 11.5.

Results

Consumption of supplementary food items

In all supplemented nests bar one (in 2005), a proportion of the food items were consumed, but in no nests was this consumption total over the whole of the nestling period. Use of supplemented food items by parents, over the whole nestling period, ranged from 70.3% of that offered to 99.2% (mean over all nests in both years = 86.6%). Consumption of supplementary food increased over the nestling period (Figure 6.1, Spearman rank correlation: $r_s = +0.502$, $n = 22$ nests, $P<0.001$). This agrees with the findings of a large-scale supplementation experiment, also on blue tits (Grieco 2001b), where consumption, measured by observation, increased with nestling age but not with brood size.

Parents carried out four different behaviours involving supplementary food items; (1) They fed nestlings directly from the supplementary food, (2) They took a mealworm from the supplementary food, flew out of the nest, perched near to the nest box and appeared to 'prepare' the food item by removing the head and then went back to the nest to feed the item to the nestlings, (3) Parents left the nest box with a supplementary item and returned later with a natural food item, in which case they were presumed to have eaten the item themselves, or (4) Parents consumed supplementary items themselves inside the nest box (pers. obs.).

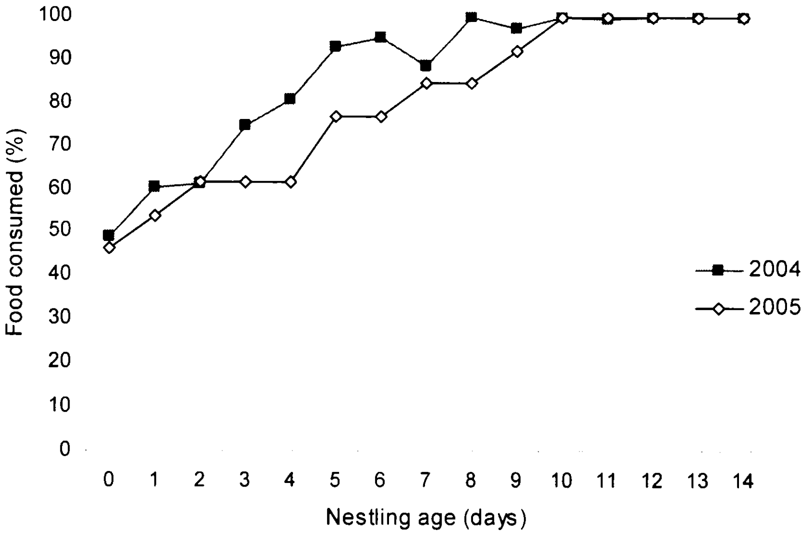


Figure 6.1. The percentage of supplementary food utilised by parents (consumed or fed to nestlings) with nestling age in 2004 (N = 11 broods) and 2005 (N = 13 broods).

Food supplementation and nestling growth

Nestling body mass was greater in food supplemented broods than in control broods at both 10 and 14 days after hatching (Repeated-measures ANOVA, $F_{1,33} = 6.929$, $P = 0.013$, Figure 6.2). The year of breeding also influenced nestling body mass, although only at 14 days after hatching (Repeated-measures ANOVA, interaction between year and nestling age: $F_{4,30} = 5.791$, $P = 0.001$, separate ANOVA at 14 days after hatching: $F_{1,39} = 14.976$, $P < 0.001$). At 14 days after hatching, nestlings were heavier in 2004 than in 2005 (Figure 6.3). Neither nestling gape width, nor nestling tarsus length, was influenced by food supplementation (Repeated-measures ANOVA, gape width: $F_{1,33} = 0.494$, $P = 0.487$, tarsus length: $F_{1,33} = 2.266$, $P = 0.142$). Both were, however, affected by the year of measurement at certain ages (Repeated-measures ANOVA interaction of nestling age and year of measurement, gape width: $F_{1,33} = 13.889$, $P = 0.001$, tarsus length: $F_{1,33} = 4.232$, $P = 0.048$). At 10 days after hatching, both nestling gape width and tarsus length were larger in 2005 than in 2004 (ANOVA, gape width: $F_{1,37} = 4.884$, $P = 0.033$, Figure 6.4, tarsus length: $F_{1,37} = 4.587$, $P = 0.039$, Figure 6.5). Tarsus asymmetry was not influenced by either food supplementation (Repeated-measures ANOVA, $F_{1,33} = 0.019$, $P = 0.893$) or the year of measurement (Repeated-measures ANOVA, $F_{1,33} = 0.916$, $P = 0.346$).

In summary, food supplementation affected nestling body mass, but not other measures of nestling development. These other measures were, however, influenced by the conditions during breeding, indicated by the effect of year on nestling mass, gape width and tarsus length. Therefore, food supplementation did not override all other environmental influences acting on the growth of offspring.

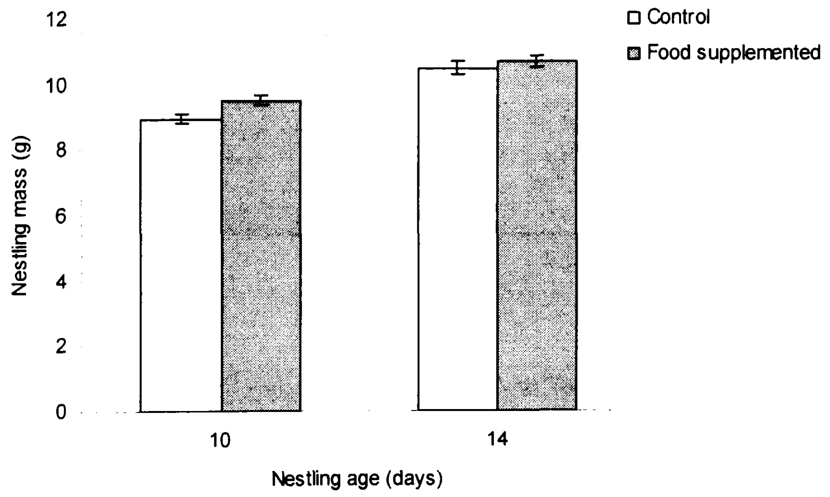


Figure 6.2. Nestling mass (mean ± SE) at 10 and 14 days after hatching for control (white bars) and food supplemented nests (shaded bars).

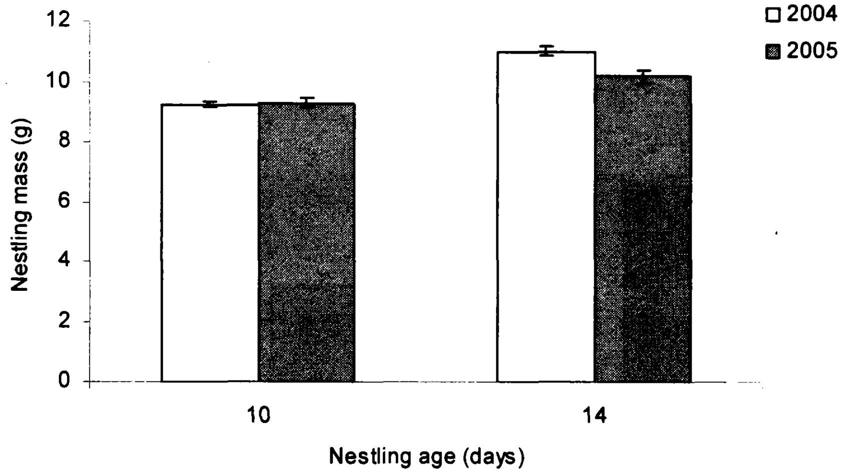


Figure 6.3. Nestling mass (mean ± SE) at 10 and 14 days after hatching in 2004 (white bars) and 2005 (shaded bars).

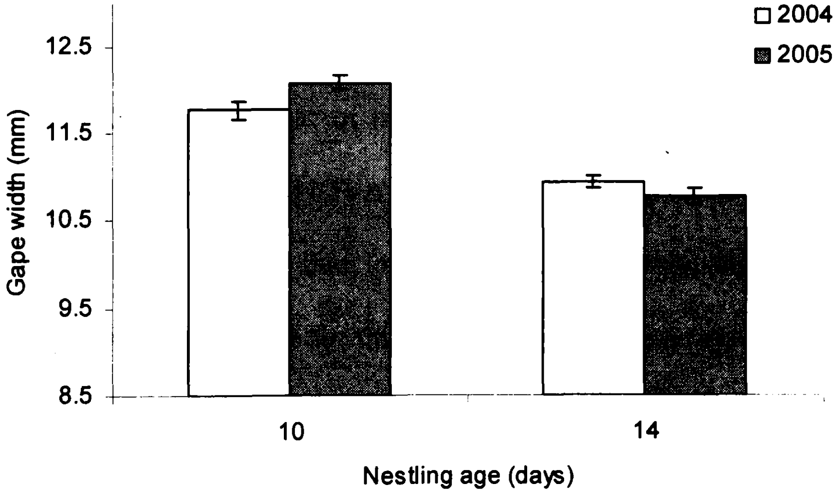


Figure 6.4. Nestling gape width (mean ± SE) at 10 and 14 days after hatching in 2004 (white bars) and 2005 (shaded bars).

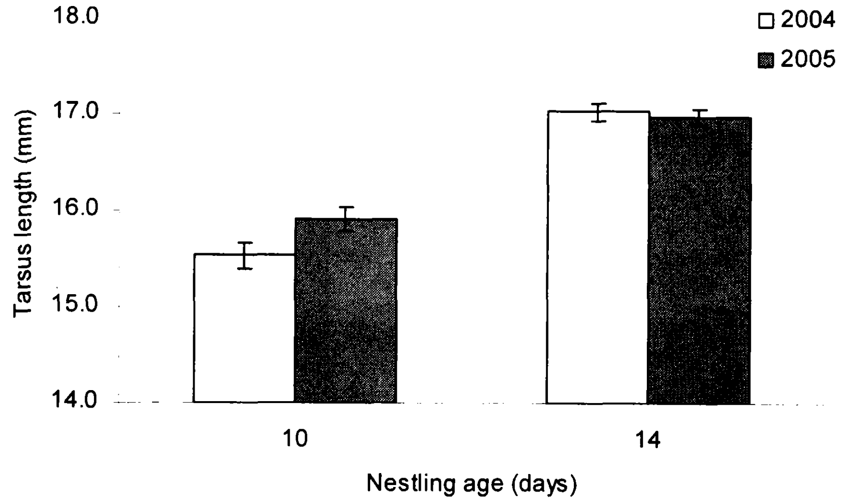


Figure 6.5. Nestling tarsus length (mean ± SE) at 10 and 14 days after hatching in 2004 (white bars) and 2005 (shaded bars).

Food supplementation did not affect within brood variation in nestling mass (repeated-measures ANOVA, $F_{1,35} = 0.110$, $P = 0.742$, Figure 6.6). There was, however, a significant effect of the year of measurement on within-brood variation in nestling mass (repeated-measures ANOVA, $F_{1,35} = 5.529$, $P = 0.024$). Within-brood variation in mass was greater in 2005 than in 2004 (Figure 6.6). Food supplementation appeared to at least partly compensate for this at day 10 (Figure 6.6 (a)), however this was not a statistically significant trend (repeated-measures ANOVA, *year*food supplementation*nestling* age interaction: $F_{1,35} = 0.740$, $P = 0.395$).

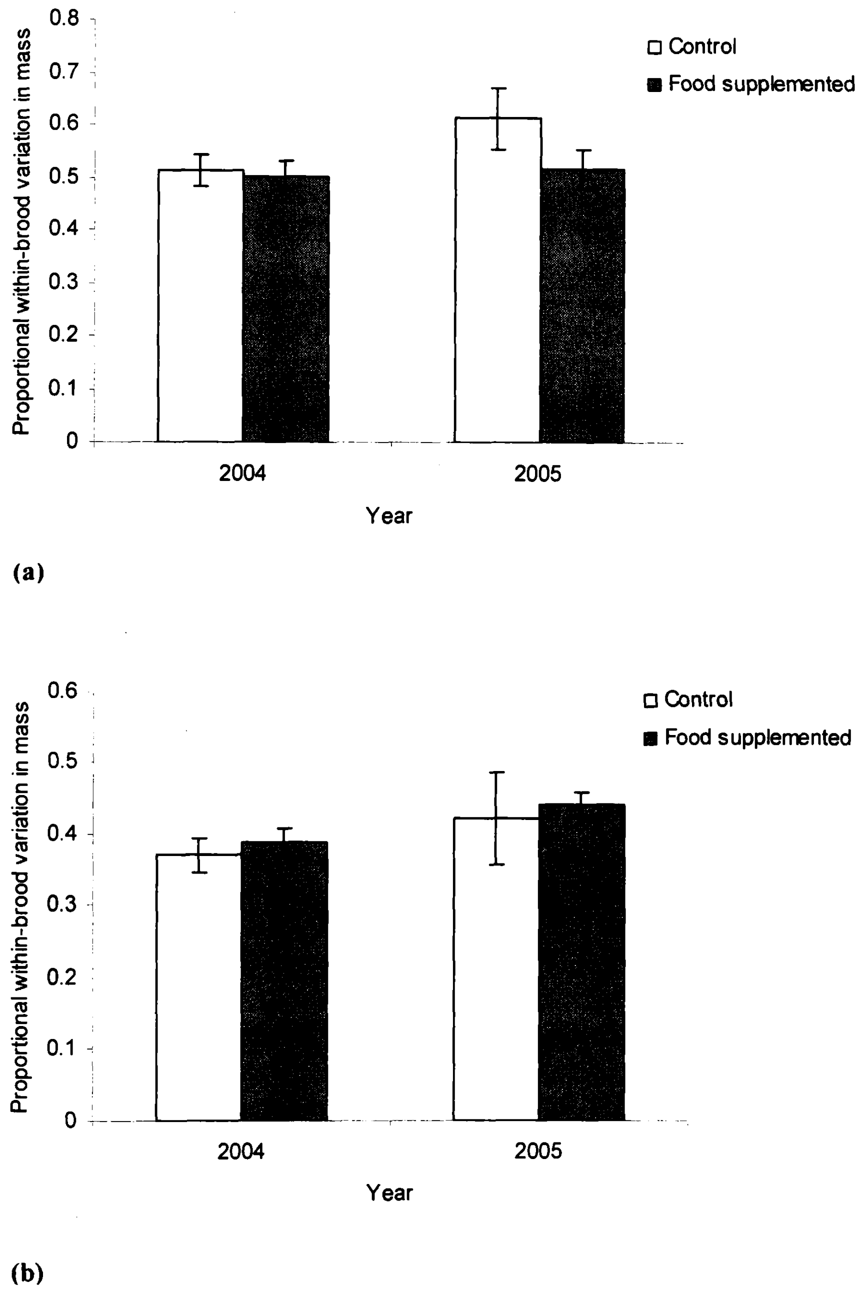


Figure 6.6. Within brood variation in nestling body mass in proportion to the mass of the largest nestling in the brood (mean ± SE) at (a) ten days after hatching and (b) fourteen days after hatching, for control (white bars) and food supplemented (shaded bars) nests during 2004 and 2005.

Fledging success and age at fledging

In 2004, there was brood reduction in three out of eleven control nests, compared to in only one out of nine food supplemented nests (Fisher's exact test: P = 0.591); in control nests fledging success ranged from 63% to 100%, while in supplemented nests it ranged from 73% to 100%. 2005 was a poor breeding year, where brood reduction was much more common than in 2004. There was brood reduction in 8 out of 10 control nests (fledging success ranged from 30% to 100%), compared to in 5 out of 13 supplemented nests (fledging success ranged from 67% to 100%), (Fisher's exact test: P = 0.090). Therefore, there was a non-significant trend for brood reduction to be more common in control nests than in food supplemented nests, especially when breeding conditions were poor.

There was a non-significant tendency for food supplemented broods to fledge at an earlier age than control broods in 2005 (t-test: t = 1.768, df = 17, P = 0.095). On average, food supplemented broods fledged a day earlier than control broods (mean fledging age in food supplemented broods = 19.42 days, SD = 1.17, n = 12 broods, mean fledging age in control broods = 20.43 days, SD = 1.27, n = 7 broods).

Food supplementation and parental allocation rules

In 2004, parents from control and food supplemented nests did not differ in how they allocated food to individual nestlings in response to nestling begging behaviour (Table 6.1). Similarly, data from 2005 showed that, within nests, parental allocation rules did not change when parents received or did not receive extra food (Table 6.2). Data from 2004 showed that when parents had access to extra food they did not change their investment with respect to nestling mass (nestling mass*food supplementation, $F_{1,71.2} = 0.43$, $P = 0.515$). These non-significant results do not appear to be due to low statistical power. The detectable effect size of these tests was small, e.g. a two sample t-test of the mean position of fed nestlings in food supplemented and control broods would give a significant result with a difference in position of 0.852 (whereas the actual average difference found was 0.175), therefore, despite small sample sizes, the results presented in Table 6.1 can be viewed with some confidence. Similarly, to give a significant result in a two sample t-test, the proportion of feeds to the smallest nestling in the brood (in 2004) would have to be 14% greater in food supplemented nests than in control nests. However, in this study, the proportion of feeds to the smallest nestling was actually, on average 6% less in food supplemented broods than in control broods. In both food supplemented and control nests, larger nestlings gained a greater number of parental feeds ($F_{1,72.5} = 4.03$, $P = 0.049$, Figure 6.7). In nests with a small brood size, there was a stronger trend for larger nestlings to be fed more than smaller nestlings, while in nests with a large brood size smaller nestlings received more food items (nestling mass*brood size, $F_{1,71.2} = 3.94$, $P = 0.047$, Figure 6.8).

Table 6.1 Mixed model examining how nestling begging behaviour (begging posture and nestling position) influenced how parents from food supplemented and control nests allocated food to individual nestlings during the 2004 breeding season. The dependent variable is 'fed' (0/1) to identify nestlings which received (1) or which did not receive (0) food at each provisioning event. Each provisioning event is 'nested' within brood as a random effect and the model has binomial errors with a logit link. Explanatory variables were assessed for significance when they were the last terms in the model, within three-way, two-way and main effects, to control for any influence of the order of terms. Non-significant terms were removed from the final model.

Model term	*df*	*F*	*P*
Begging posture	1,3373	819.00	<0.001
Nestling position	1,3373	198.45	<0.001
Food supplementation	1,10	1.79	0.2110
Begging posture*nestling position	1,3373	51.66	<0.001
Food supplementation*nestling position	1,3371	0.34	0.5588
Food supplementation*begging posture	1,3371	0.11	0.7429
Food supplementation*begging posture*nestling position	1,3370	0.54	0.4625

Table 6.2 Mixed model examining how nestling begging behaviour (begging posture and nestling position) influenced how parents allocate food to individual nestlings during the 2005 breeding season when parents either did or did not receive supplementary food. The dependent variable is 'fed' (0/1) to identify nestlings which received (1) or which did not receive (0) food at each provisioning event. Each provisioning event is 'nested' within brood as a random effect and the model has binomial errors with a logit link. Explanatory variables were assessed for significance when they were the last terms in the model, within three-way, two-way and main effects, to control for any influence of the order of terms. Non-significant terms were removed from the final model.

Model term	*df*	*F*	*P*
Begging posture	1,2050	248.99	<0.001
Nestling position	1,2050	77.13	<0.001
Food supplementation	1,2050	35.44	<0.001
Begging posture*nestling position	1,2049	1.36	0.2436
Food supplementation*nestling position	1,2047	2.31	0.1286
Food supplementation*begging posture	1,2047	0.0003	0.9860
Food supplementation*begging posture*nestling position	1,2046	0.02	0.8927

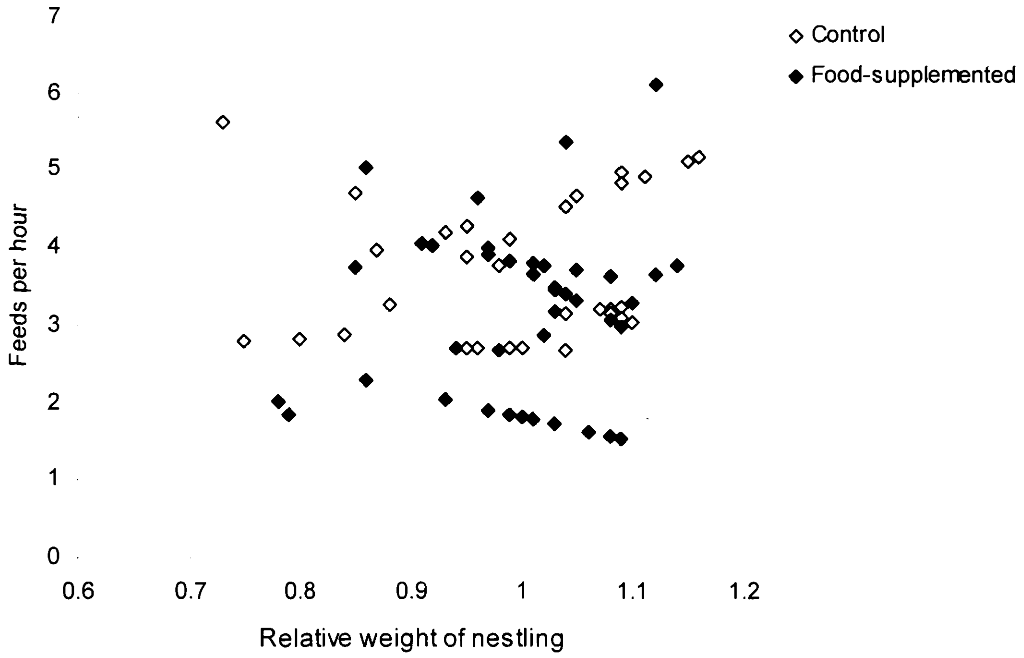
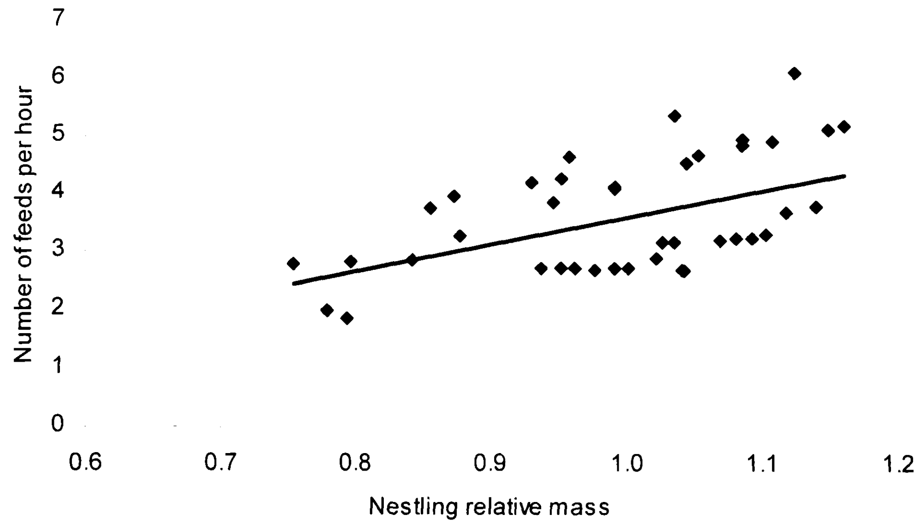
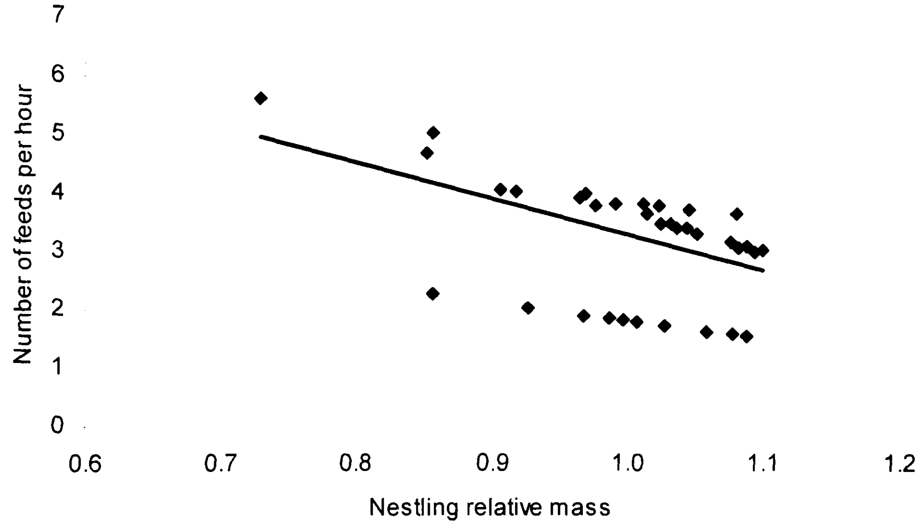


Figure 6.7. The number of parental feeds gained by nestlings per hour as a function of the relative weight of nestlings (the mass of a nestling divided by the mean mass of the brood) in control (open symbols) and food supplemented broods (closed symbols) in 2004. Each data point represents an individual nestling. The feeds gained are model estimates, back-transformed to correct for the transformation of data in the original model.

In 2004, nestlings in food supplemented broods responded to improved conditions by begging less intensely than those in control broods (Mann-Whitney test: Z = -2.242, N = 12, P = 0.025). However, despite begging at lower levels, nestlings in supplemented broods received similar amounts of food (Figure 6.9). The data from 2005 showed a similar pattern. When parents had access to supplementary food nestlings begged less intensely (Wilcoxon signed ranks test: Z = -1.956, N = 9, P = 0.050), but received similar amounts of food to when parents were not given supplementary food (Figure 6.10).



(a)



(b)

Figure 6.8. The number of feeds obtained per hour as a function of a nestling's relative mass (the mass of a nestling divided by the mean mass of the brood) in (a) broods with five to eight nestlings (small brood size) and (b) broods with nine to twelve nestlings (large brood size) in 2004. Each data point represents an individual nestling. The feeds gained are model estimates, back-transformed to correct for the transformation of data in the original model.

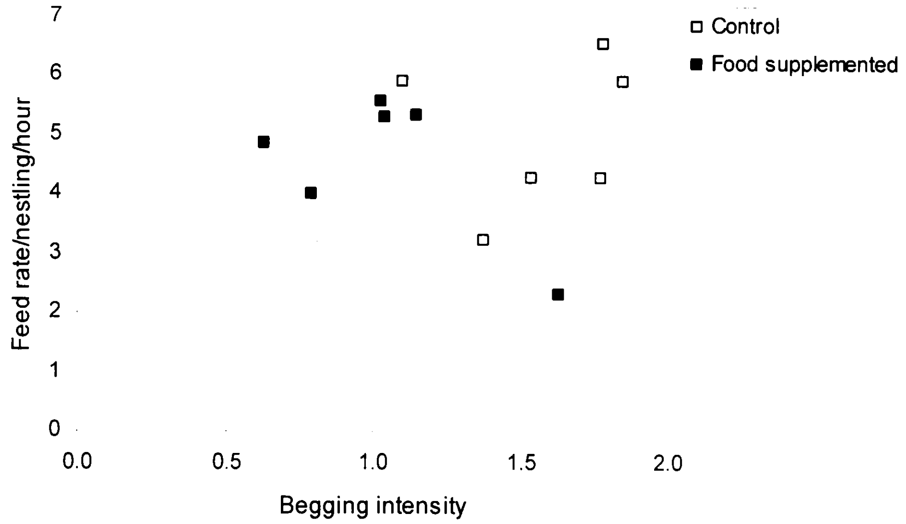


Figure 6.9. The mean begging intensity of nestlings and parental provisioning rate/nestling/hour in the control (open squares) and food supplemented (shaded squares) broods from 2004. Each data point represents the average for a brood of nestlings.

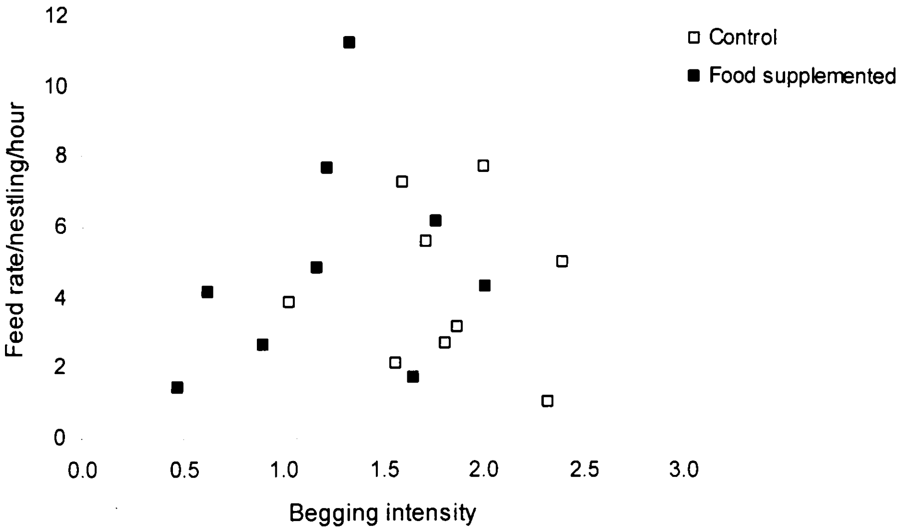


Figure 6.10. The mean begging intensity of nestlings and parental provisioning rate/nestling/hour in broods from 2005, when given supplementary food (shaded squares) and when not given supplementary food (open squares)..

Discussion

The data suggest that the food supplementation experiment was successful in creating variation in nest rearing conditions. In food supplemented nests, parents used the food provided, increasingly so as the brood reached the point where nestling growth rate was at its peak. Nestlings from food supplemented broods grew faster and reached a higher pre-fledging mass than those in control broods, suggesting that without an extra food supply parental provisioning rate is constrained. Therefore, in food supplemented broods, parents were not just replacing natural food with supplemented items of a similar value, but were supplying offspring with more food overall. Parents fed supplementary food to offspring and consumed the food themselves; both uses release them from a proportion of the energetic demands they experience during the nestling period. In supplemented broods, nestlings were heavier and begged less intensely. Thus, the experimental manipulation of parental food supply provided parents with several different cues to indicate that breeding conditions were improved. Parents, however, did not appear to respond to these cues by allocating more food to less competitive nestlings.

Grieco (2002b) also provided breeding blue tits with supplementary food and found that parents responded by provisioning nestlings with higher quality natural food items, while consuming supplementary food themselves and to a lesser extent, giving supplementary food items to nestlings. Without an extra food supply, parents may be constrained by the amount of foraging effort required to find food in the environment, either because food is time consuming to find or because parents trade-off the current foraging effort with future reproductive success, or both. When given supplementary food, parents are released from these constraints and can provide more food to offspring while expending the same, or less, foraging effort. Additionally, in the present study, the extra food supply probably buffered nestlings against periods of reduced parental provisioning effort due to environmental conditions (Keller & Vannoordwijk 1994), especially during the poor breeding season in 2005, when several days of heavy rain prevented normal foraging behaviour. In support of this, food supplementation increased nestling mass in both the good and poor breeding seasons of 2004 and 2005 respectively. Grieco (2001b) also found that providing supplementary food to provisioning parent blue tits increased the mass of nestlings, although his study differed in that while nestling mass was greater during growth in supplemented nests, nestlings did not reach a greater pre-fledging mass at day 14. This may be due to a difference in breeding conditions between the two study populations; Grieco (2001b) states that during the years of his study, fledging body mass was not limited by food availability, whereas the results of the Lancaster study suggest that it was. Conversely however, in the same population Grieco (2003) found that food supplementation decreased tarsus asymmetry, a measure of developmental precision that may indicate conditions during growth (Parsons 1992; Nilsson 1994). In the Lancaster population, food supplementation did not influence tarsus asymmetry and, suggestively, neither did the year of measurement, despite the large difference in breeding conditions between years.

There was evidence that the food supplementation in the present study did not completely ameliorate the poor breeding conditions in 2005, as brood reduction was more common in this year, even in food supplemented broods. Additionally, there was a shift in nestling growth between the years, with nestlings in 2005 having longer tarsi and larger gapes halfway through the nestling period, regardless of food supplementation. As both measures influence the success of a nestling's begging display, this may indicate that when competition between brood members was elevated in 2005, nestling development was biased in favour of structures that would increase the chances of getting fed.

Large nestlings obtained more food regardless of food supplementation and parents used allocation rules throughout that would ensure competitive offspring could bias food distribution. As a result, the difference in mass, between large and small nestlings, did not alter with food supplementation. When conditions were poor, in 2005, this difference increased, although the presence of supplementary food prevented, in some cases, mortality in the smallest nestlings. Therefore, food allocation appears to be mainly controlled by the nutritional status of the largest, most competitive nestlings in the brood. When these nestlings are satiated, smaller nestlings are allocated food. This means that in good breeding conditions all nestlings in the brood increase in mass, but smaller nestlings do not get relatively greater amounts of food and so cannot catch up with their larger nestmates. Grieco (2001b) also found that food supplementation did not decrease the gap in nestling body condition between first and last-hatched nestlings, in an experiment that also manipulated hatching asynchrony, so that in all nests last-hatched nestlings hatched three days after the first-hatched nestlings. In a four-year study on hatching asynchrony in blue tits, Slagsvold et al. (1995) found that in experimentally-created asynchronous broods, the largest nestlings in the brood were heavier than those in synchronous broods. All of these results from blue tits are consistent with those from a study on nestling growth in red-winged blackbirds (Forbes & Glassey 2000), which showed that the survival and quality of marginal offspring depends on the satiation of the core offspring in the brood. Several theoretical models have predicted this type of hierarchical pattern of food allocation (Parker et al. 1989; Forbes 1993) and it is thought to be the mechanism behind adaptive brood reduction (Forbes & Glassey 2000). The main prediction of this theory is that while food shortages affect all brood members, marginal offspring are disproportionately affected, thus promoting adaptive brood reduction in poor breeding conditions. This may also explain why, in the study presented here, there was still brood reduction in food supplemented nests. An experiment on house sparrows, *Passer domesticus*, also found that when offspring were given supplementary food, the difference in mass between the heaviest and lightest nestling was the same as in normal conditions (Mock et al. 2005). Similarly, Mondloch & Timberlake (1991) found that food availability did not have a differential effect on offspring growth within broods of pigeons, *Columba livia*. Conversely, several studies on other species have shown that size differences between nestlings are reduced when food is abundant (Graves et al. 1984; Magrath 1989; Boland et al. 1997; Forbes et al. 2002). It should be noted that in the study of Mock et al. (2005), no effect of supplementation on overall brood mass was found. Verhulst (1994) suggests that cryptic influences of supplementary feeding may produce observed effects of supplementation on offspring traits other than those measured by nestling mass and body size. For instance, Mock et al. (2005) find no effect of supplementation on nestling mass, but those nests given extra food recruit more offspring into the breeding population and this could be due to differences in how nestlings allocate available resources between developmental traits that then influence survival. This could also cause differences within broods, and should be measured before concluding that supplementation is not of greater overall benefit to marginal offspring. In addition to responding passively to offspring competitive interactions, there is some evidence that parents can bias food allocation even further in favour of competitive offspring under poor breeding conditions or when brood hunger is increased (Kilner 2002a; Smiseth et al. 2003b). Smiseth et al. (2003b) show that in bluethroats, *Luscinia s. svecica,* females temporarily provisioning as a single parent biased food allocation more towards senior nestlings than in normal conditions, even though there was no change in nestling begging behaviour. Under poor breeding conditions, parents could actively favour competitive nestlings using size as a cue to offspring quality, or as shown by work on canaries, *Serinus canaria*, they could alter their response to nestling behaviour – in this case, biasing food distribution more towards nestlings at the front of the nest, positions which less competitive offspring find hard to obtain (Kilner 1995; 2002a).

Why do parents not change their allocation rules when food availability increases? The model of Davis et al. (1999) shows that environmental quality can differentially affect the success of parental provisioning strategies, however it assumes that parents have full control over which nestling they feed, which in reality is not likely to be the case. In blue tits, parents allocate food under the pressure of maintaining a very high provisioning rate and, in addition, are assessing the begging displays from a very large brood of nestlings in a small, poorly lit nest environment. Increases in food availability, such as that provided in the experiment described here, should release parents from some portion of the time constraint under which they operate. Thus, they might be expected to actively allocate food to low quality offspring, i.e. those with the greatest long-term need. However, as shown by Grieco (2002a), blue tits can respond to a release from time constraints by foraging for higher quality prey. When able to, i.e. because of better breeding conditions, parents might also choose to decrease their reproductive effort, in order to protect future survival and fecundity (Williams 1966; Lessells 1991). In addition, where competition between nestlings is reduced, begging displays are more likely to be honest signals of offspring need. Thus, parents using the same allocation rules across a range of environmental conditions can ensure that investment in high quality offspring is prioritised, while low quality offspring obtain food when their larger siblings are satiated. In this way, parents would follow adaptive patterns of investment with no assessment cost. This is more similar to the model presented by Bonabeau et al. (1998), where competition between siblings is the mechanism whereby brood reduction is adjusted to food availability, although in their model parental decision making was limited to whether each offspring should survive or not, drastically over-simplifying the sequential decision making involved in each portion of parental investment.

Chapter 7: General discussion

Research into nestling begging behaviour has, in recent years, provided a great deal of insight into parent-offspring communication, in the context of conflict between family members over parental investment (reviewed in Kilner & Johnstone 1997; Parker et al. 2002a). This body of work has centred around debates on the information contained in nestling begging behaviour, the influence of competition between begging offspring and whether parents or offspring have control over food allocation. Independently, work on parental investment in individual offspring according to long-term need has established that in some species male and female parents respond differently to offspring demand (reviewed in Lessells 2002). This parentally biased favouritism often takes the form of the female parent investing more than the male in smaller, less valuable offspring whose long-term need is greater (e.g. Stamps et al. 1985; Leonard & Horn 1996; Krebs et al. 1999). A difference between the sexes, in patterns of food allocation, will be mediated by a difference in how the two parents assess and respond to nestling begging behaviour, possibly in combination with other cues of offspring need, such as size. Differences between the sexes in allocation rules could parallel differences in how males and females regulate their provisioning rate to the brood, in response to different elements of the begging display (reviewed in Kilner 2002b). These differences in parental investment could result from differences in male and female life history strategies (Kilner 2002b; Lessells 2002).

In a species like the blue tit, *Cyanistes caeruleus*, with large brood sizes and where breeding success is strongly dependent upon a seasonal food supply, brood reduction is common (Perrins 1979; Slagsvold et al. 1995). Mortality rates are also high immediately after offspring leave the nest, and are probably largely dependent on fledging body mass (Perrins 1979; Nur 1984a). There will be, therefore, strong selective pressure on nestling competitive ability and this may manifest itself in strategic and context-dependent nestling begging behaviour (Glassey & Forbes 2002b; Johnstone 2004). Despite the strong influence of hatching asynchrony on the fitness of individual nestlings, size differences between nestlings within nests are often slight, with the result that parents may be unable to independently assess offspring long-term need. This is especially the case as parents are tightly constrained by a demanding schedule of foraging to provide nestlings with food and spend little time assessing offspring before allocating a feed. Indeed, during the nestling period, foraging is the main parental occupation (Naef-Daenzer & Keller 1999; Grieco 2001b), is extremely energetically costly for parents (Tinbergen & Dietz 1994; Thomas et al. 2001), and is likely to be a significant factor in the evolution of parent-offspring communication in this system. Thus, this study has also examined patterns of food allocation when parents are partially released from this constraint, by experimentally increasing the food available to provisioning parents. As provisioning parents usually deal with a brood of begging nestlings, which they must choose between, and as there is currently debate over whether offspring begging is an honest signal of need (Royle et al. 2002), this concluding chapter begins with an examination of nestling begging strategies in the blue tit, with relation to nestling need, competitive ability and the effect of soliciting more than one care-giver.

Nestling begging strategies

One of the main questions which results from the begging literature is whether offspring begging behaviour is strategic, being context-dependent, or whether begging is always an honest signal of offspring need (Johnstone & Godfray 2002; Royle et al. 2002). There is convincing evidence that while begging behaviours reflect offspring need, they are also dependent upon factors such as past experience, parental response and the competitive environment in which they are performed, and therefore can be viewed as competitive strategies (Price et al. 1996; Leonard & Horn 1998; Kedar et al. 2000; Leonard et al. 2000; Rodriguez-Girones et al. 2002). Parents must, therefore, control for these factors when obtaining information on offspring need from begging displays (Kilner & Johnstone 1997). This thesis has presented results showing that in blue tits, nestling begging related to short-term need (hunger due to the experimental treatment) and therefore conveyed information, to provisioning parents (Chapter 3). However, begging did not contain information on nestling long-term need, as smaller nestlings with greater long-term food requirements did not beg more than their larger siblings. Furthermore, nestling position in the nest relative to the provisioning adult was related in a complex way to nestling hunger, size and the sex of the provisioning adult (Chapter 3). Therefore, at least one aspect of begging behaviour was influenced by factors other than nestling need, affecting the information conveyed to parents in begging displays. In fact, the two parents may be receiving different sets of information on nestling state, as there appears to be differential competition for positions close to the male and female parent. Nestlings compete for positions close to the male parent, while no such behaviour was observed towards the female parent. As a result of this interaction between nestling hunger and competitive ability and the sex of the provisioning adult, each parent receives a different impression of offspring need according to the position of nestlings relative to the feeding position used by that parent. In a similar way, parents gain a different impression of nestling need according to whether or not they give a feed call when they enter the nest with food, as the stimulus to beg influences nestling begging (Chapter 4). At the stage in the nestling period when this study was carried out, there do not appear to be differences within broods in the development of the senses that would influence how nestlings react to the stimulus to beg (i.e. how fast nestlings were to respond to the arrival of the adult, with or without a feed call). This means that parents would not have to control for nestling size when responding to nestling begging at feeds when the arrival of the adult was more ambiguous, specifically when the adult did not give a feed call. However, at earlier stages in the nestling period, when disparities between nestling perceptual ability are larger, this may be a real issue for parents and may be one reason why the parent's feed call is used more when nestlings are younger. The link between nestling motivation and begging was influenced by the reliability of the stimulus to beg. When the parent gave the feed call, signalling that there was about to be a feed, all nestlings were quick to respond, whereas when the stimulus was more ambiguous, being the sound of the adult arriving at the nest, only nestlings that were highly motivated to beg, due to hunger, were quick to respond. This aspect of begging, therefore, was only honest when the parent refrained from giving the feed call, and this may be a factor selecting against the use of the call. The cost of begging in error, when there is no imminent feed, may be what keeps the speed that nestlings respond to the stimulus honest. When this cost is removed, all nestlings respond quickly, as their response speed is likely to influence their chances of being fed. This is backed up by the results showing how nestlings respond to unreliable stimuli – those stimuli that produced false alarm begging. When nestlings were motivated to beg to the adult, they were also more likely to commit an error by begging during a false alarm, suggesting that motivated nestlings reduce the stimulus threshold above which they respond.

In this sense, nestling begging is not simply a signal of need, as begging behaviour is dependent upon the costs and benefits involved for individual nestlings, within the context of each particular begging event. This has implications for how parents should respond, as well as for the interpretation of the numerous studies of nestling begging behaviour, especially those studies where begging behaviour is induced by an artificial stimulus (as suggested by Leonard et al. 2005). Intriguingly, the results presented in Chapter 4 suggest that male and female blue tits differ in how frequently they use the feed call, although this needs to be investigated further, as the sample size was low. This could be due to the sexes differing in their investment patterns. The male could use the feed call in order to increase competitive interactions between offspring, as well as maximising foraging efficiency, while the female, by using the feed call less often, retains information on nestling need, in order to allocate food to those offspring whose need is greatest. Further experiments, involving both manipulating nestling hunger within the nest and observing the use of the adult's feed call and subsequent allocation patterns, and experiments on nestlings in controlled environments, to detail how the feed call influences nestling begging, would help us to understand the adaptive significance of the feed call to each of the parents. These experiments should be done over a range of nestling ages, in order to examine the possibility that the feed call can act to remove perceptual disparities between nest mates and to elucidate the function(s) of the feed call in detail.

Parental food allocation rules

In blue tits, parents responded to nestling begging behaviour and this resulted in them preferentially feeding hungry offspring, supporting the theory that begging is an honest signal of offspring need (Kilner & Johnstone 1997). However, when deciding whom to feed, parents also integrated the position of nestlings with nestling begging and this would allow more competitive offspring to bias food allocation in their favour, regardless of need. Certainly, paternal feeding rules, coupled with competition between nestlings to get close to the male parent is likely to result in large nestlings obtaining more food from the male over the whole nestling period. This was shown quite clearly in how nestlings positioned themselves in the nest, relative to the provisioning male parent, over time (Chapter 3: Figure 3.6). When nestling hunger was experimentally controlled, large hungry nestlings in positions close to the male parent exchanged places with small hungry nestlings over time, suggesting that due to competitive asymmetries, small nestlings have to wait until large nestlings are satiated before they can obtain positions close to the male. Furthermore, large nestlings were more successful than small nestlings at obtaining feeds when competing by begging intensely. This may be due to their size conferring on them an added advantage over smaller nestmates when parents are comparing begging signals between offspring. Parents may assess the intensity of begging signals partly by the height that nestlings reach when begging upwards towards the provisioning adult. This result also shows that parents do not control for nestling size when assessing nestling begging posture.

The situation with food allocation by the female parent is slightly different. Although the female does not appear to preferentially feed small nestlings overall, as has been found in several other species (reviewed in Lessells 2002), she does use provisioning rules that favour small nestlings under certain circumstances. Females have a stronger preference than males to feed nestlings that are further away in the nest, which could result in the female feeding small nestlings more than the male in situations where there is increased competition for feeds amongst siblings. Furthermore, females are more likely to feed small nestlings than large nestlings when they are further away from the provisioning adult, suggesting that the female controls for size when assessing offspring need according to the position of nestlings in the nest cup. These differences in allocation rules between the sexes could mediate parentally biased favouritism, especially where size differences between offspring are larger or in situations where competition for food is increased. Slagsvold et al. (1994) show that when the brood hatches more asynchronously, post-breeding survival rates for female blue tit parents are lower than when the brood hatches synchronously. Behavioural observations suggest this is due to the female providing more care than her male partner to the smaller fledglings in asynchronous broods. Apparently, when broods hatch synchronously and size differences between nestlings are small, male parents contribute more, presumably because the length of post-fledging care for larger offspring is extended relative to asynchronously hatching broods. Females deciding when to commence incubation would therefore face a trade-off, between the possible advantages of creating asynchrony within the brood (reviewed in Magrath 1990) and maximising their partner's contribution to parental investment. Female provisioning rules in the nestling stage may also be an attempt to minimise size differences between offspring in order to maximise the extent of paternal care.

Chapter 6 showed that in blue tits, parents do not change their allocation rules in response to food availability, allowing larger nestlings to gain a higher proportion of parental feeds even when food availability was experimentally enhanced. This inflexibility contrasts with the more flexible provisioning rules found in canaries, *Serinus canaria* (Kilner 2002a) in response to nestling hunger and in bluethroats *Luscinia s. svecica,* (Smiseth et al. 2003b) in response to food limitation. However, in both of these previous studies, parents changed provisioning rules in response to increased levels of competition within the brood and changed them so that food allocation was more biased in favour of competitive offspring. This suggests that under normal conditions parents play a more active role in food allocation, but when conditions are bad, either because the brood is hungrier or because the food supply is limited, parents become more passive, allowing competitive interactions between nestlings to dictate allocation patterns. This may be the most efficient pattern of investment for parents under these conditions, both as it promotes adaptive brood reduction, and as it liberates parents from time-consuming allocation decisions, allowing them to increase provisioning rate. In the experiment presented in this thesis, food supply was enhanced above normal conditions and this may explain the difference between this and the previous studies. If parents are already actively allocating food according to both the nestling begging display and the position of nestlings, which represents a composite of nestling need and competitive ability, then there may be no advantages to changing this investment pattern when feeding conditions improve. Once more food is available to the brood, competition for food will decrease and less competitive nestlings will automatically be able to obtain better positions to solicit and be fed by provisioning parents. Where competition between nestlings is reduced, begging displays are more likely to be honest signals of need. These observations lead directly to the question of whether parents or offspring control food allocation, which has been the major issue in recent discussions of parent-offspring communication and conflict over parental investment (Royle et al. 2002).

Do parents or offspring control food allocation?

The difference in provisioning rules between the parents implies that each parent trades-off the costs and benefits of responding to different aspects of the begging display. A major constraint for both may be the time cost of assessing begging displays and other cues of offspring need, when provisioning rate is limited by food availability. Conversely, this constraint may be less important if it is in the interest of parents to allocate food according to competitive interactions more passively, if this results in investment in high quality offspring when food is limited and more equitable food distribution when food availability is high. The individual trade-off between these factors and the reproductive effort of each parent is likely to differ between the sexes, and possibly between individuals (for example with parental age). Male parents appear to respond more passively to offspring solicitation, with the result that they allocate food according to the result of nestling interactions as well as to the begging display. This may be because they are less willing than females to invest time in assessing nestling begging behaviour, due to trade-offs with other behaviours, e.g. body moult (Svensson & Nilsson 1997). Additionally, they may be selected to invest more than the female in highly competitive offspring, due to differences in life-history trade-offs or due to the presence of extra-pair offspring. Blue tit nestlings appear to adjust their begging strategy according to the difference in allocation rules between the sexes, although it cannot be ruled out that nestlings compete to be closer to the male parent because the male provides a better food supply (Slagsvold 1997). Females appear to control to some degree, for offspring competitive interactions when allocating food. Spending longer at the nest than the male, due to cleaning the nest and brooding nestlings, female blue tits may have more information than the male on offspring and brood state, without incurring additional assessment costs. This may make it easier for the female to override competition between offspring during solicitation. Additionally, the female may be more interested than the male in investing in lower quality offspring.

It would be hard to determine whether the response of males implies a lack of control over allocation, due to constraints, or whether males are selected to invest according to the outcome of competitive interactions. The distribution of food is more equitable when competitive offspring cannot dominate positions close to the parents (Ostreiher 2001), suggesting that parents may prefer to bias investment away from competitive offspring. This may also apply to blue tits. Alternatively, in a study on great tits, *Parus major*, Kolliker et al. (1998) suggest that parents may actually manipulate sibling competitive behaviour, so that they can invest in preferred offspring without making time consuming choices. In great tits, parents often feed from different locations around the nest cup. The male parent feeds nestlings begging at higher postures than the female, possibly as a result hungry nestlings move closer to the female parent, so that they can obtain food at the lowest possible cost. Parents may feed from different locations and respond differently to nestling begging behaviour in order to influence the positioning of nestlings in the nest cup. This will also restrain dominant offspring from completely biasing food distribution. Conversely, parents may refrain from feeding from random locations around the nest cup, as this would reduce information to be gained about nestling state from the position of the nestlings relative to the feeding location. Indeed, in those species where it has been measured, parents appear to feed from relatively fixed, predictable locations (McRae et al. 1993, this study; Kolliker et al. 1998; Kolliker & Richner 2004). Interestingly, in blue tits, parents fed from different locations in only half of the nests observed. In contrast to the great tit (Kolliker et al. 1998), parents rarely moved to the back of the nest to feed, although the female was more likely to do so than the male. Instead, parents fed from between 45-90 degrees from the nest entrance. They may, therefore, be more interested in feeding according to the outcome of nestling competition than the great tit. This could be due to the larger brood size and higher provisioning rate in blue tits. In support, great tits appear to spend more time assessing nestling begging behaviour before allocating food (an average of 2.59 seconds, Kolliker et al. 1998) compared to blue tits (1.37 seconds, this study). It would be interesting to find out whether blue tit parental feeding locations are fixed over successive breeding attempts or whether positions are adjusted to the partner's position, and to discover why parents do not feed from separate locations in all nests. In the great tit also, a significant proportion of parents feed from similar locations (34% of nests, Kolliker et al. 1998). Slagsvold (1997) suggests, in his 'parental approaching hypothesis' that parents might alter their feeding positions, with respect to each other, in order to adapt their investment patterns to food availability. When food is very scarce, parents would both use the same feeding position in order to feed the most valuable nestling. When food is less scarce, parents would feed from different locations, or from variable locations, in order to feed a different subset of nestlings. Differences between species, even those with similar breeding ecology, like great and blue tits, may be explained by differences in how parents trade-off investment in current and future reproduction, together with other aspects of the breeding ecology of each species, such as the frequency of extra-pair fertilisations and the level of sibling competition within broods. In parrots, where hatching is extremely asynchronous, parents control food allocation, using cues such as offspring size to allocate food in preference to offspring begging behaviour (Stamps et al. 1985; Krebs 2002). This degree of parental control may be possible because large size differences between offspring make their long-term need apparent, while very low provisioning rates release parents from time constraints when assessing offspring need (Krebs 2002). Even so, there is evidence that male and female parents can differ in the degree of control that they exert when responding to offspring demand. For instance, in budgerigars, *Melopsittacus undulatus*, female parents feed offspring primarily according to size, biasing investment towards smaller young, but their provisioning rate is only half as fast as male parents, who feed young according to their begging display (Stamps et al. 1985).

In conclusion, in blue tits, parents appear to allow nestlings to control food allocation to a greater extent, and this may be due to several attributes of their breeding system, for instance large brood sizes and high parental provisioning rates. Breeding success in this species is highly vulnerable to short-term changes in food availability, but even when parents were provided with extra food they continued to allocate more food to larger offspring. This may be because under good breeding conditions, the best parental investment policy is to respond to nestling short-term need, as indicated by nestling begging behaviour. Although this will result in large offspring gaining more food items, this may be to the parent's advantage, as it maintains size differences between offspring, allowing adaptive brood reduction should environmental conditions decline during the breeding attempt. However, despite this overall pattern of investment, female parents controlled for nestling size when allocating food and this, in combination with different parental feeding locations, may partially counteract the bias in food allocation due to competitive interactions between offspring.

It is apparent that issues relating to how parents and offspring negotiate the flow of parental investment will be resolved differently according to the particular breeding ecology of each species. For instance, in blue tits parental investment patterns are probably constrained by large brood sizes and high provisioning rates during the nestling period. In species of birds where parents have more control over food allocation, competitive interactions between siblings will have less influence. With low provisioning rates and long nestling periods, parents can allocate investment into individual offspring with exactitude and appear to do so in very complex ways (Krebs et al. 1999; Krebs & Magrath 2000). At the same time, features of the nest site or parental provisioning behaviour will influence the degree to which interactions between siblings influence food allocation (Ostreiher 2001; Smith et al. 2005). Studies on single-brooded species can shed light on parent-offspring interactions when sibling competition within broods is not influencing parental investment (Quillfeldt 2002; Quillfeldt et al. 2004). However, on the whole, parent-offspring interactions within systems of care other than in nidicolous birds pre-fledging have been less well studied. For instance, in some precocial species of birds, young are fed by parents and solicit parental care through begging behaviour and through ornamented plumage (Lyon et al. 1994; Krebs & Putland 2004) but this has not yet been examined in much detail.

As well as differing between species, the nature of interactions between parents and offspring is likely to change over the period of parental care. This thesis has presented results taken from the middle of the nestling period in blue tits. However, the degree to which parents can control food allocation shifts from full control at the start of the nestling period, to a much more passive response shortly before fledging, when older nestlings dominate positions immediately adjacent to the entrance hole, with the result that the parent often feeds from outside the nest entrance. It is interesting to note that shortly after fledging, offspring are usually not very mobile, and at this point parents may regain full control over food allocation. Unfortunately, in blue tits at least, at this stage nestlings are hard to locate, so that taking observations of potentially very interesting interactions between parents and offspring is extremely difficult. In other species, parental tactics may actively change over time, in order to adaptively control brood reduction at different stages of parental care (e.g. Kloskowski 2001). Therefore, both across and within species, the begging behaviour of offspring and the way that parents respond to offspring solicitation is variable and context dependent, being influenced by the degree to which family members have control over the flow of parental investment and by the amount of conflict between them.

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