



Parental allocation of food to nestling tree swallows: the influence of nestling behaviour, sex and paternity

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Parents are expected to invest more in young that provide the greatest fitness returns. The cues that parents use to allocate resources between their offspring have received much recent attention. In birds, parents may use begging intensity, position in the nest or nestling size as cues to provision the most competitive young or those most likely to survive. It may also benefit parents to invest in young differentially by sex or relatedness if the fitness returns of sons and daughters differ or broods are sired by multiple males. We examined the allocation of food to tree swallow, *Tachycineta bicolor*, nestlings in relation to their begging behaviour, size, sex and paternity. Provisioning by parents was not related to nestling size, sex or paternity. The begging behaviour of nestlings did not differ with respect to sex or paternity. Both parents were more likely to feed nestlings that begged first or were closer to the nest entrance, suggesting that parents allocate food resources in response to cues that nestlings control. As a consequence, brood reduction was facilitated by biased provisioning within the brood in addition to the nestling size hierarchies created by hatching asynchrony.

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In many animals, parents invest substantially in the care of their young. To maximize their fitness, parents are expected to provide care in relation to the reproductive value of offspring (Clutton-Brock 1991). As a result, there has been much interest in variation in parental care in relation to benefits, such as offspring number, age and quality (e.g. Clutton-Brock 1991; Sargent & Gross 1993). Much of the original focus has been on relative parental investment between young in different reproductive episodes. However, in many species, parents have the opportunity to invest differentially between their offspring within a brood and must make decisions about the allocation of limited resources between them. In birds with altricial young, for example, parents return to the nest with food and are confronted with the competing displays of several begging nestlings. Usually the parent feeds only one or two of the young at a given feeding visit, but which one(s)?

In the context of parent-offspring conflict theory (Trivers 1974), there has been considerable recent interest in the honesty of nestling begging signals and the influence of these signals on the allocation of food by parents (Cotton et al. 1996; Leonard & Horn 1996; Krebs et al.

1999). Parent-offspring conflict theory proposes that offspring increase their fitness by extracting more resources from their parents than is optimal in terms of parental fitness, suggesting that offspring are selected to manipulate parents and outcompete siblings (Trivers 1974; Parker 1985; Harper 1986). The conflicts are likely to be even greater in broods with mixed paternity (Parker 1985), because some nestlings within a brood are full siblings and related to both of the caregiving parents, but others are half-siblings and related to only one of the caregiving 'parents'.

Parents may respond to several cues that indicate nestling vigour and competitive ability, such as position in the nest and begging intensity (under nestling control) or nestling size (independent of nestling behaviour; reviewed in Mock & Parker 1997). When parents arrive at the nest in a predictable location, and favour feeding nestlings at certain positions in the nest, nestlings can manipulate parental behaviour and receive more food if they compete among themselves for the favoured nest position (McRae et al. 1993; Kacelnik et al. 1995). Nestlings may also be able to manipulate parental behaviour by changing their begging intensity and gain more than their share of the resources from parents. Although there is strong support for the idea that parents often provide food based on begging intensity, several studies suggest that parents are not being manipulated; instead, begging intensity is a reliable indicator of nestling hunger

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and need (Cotton et al. 1996; Price et al. 1996; Kilner & Johnstone 1997).

The allocation of resources in relation to begging intensity and, therefore, hunger may often be beneficial, but there will be instances in which the hungriest nestling does not provide the greatest fitness returns. For example, small nestlings may beg more often than their larger nestmates (Bengtsson & Ryden 1983; Price & Ydenberg 1995), but their chances of survival are often lower (Magrath 1990; Stoleson & Beissinger 1995; Boland et al. 1997). Thus, parents may benefit more by investing in larger nestlings, especially when food is limited (Lack 1968). Nestling size may be a good indicator of nestling survival prospects, because larger nestlings are closer to fledging mass (and independence) than smaller nestlings. Hence, begging may not signal offspring value as reliably as alternative cues, such as size, and parents may, therefore, rely on the latter as a cue to optimize their allocation of food. In many species, size hierarchies exist between brood members and can arise when young hatch asynchronously or when there are size differences between the sexes. In such cases, it may be unlikely that all young within a brood benefit equally from a unit of parental investment, and parents are expected to allocate food selectively between the young within a brood (Clutton-Brock 1991). Size may directly indicate the value of young to the parents, but it may also be related to other important factors influencing parental fitness, such as nestling sex and their paternity.

Selective parental investment in relation to paternity would be beneficial for males, especially in species with frequent extrapair paternity. Although male birds cannot recognize genetic descendents and, therefore, cannot bias investment directly (reviewed by Beecher 1988; Whittingham & Dunn 2001a), it may be possible for males to bias investment based on cues that are correlated with paternity. For example, if within-pair young are more likely to occur early in the laying order and hatch earlier (Gottlander 1987; Kölliker et al. 1998), then males using size as a cue and provisioning larger nestlings would be more likely to feed within-pair young. In contrast to the focus on parental provisioning in response to nestling begging intensity, the allocation of resources in relation to nestling sex or paternity has received relatively less study (but see Westneat et al. 1995).

Parents may also benefit if they bias provisioning in relation to nestling sex. Sex-biased provisioning may be favoured when the fitness returns of sons and daughters differ (Trivers & Willard 1973; Clutton-Brock & Albon 1982). For example, when the energetic demands of male and female nestlings differ, or when a successful son has the potential to produce more offspring than a successful daughter (Trivers & Willard 1973). Parents could also bias provisioning in relation to the sex or paternity of the young if male and female nestlings or within-pair and extrapair young behaved differently when soliciting food from parents. This idea has received little study.

We examined the allocation of food to nestlings in the socially monogamous tree swallow, *Tachycineta bicolor*. Tree swallows are a good model species for this study because: (1) both parents feed young (Leffelaar &

Robertson 1986), (2) broods hatch asynchronously, creating a size hierarchy between brood members (Zach 1982), (3) male nestlings are larger than female nestlings (Whittingham & Dunn 2000), (4) male parents are more likely to feed larger nestlings (Leonard & Horn 1996) and (5) most broods have mixed paternity (Dunn et al. 1994; Whittingham & Dunn 2001b). We examined whether parents fed nestlings in response to cues under nestling control (e.g. begging behaviour or position in the nest) or in relation to cues likely to be independent of nestling behaviour (e.g. nestling body size), which could also indicate the sex or paternity of the young. We also examined whether differences in nestling behaviour related to sex or parentage influenced provisioning by parents.

METHODS

Study Area and Species

We studied tree swallows in 1997 and 1998 in a box-nesting population at the University of Wisconsin-Milwaukee Field Station near Saukville, Wisconsin, U.S.A. (43°23'N, 88°01'W). Our population consisted of 85 nestboxes, which were similar in density to natural tree swallow populations (Whittingham & Dunn 2000). Nestboxes were checked daily to record progress in nest building and egg laying, and checked every 1–2 h during hatching. All nestlings and adults were marked for individual identification. Each nestling was marked with coloured, nontoxic felt tip markers within 1–2 h of hatching (Clotfelter et al. 2000) and ranked according to hatch order within the brood. When two nestlings hatched at the same time, they both received a mean hatch rank. For example, if both the third and fourth nestlings hatched at the same time, they both received the rank of 3.5, and the next nestling to hatch received the rank of 5. Nestlings were re-marked with felt-tip markers until 4 days of age (hatching=day 0), when they received a coloured plastic leg band. On day 12, nestlings were given a U.S. Fish & Wildlife Service (USFWS) aluminium band, measured (wing and tarsus length) and weighed. Adults were caught during nest building, measured and weighed, and given a USFWS aluminium band. For individual identification, adults were also marked with nontoxic colours on the breast (felt-tip markers), wings or tail (acrylic paint; Dunn et al. 1994). A small (about 50 µl) blood sample was taken from the brachial vein of all adults and 12-day-old nestlings for DNA analyses.

Nestling Sex Determination and Assessment of Paternity

We conducted DNA analyses to determine nestling sex and parentage for 192 nestlings in 39 broods of tree swallows (16 broods in 1997 and 23 broods in 1998). DNA was extracted from the blood of parents and offspring by salt extraction (Miller et al. 1988). To determine the sex of nestlings, we amplified an intron in the CHD-1 gene (Griffiths et al. 1998). Details of the polymerase chain

reaction conditions are provided in Whittingham & Dunn (2000).

Paternity exclusions were made based on allelic variation at two highly polymorphic microsatellite loci: HrU6 and HrU10 (Primmer et al. 1995, 1996). Details are provided in Whittingham & Dunn (2001b). Briefly, extrapair young were identified as those that did not share an allele with their putative father at one or both of the two loci. Each locus used in this study had a high probability of paternity exclusion (0.881 and 0.965 for HrU6 and HrU10, respectively), which is the probability that a randomly chosen male will not share the paternal allele found in the young, given that the maternal allele is known (Jamieson 1994). The total probability of exclusion in this study was 0.996 for both loci combined. Nine young had an allele that did not match their putative father at just one locus. For these nestlings, we calculated the probability of chance inclusion at the matching locus, which is the probability that a randomly chosen adult would share the same allele as the nestling (Jeffreys et al. 1992). The probability of chance inclusion was calculated as $2p_i - p_i^2$ for each locus, where p_i is the observed frequency of the matching allele in our population. If the nestling had a relatively high probability ($P > 0.01$) of chance inclusion, then we concluded that the nestling was sired by an extrapair male. Conversely, if the nestling had a low probability of chance inclusion, then we concluded that the nestling was sired by the attending male, but the mismatch was caused by mutation, which occurs at a rate of 0.004 per meiotic event at HrU6 (Ellegren et al. 1997). Among the nine nestlings, the probability of chance inclusion at the matching locus was relatively high for both HrU6 (range 0.02–0.51) and HrU10 (range 0.07–0.11). Thus, we concluded that nestlings with a mismatched allele at one locus were probably sired by extrapair males.

Video Analysis of Nestling Behaviour and Parental Provisioning

We used video cameras to record nestling begging and parental provisioning behaviour when broods were 10, 12 and 14 days old (day 0 represents hatching). Broods of four to six eggs hatched over 2–70 h. We used a custom-made colour CCD video camera (Midwest Electronics, Inc.) with a 4 mm lens and audio pickup contained in a plastic housing (14 × 9 × 3 cm). Illumination through the nestbox entrance was sufficient to identify parents and young. The camera housing was attached to the inside of the roof of each nestbox with Velcro. A long cable connected each video camera to a video-cassette recorder that was powered by a 12-V DC battery and hidden in the vegetation 2 m from the nestbox. Each brood was recorded for 2 h, on each of the 3 days, between 0600 and 1400 hours Central Standard Time (mean ± SE start time = 0709 h ± 17 min). Birds acclimated quickly to the video camera; in all cases adults began visiting the nestbox within 5 min of the start of recording. Video recordings were not always made at every nest on all 3 days due to inclement weather or equipment failure. Each nest was recorded two or three times (mean ± SE 2.5 ± 0.1): 32

nests on day 10, 34 nests on day 12 and 32 nests on day 14. The mean ± SE recording period was 116 ± 1.1 min. During videotaping, mean ± SE brood size was 5 ± 0.07 nestlings, and there was no nestling mortality between days 9 and 14.

For individual identification during videotaping, we marked each nestling within a brood with a unique combination of one to two dots of nontoxic coloured acrylic paint on top of the head. Nestlings were marked with paint on day 9 and re-marked if necessary on days 11 and 13. Thus, nestlings were not moved or disturbed before inserting the video camera into the nestbox. On day 12, nestlings were weighed following videotaping. When nestlings were 6 days old, adults were caught and marked with a spot of coloured (sex-specific) acrylic paint on the top of the head so that the sex of the parent could also be determined on videotape.

During videotape analysis, we examined each feeding visit and recorded (1) the first nestling to beg (defined as the first nestling to open its mouth), (2) the nestling closest to the nestbox entrance, (3) the nestling fed by the parent and (4) sex of the parent providing food. When two nestlings tied as 'the first to beg', both were recorded as 'first'. Similarly, if two nestlings were closest to the nestbox hole, then they were both recorded as 'closest'. Most of the videotape analyses were conducted by individuals blind to the predictions of the study and before any genetic results were known.

Statistical Analyses

Analyses were performed using JMP 3.0 (SAS Institute 1997). In analyses of male and female feeding behaviour, we accounted for the nonindependence of nestlings within the same nest by summarizing the data on a per nest basis ($N = 39$ nests) or by performing nested analyses of variance (ANOVAs) in which nest was used as the nesting variable. Interactions were nonsignificant unless stated otherwise. We tested dependent variables for normality using the Shapiro–Wilk test (SAS Institute 1997), and non-normal variables were square-root transformed to achieve normality. The relationship between paternity (extrapair or within-pair) and hatching order was tested with an ordinal logistic regression in which both hatching order and clutch size were used as predictors to account for differences in the number of young between nests. Means are presented + SE.

RESULTS

We recorded 4140 feeding trips by parents during 189 h of observation at 39 nests. The rate at which parents provisioned nestlings (square-root transformation of feeding visits/nestling/30 min) differed between male and female parents ($F_{1,125} = 20.9$, $P < 0.0001$) and observation sessions (nestling ages 10, 12 and 14 days; $F_{34,125} = 1.5$, $P = 0.047$), but did not differ between years ($F_{1,125} = 0.1$, $P = 0.78$) in a nested ANOVA (nest was the nesting variable). Females fed young more often (1.3 ± 0.06

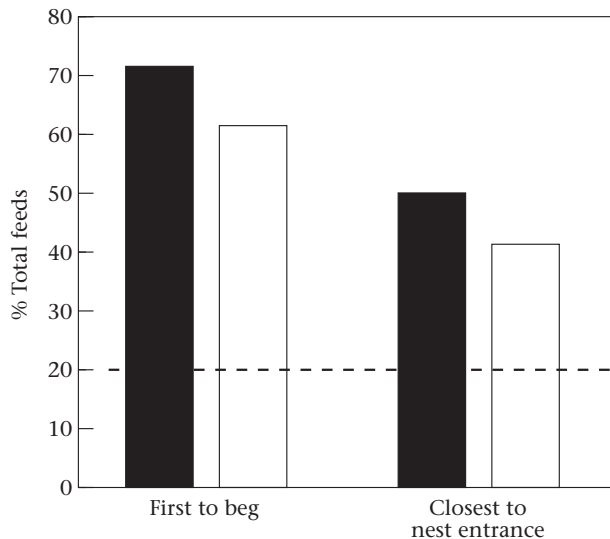


Figure 1. The percentage of total feeds by male (■) and female (□) parents to young that were the first to beg or closest to the nest entrance. Data are from broods of five young ($N=18$). All bars were significantly greater than expected based on random allocation between five nestlings (20%; dashed horizontal line).

visits/nestling/30 min) than males (1.0 ± 0.05 visits/nestling/30 min), and both parents fed nestlings more on days 10 and 12 (both 1.2 ± 0.07 visits/nestling/30 min) than on day 14 (1.0 ± 0.07 visits/nestling/30 min). Provisioning rates were not related to the time of day in which video observations were conducted ($r^2=0.003$, $P=0.6$). Parents fed only one nestling per visit and rarely visited the nest without feeding (4% of visits).

Begging First

Overall, nestlings that begged first were more likely to be fed than were their nestmates. For example, in the most common brood size of five, any given nestling will be fed 20% of the time if feedings are distributed randomly; however, the first nestling to beg was fed on 65% of visits (one-sample t test: $t_{17}=23.8$, $P<0.001$; Fig. 1). We found a similar response to the first nestling to beg in all other brood sizes (one-sample t tests, all $P<0.004$). Male parents were more likely to feed the first nestling to beg than were female parents at the same nest (paired t test: $t_{38}=3.6$, $P=0.001$; Fig. 1).

Proximity to Nest Entrance

Nestlings closer to the nestbox entrance were more likely to be fed than were their nestmates. For example, in the most common brood size of five, the closest nestling to the entrance hole was fed on 44% of visits, which is more often than expected based on random allocation among five nestlings (20%; one-sample t test: $t_{17}=10.9$, $P<0.001$; Fig. 1). A similar response to the closest nestling was found in all other brood sizes (one-sample t tests: all $P<0.025$). In a paired analysis of males and females at the same nest, we found that the male fed the nestling closest

to the entrance 9% more often than the female (paired t test: $t_{38}=4.4$, $P<0.001$; Fig. 1). Although there was an advantage for nestlings to be closer to the nestbox entrance, they did not scramble to improve their position when the parents arrived with food. Nestlings usually changed position within the nest cup upon ejection of a faecal sac at the end of a parental visit or during the absence of the parents between feeding visits.

Body Mass

Did parents respond to cues that were not under nestling control? We examined the relationship between nestling mass and the percentage of all feeds by each parent to a given nestling (square-root transformed) in a nested ANOVA with nestling mass and parent sex as predictors (day 12 nestling mass nested within nest). Overall, heavier nestlings tended to receive a greater proportion of feeds (mass effect: $F_{38,299}=1.4$, $P=0.065$). Male parents did not make a relatively greater feeding contribution than females for the same-size nestling (parent effect: $F_{1,299}=0.2$, $P=0.69$). Heavier nestlings did not receive a greater proportion of feeds as a consequence of their behaviour; they were not more likely to beg first (nested ANOVA: $F_{38,112}=1.0$, $P=0.44$) or position themselves close to the nest entrance ($F_{38,112}=1.2$, $P=0.19$). In a nested ANOVA (hatching order nested within nest), we found that day 12 nestling mass was influenced by hatch order ($F_{36,104}=2.2$, $P=0.001$) and nestling sex (males were heavier than females; $F_{1,104}=13.5$, $P<0.001$). Thus by day 12, later-hatched nestlings were still smaller and had not 'caught up' to earlier-hatched nestlings (see also Clotfelter et al. 2000).

Nestling Sex and Paternity

We also examined whether parents bias their provisioning in relation to nestling sex and paternity. Overall, 53% (101/192) of young in 85% (33/39) of broods were sired by extrapair males. Male nestlings at day 12 were heavier (21.3 ± 0.2 g) than females (20.4 ± 0.2 g), and thus size could have been a cue to nestling sex. However, males did not provide a greater percentage of their feeds (square-root transformed) to within-pair offspring (nested ANOVA: $F_{27,85}=1.1$, $P=0.32$), nor did they favour one sex (nested ANOVA: $F_{34,85}=0.99$, $P=0.50$). Similarly, the percentage of female feeds (square-root transformed) was not related to nestling sex (nested ANOVA: $F_{37,112}=0.8$, $P=0.7$). If within-pair young are more likely to hatch earlier within a brood, then they may be larger and more likely to be fed. However, we found no relation between paternity and hatch order ($\chi^2_5=4.38$, $P=0.88$) or clutch size ($\chi^2_1=1.67$, $P=0.2$) in an ordinal logistic regression with both hatch order and clutch size as predictors. Within nests, there were no differences in the mass of within-pair and extrapair young at 12 days of age for either males (paired t test: $t_{17}=0.29$, $P=0.78$; within-pair young were 0.1 g heavier than extrapair young) or females (paired t test: $t_{12}=0.16$, $P=0.87$; extrapair young were 0.1 g heavier than within-pair young).

There was no evidence that paternity or sex affected the behaviour of nestlings. Within nests that had both within-pair and extrapair young, nestlings were not more likely to beg first if they were sired by extrapair males (paired t test: $t_{29}=0.98$, $P=0.33$), nor were they more likely to be close to the nestbox entrance if they were sired by extrapair males (paired t test: $t_{29}=0.91$, $P=0.37$). Similarly, male and female nestlings in the same nest did not differ in their likelihood of begging first (paired t test: $t_{35}=0.14$, $P=0.89$) or being close to the nestbox entrance (paired t test: $t_{35}=0.16$, $P=0.87$).

Multivariate Patterns

In the bivariate analyses above, begging first, proximity to the nest entrance and nestling mass all tended to influence the probability of being fed by a parent. To assess the relative importance of each of these three variables as well as paternity and nestling sex, we analysed them in a nested ANOVA of the percentage of feeds to each nestling. The percentage of feeds to a particular nestling (square-root transformed) was related only to the percentage of visits that the nestling was closest to the nest entrance ($F_{29,35}=3.5$, $P<0.001$) or begged first ($F_{33,35}=1.8$, $P=0.049$). Nestling mass on day 12 ($F_{29,35}=1.0$, $P=0.52$), paternity ($F_{1,35}=3.0$, $P=0.09$), sex ($F_{1,35}<0.1$, $P=0.99$) and the interaction between sex and paternity ($F_{1,35}=1.3$, $P=0.27$) were not related to the percentage of feeds to the nestling. Thus, after controlling statistically for begging first and proximity to the nest entrance, nestlings that were larger were not more likely to be fed by their parents.

Distribution of Food Between Nestlings

At most nests (82%, 32/39) food was distributed equitably between members of the brood (not significantly different from a uniform distribution within each brood; all $\chi^2_1<7.2$, all $P>0.13$). However, at five nests, the distribution of food between nestlings was significantly nonuniform (all $\chi^2_1>9.85$, all $P<0.02$), and at two additional nests, food allocation was also somewhat biased ($P=0.06$). In all cases, there was no apparent difference in male and female behaviour with respect to the distribution of food between brood members. At six of the seven biased broods, at least one nestling died sometime after the last videotaping on day 14. At each of these seven nests, the dead nestling was the smallest in the brood and usually the one that had received the smallest number of total feedings during videotaping (6/7 nests). Interestingly, the dead nestling was usually not the last to hatch (6/7 nests).

DISCUSSION

Tree swallow parents were more likely to feed nestlings that begged first and were closer to the nest entrance when the parent returned with food. Provisioning by parents did not appear to be influenced by nestling size, sex or paternity. Few studies have examined sex biases in

parental provisioning and possible differences in nestling behaviour in relation to their sex or parentage. In contrast to previous studies on tree swallows and other species of birds, we found that although larger nestlings tended to be more successful at gaining food from their parents, this trend disappeared when we controlled for nestling behaviour (begging first and proximity to the nest entrance).

Biased investment in relation to parentage would clearly benefit male tree swallows because broods with extrapair young are so common and males do not reduce their overall parental investment in relation to their paternity in a brood (Whittingham et al. 1993; Kempnaers et al. 1998). If males are more likely to sire eggs laid early in the laying sequence and these become the largest nestlings, then males might avoid large investments in unrelated young if they feed nestlings that are relatively large. Paternity varies predictably in some species, with extrapair young more likely to occur later in the clutch in house martins, *Delichon urbica* (Riley et al. 1995) and snow geese, *Chen caerulescens* (Dunn et al. 1999), and earlier in the laying sequence in house sparrows, *Passer domesticus* (Cordero et al. 1999). However, in tree swallows, the occurrence of extrapair young in the brood did not vary with hatching order (see also Barber 1997), and there was no relationship between parentage and nestling mass at 12 days of age. Thus, males had no size cues to their paternity.

Sex-biased provisioning could occur through active discrimination of male and female nestlings based on plumage differences, or as a result of differences between male and female nestlings in behaviour (e.g. begging intensity). Sex-biased provisioning has been reported in a few sexually dimorphic species; larger male nestlings, which beg more, are fed more often by parents than smaller female nestlings (red-winged blackbirds, *Agelaius phoeniceus*: Teather 1992; Westneat et al. 1995; yellow-headed blackbirds, *Xanthocephalus xanthocephalus*: Price & Ydenberg 1995). In tree swallows, fitness gains for females are potentially large from sex-biased investment in sons, because the high level of extrapair paternity creates a high variance in male reproductive success, and larger males are apparently more likely to be extrapair sires (Kempnaers et al. 2001). Although 12-day-old male nestlings were larger than females, we found no bias in food allocation towards male (or larger) nestlings. However, the sexual size dimorphism in nestling tree swallows was slight (4%) and may not provide as strong a signal as in species in which nestlings are more dimorphic (e.g. red-winged and yellow-headed blackbirds). Furthermore, we found no indication that male and female nestlings tree swallows begged differently.

Tree swallow nestlings were most likely to be fed as a result of their own behaviour, as has been found in some other species (European starling, *Sturnus vulgaris*: Kacelnik et al. 1995; canary, *Serinus canarius*: Kilner 1995). Nestlings often compete for a preferred position in the nest from which they receive more food from the parents (McRae et al. 1993). This is particularly common in cavity-nesting species in which the position of parent

arrival at the nest is predictable and nestlings compete to be closest to the nest entrance (pied flycatchers, *Ficedula hypoleuca*: Gottlander 1987; European starlings: Kacelnik et al. 1995; tree swallows: Leonard & Horn 1996; this study; but see great tits, *Parus major*: Kölliker et al. 1998). The ability of a nestling to occupy the preferred position could be highly correlated with size. In food deprivation experiments, larger nestlings were more likely to monopolize preferred positions within the nest (Gottlander 1987; Kilner 1995), but size was not correlated with gaining preferred nest positions under natural conditions (Gottlander 1987; Leonard & Horn 1996; this study; but see Slagsvold & Rohwer 2000). Thus, closeness to the nest entrance is a correlate of parental provisioning that is independent of nestling size.

Begging first has also been identified as an important cue for parents feeding young, but it is often correlated with larger nestling size (Price & Ydenberg 1995). Our study suggests that begging first can be an important cue for parents feeding nestlings independent of their size. Our results differ from a previous study of tree swallows (Leonard & Horn 1996) in which both parents were more likely to feed nestlings that begged first, but males preferentially fed larger nestlings while females preferentially fed smaller nestlings. Selective feeding of smaller nestlings by females has been reported in a few species (Stamps et al. 1985; Gottlander 1987; Krebs et al. 1999) and may be related to abundant food (e.g. Stamps et al. 1985; Kölliker et al. 1998). In our study, nestling size did not influence the likelihood of being fed by either parent. Instead, parents allocated food based on the outcome of competitive interactions between nestlings (i.e. begging first; Mock & Parker 1997), which may allow parents to invest in nestlings more likely to survive when food is limited.

In the majority of species studied, nestling body size significantly affected parental provisioning and larger nestlings were fed more frequently even when they begged less often than their smaller nestmates (Bengtsson & Ryden 1981; Cotton et al. 1996; Leonard & Horn 1996; Thomas & Shutler 2001). However, few studies have conducted multivariate analyses to determine whether nestling size affects parental provisioning after controlling for other potentially confounding variables such as begging first and nestling position. In contrast to most of the empirical evidence, models of parent food allocation to small versus large nestlings predict that parents should selectively provision the smallest or intermediate chicks to maximize their fitness gains (Cotton et al. 1999). They reason that the fitness gain of a chick from parental provisioning decreases as its condition improves, and predict that fitness gains are greater from feeding hungrier chicks in poor or intermediate condition. However, the models assume that all chicks fledging at a certain target mass have the same fitness payoff to parents. McCarty (2001) showed that this assumption does not hold for tree swallows, because nestlings that suffered delayed growth during the nestling period were less likely to survive and recruit, even though they reached the same fledging mass as nestlings that did not experience delayed growth. This critical evidence suggests

that a pattern of investment based on early begging and nest position may be a better strategy for tree swallow parents, and that simply increasing the mass of smaller nestlings may not be enough to improve survival.

Lack (1968) suggested that hatching asynchrony produces size and competitive differences between nestlings that may determine access to food and facilitate brood reduction when food is scarce, without any direct manipulation of food provisioning by the parents. In tree swallows, nestlings that died following day 14 were the smallest and least often fed in their brood, but usually not the last-hatched nestling. Thus, although the effects of hatching asynchrony on mortality appear to be most important early in the nestling period (before day 8; Clotfelter et al. 2000), we found that the influence of biased parental provisioning on nestling mortality appears to occur late in the nestling period (after day 14).

In our study, parent tree swallows were more likely to feed nestlings based on cues that the nestlings controlled (i.e. begging first and proximity to the nest entrance) than on independent cues not under nestling control (i.e. size, sex or paternity). Differences between our results and those of Leonard & Horn (1996) may be related to differences in food supply, which may influence parent allocation strategies. Females may be more likely to allocate their parental care to smaller nestlings (as found by Leonard & Horn 1996) in areas with plentiful food supplies, because in these circumstances it may pay parents to provide 'extra' assistance to young that would normally die as a result of competitive hierarchies. Boland et al. (1997) and Krebs & Magrath (2000) provided experimental evidence for such a shift in provisioning tactics of parents. Further work addressing the effect of food supply on parental allocation of resources among young is needed.

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