Site- and sex-level differences in adult feeding behaviour and its consequences to offspring quality in tree swallows (*Tachycineta bicolor*) following brood-size manipulation

D.R. Ardia

Abstract: In species with biparental care, males tend to invest less in offspring than do females, likely because of differences in the costs and benefits associated with parental effort. Here I test for sex differences in the response of tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) to a brood-size manipulation at two locations differing in food resources, Alaska and New York. I tested sex and habitat differences in how swallows responded to changes in offspring demand. At both sites, both sexes increased effort when feeding enlarged broods, although Alaskan males increased feeding less than Alaskan females. Males decreased feeding effort more to reduced broods than females, but only in Alaska. Food abundance was higher in Alaska than in New York, and Alaskan tree swallows made more feeding visits than New York tree swallows. In New York, food availability did not predict feeding rate and there was no sex difference in the response to brood manipulation. In both sites, male feeding effort was linked with nestling residual body mass, while female feeding effort was correlated with nestling growth rate. This study demonstrates that male tree swallows differ from females by being the first to reduce feeding effort under certain conditions and that male and female feeding rate affects offspring quality differently.

Résumé : Lorsque les soins parentaux chez une espèce sont partagés par les deux parents, les mâles ont tendance à investir moins que les femelles dans leurs petits, probablement à cause de différences dans les coûts et bénéfices associés à l'effort parental. La présente étude vérifie l'existence de différences sexuelles dans les réactions d'hirondelles bicolores (*Tachycineta bicolor* (Vieillot, 1808)) à une manipulation de la taille de leur couvée à deux localités à ressources alimentaires différentes, dans le New York et en Alaska. Les différences reliées au sexe et à l'habitat dans les réactions des hirondelles aux demandes de leurs rejetons ont été vérifiées. Aux deux localités, les parents des deux sexes augmentent leur effort pour nourrir leurs couvées agrandies, bien que les mâles d'Alaska haussent leur effort d'alimentation moins que les femelles d'Alaska. En présence de couvées réduites, les mâles diminuent leur effort d'alimentation plus que les femelles, mais seulement en Alaska. L'abondance de nourriture est plus grande en Alaska que dans le New York et les hirondelles bicolores d'Alaska font plus de visites d'alimentation que les hirondelles du New York. Dans l'état de New York, la disponibilité de la nourriture n'explique pas le taux d'alimentation et il n'y a pas de différence sexuelle dans les réactions à la manipulation de la couvée. Aux deux endroits, l'effort d'alimentation des mâles est en corrélation avec la masse corporelle résiduelle des petits au nid, alors que l'effort d'alimentation des femelles est lié au taux de croissance des petits au nid. Cette étude démontre que les hirondelles bicolores mâles différent des femelles en étant les premières à réduire leur effort d'alimentation sous certaines conditions; de plus, les taux d'alimentation des mâles et des femelles affectent la qualité des petits de façon différente.

[Traduit par la Rédaction]

Introduction

In species with biparental care, there is a conflict of interest between males and females as each strives to maximize offspring survival while minimizing costs to their own future reproductive success (Stearns 1992; McNamara et al. 1999; Houston et al. 2005). Thus, as one sex adjusts to conditions, the other sex should never compensate fully for reduction in care (Chase 1980; Houston and Davies 1985; Winkler 1987; Hinde and Kilner 2007). Parental care should vary based on the costs and benefits to each sex of changing effort (Queller 1997; Sanz et al. 2000). In this study, I tested for sex differences in the response of tree swallows (*Tachycineta bicolor* (Vieillot, 1808)) to a brood-size manipulation at two sites that differed in food availability. Brood-size manipulation allows for an assessment of the response of both parents to an experimental change and can indicate willingness of both parents to feed offspring (Leffelaar and Robertson 1986). The tree swallow has been a good model for examining parental care (Leffelaar and Robertson 1986; Lombardo 1991; Dunn and Robertson 1992; Whittingham et al. 1993, 1994). Tree swallows are socially monogamous;

D.R. Ardia.[1] Department of Ecology and Evolutionary Biology, Cornell University, Ithaca, NY 14853, USA.

[1]Present address: Department of Biology, Franklin and Marshall College, Lancaster, PA 17064, USA (e-mail: daniel.ardia@fandm.edu).

both parents feed offspring, but only female tree swallows incubate and brood (Robertson et al. 1992).

First, I tested for sex differences in response to brood-size changes using feeding behaviour as a measure of parental care. Males and females may differ in their response to brood size because of differences in relatedness to offspring caused by high levels in extra-pair paternity (Kempenaers et al. 1998). However, the sexes may respond differently because their roles during the nestling period may vary, with one sex generally contributing less to feeding behaviour and more to other aspects of care, such as nest defense.

Second, I tested for the effect of habitat variation as differences in resources and environmental conditions among sites can greatly affect parental strategies (Tremblay et al. 2003). In tree swallows, Dunn and Robertson (1992) compared the importance of male parental care (via male removal) between two sites differing in food abundance and found that females were most strongly affected by the loss of their mate in the site with lower food abundance. In this study, I compared sex differences in response to brood-size manipulations in two sites that differed greatly in food abundance (Alaska and New York, USA). If indeed differences in costs and benefits between males and females lead to sex differences in parental care, then males may show less difference relative to females at the site where food supply is most important to raising offspring. Thus, I predicted that the site with the highest food availability would show the smallest decrease in male care, especially when broods are enlarged. I tested (*i*) whether parental care, as measured via offspring feeding, differed between sites and (*ii*) whether males showed a greater reduction in care to reduced broods in the site with the higher food availability.

Lastly, examining parental care without its consequences to offspring quality or condition is incomplete, as the ability to maintain offspring quality under experimental conditions may reflect parental care better than feeding rates alone (Whittingham et al. 1994). Increased parental care, reflected in feeding rates, should lead to increased offspring condition; however, the changes induced in this experiment by manipulating brood size may lead to differences in the effect of male vs. female provisioning behaviour on offspring measures. Overall, in this study, I tested sex differences in changes in feeding effort in response to changes in brood size and the consequences of those changes on offspring condition (growth rate and residual body mass).

Materials and methods

I studied tree swallows breeding in nestboxes erected for their use in Tompkins County (centered on 42°29′N, 76°27′W, elevation 118 m), New York, USA, in 2000 and in Fairbanks (centered on 64°49′N, 147°52′W, 138 m), Alaska, USA, in 2002. Clutch initiation date varied among sites (median date — New York: 10 May; Alaska: 1 June); the experiment was conducted on nests spanning 82%–85% of the breeding season at each site. Ninety percent of tree swallows initiate clutches within 60 days of one another in New York and within 35 days in Alaska. Nests were checked daily to determine date of clutch initiation and clutch size. Neither clutch size (Alaska: 5.67 ± 0.655 (mean ± SD), New York: 5.62 ± 0.71; $t_{[145]} = 0.45$, $P =$

0.50) nor mean daily temperature differed between sites (Ardia 2006). In all nests, breeding females were captured, banded, and aged as either 2nd year or after 2nd year by plumage (Robertson et al. 1992). To record nest visitation rates, three 60 min behavioural observations stratified over the daylight hours were conducted using video cameras recording from at least 20 m outside the box between nestling days 8–11 for each breeding pair, the period of peak nestling growth (Zach and Mayoh 1982) and high energetic demand (Burness et al. 2000). Prey delivery rate reflects prey mass in tree swallows (McCarty 2002). Sexes were differentiated in video observations by marking females with a small dot of white paint on the back; all observations had at least a single visit by both the male and the female in each pair. For each observation, cameras were set with timers to begin recording 15 min after setup to minimize the effect of human disturbance on provisioning behaviour. No more than one observation was conducted on any single day. Mean feeding visits per observation were used in analyses, except for analyses of the effect of feeding on nestling growth and residual body mass, when the number of feeding visits per observation per hour of daylight was used. With few exceptions, tree swallows feeding nestlings at this age bring food during nest visits (personal observation).

First broods with the same hatching date were randomly assigned to one of three partial cross-fostering brood manipulation treatments: (1) increased, (2) decreased, or (3) control. This created broods that were roughly 50% larger or smaller than the original clutch size (natural range 4–7 eggs) (mean number of nestlings on day 4 — New York: decreased 2.97 ($N = 17$), control 5.01 ($N = 16$), increased 7.81 ($N = 16$); Alaska: reduced 2.94 ($N = 16$), control 5.08 ($N = 17$), enlarged 7.88 ($N = 16$)). Chicks were individually marked and swapped for all treatments on day 3 of the nestling period. Every nest contained partially cross-fostered nestlings (i.e., a mix of nestlings hatched in the nest and hatched in other nests). Offspring were measured on days 4, 6, 10, and 12 of the nestling period. During each visit, body mass (±0.1 g), flattened left wing length (±0.5 mm), head–bill length (back of skull to tip of bill), and tarsus length (±0.05 mm) were recorded by the same individual at both sites.

Insect availability was determined using two 2 m aerial insect samplers powered by a Robbins and Myers 1650 rev/min 0.08 horsepower motor (12.95 m/s) (McCarty and Winkler 1999) to collect daily samples of aerial insect abundance during the breeding season. Samplers were set on timers to collect insect availability over approximately 70% of daylight hours; each daily sample was divided by the number of hours of operation to correct for longer periods of daylight hours in Alaska. Packed insect volume was measured by centrifuging samples at 5000 r/min (31.4 m/s², 4500g) for 75 min after removing seeds and other debris. Prey availability was calculated for each pair by summing the insect volume measured on the 3 days the feeding observations occurred.

Females were part of a larger experiment on tradeoffs between immune function and offspring quality in breeding females (Ardia 2005a, 2005b). Females raising cross-fostered broods (control, reduced, enlarged) were given two immunochallenges: sheep red blood cells and phytohaemagglutinin on day 4 of the nestling period. To assess whether immuno-

challenges affected female feeding behaviour, I compared injected females raising control broods to females handled the same but given injections of saline. There was no difference in the number of feeding visits between females exposed to immunochallenges and females exposed to saline (injected: 8.73 ± 1.13 visits (mean $\pm$ SD), not injected: 8.67 ± 1.07 visits; $F_{[1,33]} = 0.56$, $P = 0.65$); females were assigned to immunochallenges and saline controls balanced for clutch size and lay date. In addition, both male visits and total feeding visits (female + male visits) did not differ between immunochallenged female pairs and saline-injected female pairs (male — injected: 5.8 ± 1.07 visits, not injected: 6.0 ± 1.12 visits, $F_{[1,33]} = 0.43$, $P = 0.81$; total visits — injected: 14.53 ± 1.71 vistis, not injected: 14.67 ± 1.68 visits, $F_{[1,33]} = 0.61$, $P = 0.63$), indicating no difference in how males responded to females being immunochallenged. These results suggest that any change in female feeding behaviour in the present study reflects the effect of the brood-size manipulation and not the direct effect of mounting an immune challenge.

All work was done with the approval of the Institutional Animal Care and Use Committee of Cornell University.

Statistical analyses

I first tested for site and sex differences with a two-way ANOVA examining feeding rate with site and sex as main effects, as well as a site × sex interaction. Factors predicting feeding effort were then assessed separately for each site using an ANCOVA (PROC GLM) (SAS Institute Inc. 1988) with the following effects: sex, brood-size manipulation treatment (reduced, control, enlarged), food availability on the days of the observations, sex × treatment interaction, and sex × food availability. To avoid pseudoreplication, nest was included as a random effect. In addition, the following variables were included as covariates: standardized clutch initiation date, female age (after 2nd year vs. 2nd year), and initial clutch size. Clutch initiation date was standardized to a mean of 0 for each year while maintaining the normal range of variation. Post hoc tests of means were conducted using significant differences in pairwise comparisons of least square means (means correcting for covariation with other variables). Insect availability over time was analyzed using simple regression. All variables were normally distributed (Shapiro–Wilk's $W > 0.97$, $P > 0.20$).

Nestling development was characterized using two variables: (1) growth rate and (2) residual body mass. Growth rate from day 4 to day 12 was calculated as the growth rate constant K of a logistic growth function (Starck and Ricklefs 1998) for three nestling measures (ninth primary wing feather length, tarsus length, and head–bill length), an approach used previously for tree swallows with a similar number of data points (Zach and Mayoh 1982; McCarty 2001). For these sites, previous analyses showed that fitting a logistic equation was the best fit for tree swallow growth (Ardia 2006). The following asymptotic values were used to calculate K: ninth primary wing feather length (85 mm), tarsus length (16.5 mm), and head–bill length (28 mm). Because the three nestling measures are highly correlated, K values were combined in a principal component analysis and the first principal component (which explained 82% of the variation) was used in statistical analyses. Nestling resid-

ual body mass on nestling day 12 was calculated as the residual of a regression of body mass against head–bill length, a structural measure of body size. Residual body mass values were calculated separately for each site because of differences in overall body mass between sites (Ardia 2006).

The effect of provisioning behaviour on nestling measures was examined in a forward-selection multiple regression model (entry probability = 0.15) analyzing both growth rate and residual body mass simultaneously. The following variables were included in the initial analysis: standardized clutch initiation date, the number of chicks in the nest on nestling day 12, the difference between the original clutch size and the number of chicks on day 12, prey availability index, the number of female visits, and the number of male visits. I used partial regression plots to examine relationships between predictors and the variable of interest while taking other variables into account. Partial regression plots are the best method of examining the relationship between two variables while accounting for covariation with other independent variables in a model (Neter et al. 1996). Partial regression plots for a pair of variables are created by plotting the residuals of two regression analyses: the first variable of interest against all independent variables vs. the first variable of interest against all independent variables excluding the second variable.

Results

Insect availability showed considerable daily variation at both sites, but overall prey availability showed a positive linear trend as the breeding season progressed (Julian date vs. packed insect volume (mm^3) — Alaska: $\beta = 5.70$, $F_{[1,67]} = 5.12$, $P = 0.02$, $R^2 = 0.13$; New York: $\beta = 2.05$, $F_{[1,111]} = 4.22$, $P = 0.04$, $R^2 = 0.10$). There were more insects available in Alaska than in New York (site-level difference in abundance: $F_{[1,202]} = 11.16$, $P < 0.001$).

There were significant sex- and site-level differences in feeding behaviour. Alaska tree swallows made more feeding visits than New York tree swallows ($F_{[1,94]} = 37.3$, $P < 0.001$). Female tree swallows made more feeding visits than male tree swallows ($F_{[1,94]} = 4.39$, $P = 0.03$), with no difference in the magnitude between sites (sex × site interaction $F_{[1,94]} = 0.3$, $P = 0.59$; least square mean ($\pm$SE) feeding visits / h — Alaska: male 13.1 ± 1.0, female 15.3 ± 1.2; New York: male 6.0 ± 0.9, female 8.8 ± 1.0). The effect of brood manipulation varied by site; there was a significant three-way interaction between site × sex × brood manipulation ($F_{[2,94]} = 6.1$, $P = 0.01$).

To aid in the interpretation of a three-way interaction, the effect of brood manipulation on male and female tree swallows was then examined separately among sites. In Alaska, males and females responded to brood-size manipulation differently (Fig. 1; overall model: $R^2 = 0.74$; sex: $F_{[1,60]} = 33.0$, $P < 0.001$; brood-size manipulation: $F_{[2,60]} = 51.8$, $P < 0.001$; sex × manipulation: $F_{[2,60]} = 5.9$, $P = 0.004$). Relative to control broods, both sexes increased feeding rate to enlarged broods, with males increasing feedings by 29% and females by 43% (Fig. 1). In reduced broods, males decreased feeding more than females, showing a 55% reduction in feeding rate relative to controls, while females decreased by only 5%. In Alaska, food availability predicted
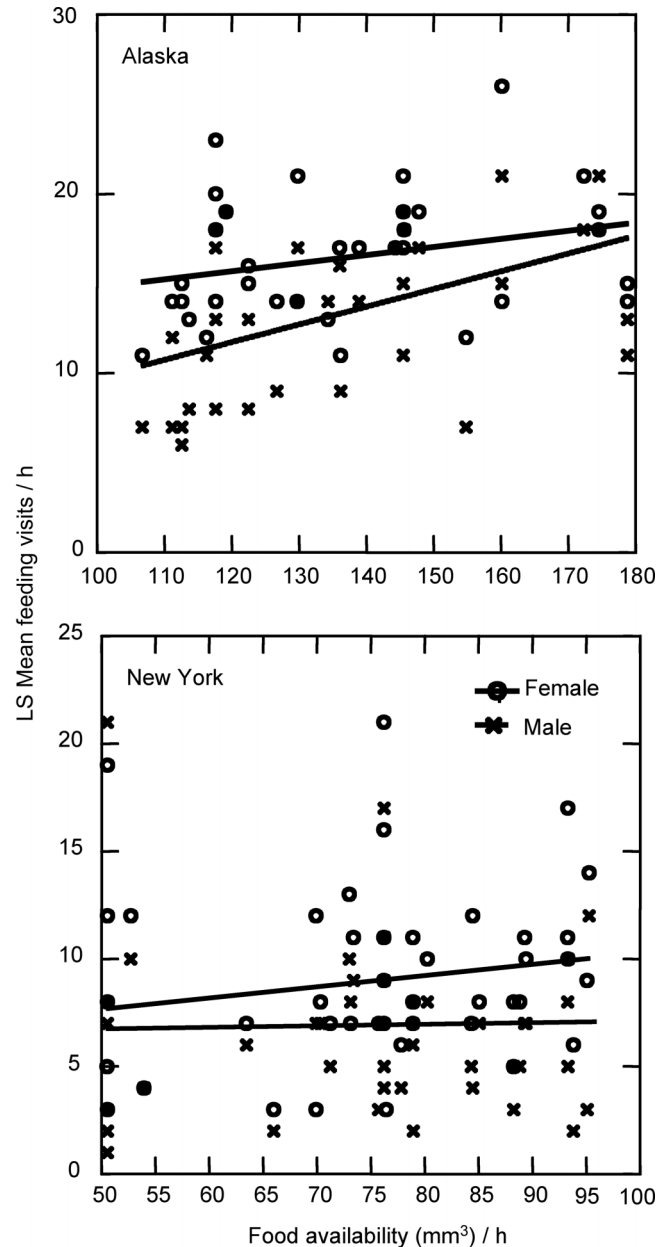
Fig. 1. Feeding rate of male and female tree swallows (*Tachycineta bicolor*) feeding 8- to 11-day-old nestlings following brood-size manipulation at two sites (Alaska and New York). Letters refer to least square (LS) mean differences at $P < 0.05$ within each site. Note the different scale for each site.

Fig. 2. Effect of food availability (measured as packed volume) on feeding rate of male and female tree swallows feeding 8- to 11-day-old nestlings at two sites (Alaska and New York). Note the different scale for each site.
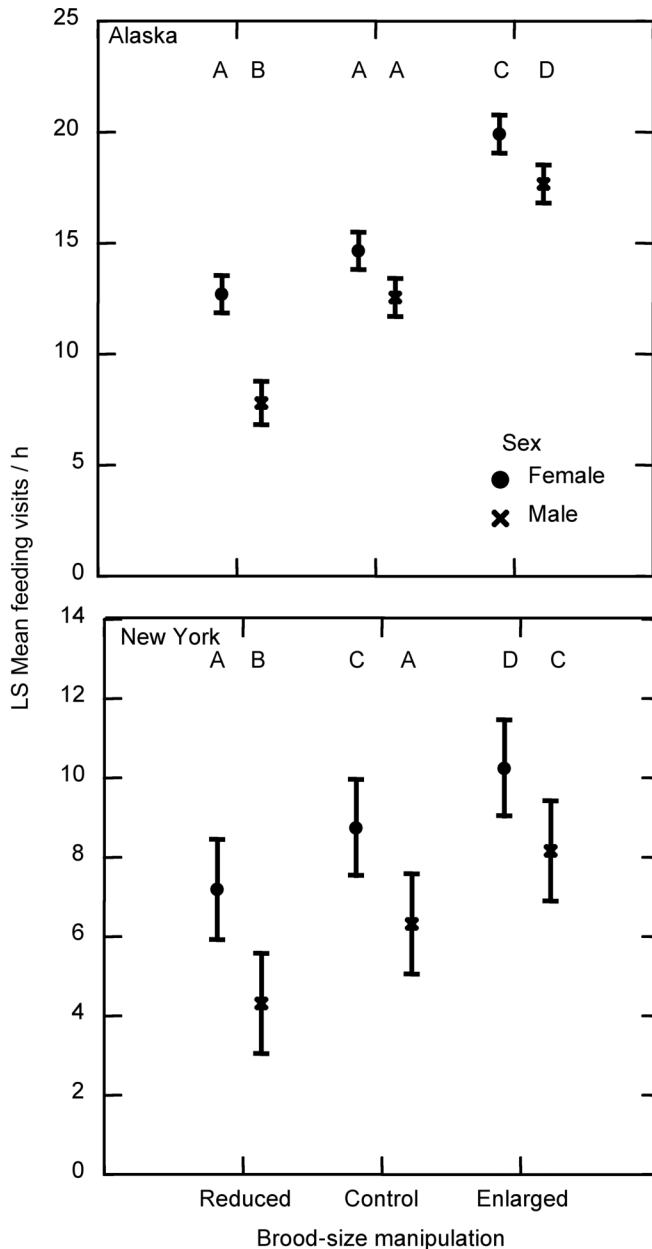
feeding rate (Fig. 2; $F_{[1,60]} = 7.8$, $P = 0.007$), but there was no sex difference in the effect of food on feeding rate (sex × food interaction: $F_{[1,60]} = 0.5$, $P = 0.49$). There was no effect of female age, clutch initiation date, or initial clutch size on visitation ($F_{[1,60]} \leq 1.3$, $P \geq 0.26$).

In New York, males and females responded similarly; both sexes increased feedings to enlarged broods and decreased feedings to reduced broods (Fig. 1; overall model: $R^2 = 0.46$; sex: $F_{[1,85]} = 9.7$, $P = 0.004$; brood-size manipulation: $F_{[2,86]} = 3.8$, $P = 0.02$; sex × manipulation: $F_{[2,60]} = 0.1$, $P = 0.91$). Relative to control broods, males and females showed a similar increase in feeding rate to enlarged broods

(25% vs. 28%) and a similar decrease to reduced broods (30% vs. 25%). There was neither an effect of food availability on visitation (Fig. 2; $F_{[1,86]} = 0.2$, $P = 0.67$) nor any effects of female age, clutch initiation date, initial clutch size, or food availability on visitation ($F_{[1,86]} \leq 2.1$, $P \geq 0.15$).

There was no difference in factors affecting offspring quality when each site was analyzed separately, so both sites were combined in the final analysis. Increased feeding rate was correlated with offspring quality, with male and female feeding visits affecting offspring differently. Male feeding visits were correlated with nestling residual body mass ($\beta = 0.198$, $F_{[1,82]} = 29.3$, $P = 0.0001$, $R^2 = 0.31$; Fig. 3), but male visits had no effect on nestling growth rate ($P > 0.24$).

Fig. 3. Partial regression plot of the effect of residual male and female tree swallow feeding visits on residual nestling growth and residual body mass. Growth rate is a composite of growth of three structural measures: head–bill length, tarsus length, and ninth primary wing feather. Residual body mass is the residual of a regression of head–bill length vs. body mass. See text for description of how partial regression plots were calculated.
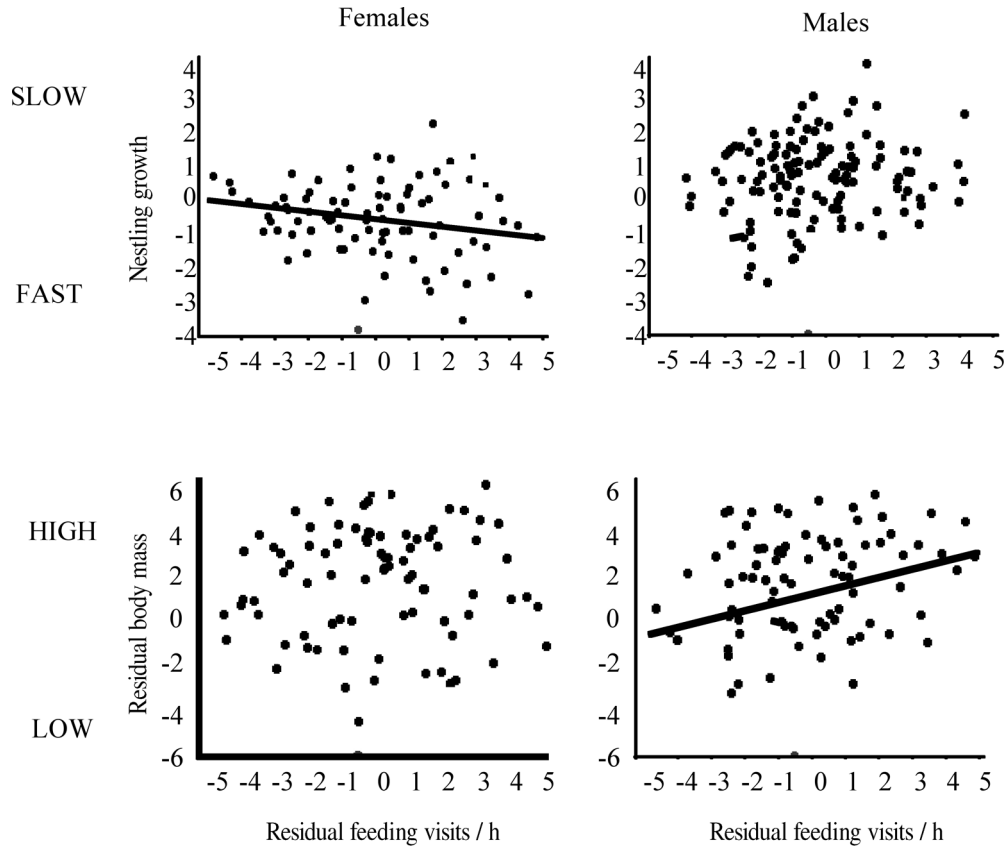
The converse was true for females; female feeding visits were correlated with nestling growth rate ($\beta = -0.10$, $F_{[1,82]} = 17.26$, $P = 0.0001$, $R^2 = 0.18$) but not with residual body mass ($P > 0.22$; Fig. 3). There was no effect of the number of nest mates or difference in number of nest mates prior to brood-size manipulation on either residual body mass or growth rate ($P \geq 0.42$).

Discussion

In species with biparental care, differences in the costs and benefits of reproductive effort may lead males to show different sensitivity to changes in offspring demand compared with females. Males responded differently compared with females following an experimental manipulation, but only in one site, Alaska. In Alaska, males reduce provisioning to a greater extent than females (55% vs. 5%), while in New York, both sexes reduced provisioning similarly (25%–30%). At both sites, males and females increased feeding effort in enlarged broods, but the difference between males and females was much larger in Alaska (29% vs. 43%) than in New York (28%–30%). Differences in food availability and its link with foraging appears to underlie these differences, supporting studies finding a link between habitat and parental care (Bryant and Westerterp 1983; Tremblay et al. 2003).

The pattern reported here reflect a correlative link be-

tween food availability and parental care in only one site. Food availability was higher in Alaska and feeding rates (both males and females) were higher. In addition, increasing food abundance was correlated with increased feeding visits in Alaska, but not in New York. Differences between breeding sites reported here suggest that when food availability is high, males will make more feeding visits, and that when food availability is correlated with feeding rate, males will be less likely to reduce care. This may be due to overall higher food abundance in Alaska, which may allow males to reduce care without cost to offspring. In New York, there was no link between food abundance and feeding rate and no sex difference in response to the brood-size manipulation. Prey-delivery rate reflects prey mass in tree swallows (McCarty 2002), so differences in prey deliveries should reflect differences in total food ingested by broods, a key component of parental care. Interpreting the role of food availability in driving parental care is difficult; work done in blue tits (*Cyanistes caeruleus* (L., 1758)) in variable habitats (Tremblay et al. 2003) suggests that only in extremely rich habitats will the link between feeding and food become uncoupled. Thus, even though food is abundant in Alaska, it may not be at a level where parental care is unaffected by changes in food availability.

Females fed more than males regardless of site or brood manipulation treatment, a pattern found in other studies in tree swallows (Lombardo 1991). This pattern suggests that

male and female tree swallows may differ in either the cost of foraging and (or) the benefit of investing in young. Without specific information, for example, on the energetic costs of foraging, it is difficult to assess costs. Work done on blue tits suggests that individuals in poorer habitats travel farther in search of food (Tremblay et al. 2005). Costs and benefits to each sex may differ based in part on differences in expectation of relatedness between the sexes (Trivers 1972); however, this does not explain why there might be a site-level difference without knowing whether extra-pair paternity differs between sites. Another difference in benefit between the sexes may be the value of parental care to offspring. The pattern reported here suggests that males show differences in parental care, reflected in feeding behaviour, only under certain conditions; in this case, a site where insect abundance is high and influences feeding rate. This correlation may indicate that feeding rate is more sensitive to food supply and may thus be more costly. Interestingly, I found an increase in feeding rate in enlarged broods in contrast to a previous brood-size manipulation of tree swallows that reported a maximal feeding rate at control brood sizes (Murphy et al. 2000). This suggests that both sites may have higher food availability than in other locations. These results fit with other studies that show sex differences in either responses to offspring in common canaries (*Serinus canaria* (L., 17580) (Kilner 2002) or the effect of foraging in European starlings (*Sturnus vulgaris* L., 1758) (Wright and Cuthill 1990).

Site differences are likely caused by a variety of factors in addition to differences in food availability. I found no differences in clutch size, egg mass, and ambient temperature between sites (Ardia 2005*a*, 2005*b*; Ardia 2006), suggesting that food supply may be the best indicator of environmental conditions between sites. In addition to greater food supply, Alaskan swallows may also be more sensitive to changes in offspring because of differences in longevity, as previous work showed that Alaska tree swallows have lower return rates relative to locations farther south (Ardia 2005*b*). Return rates are not necessarily indicative of survival, but even if these differences in return rates reflect survival, they are difficult to interpret. On the one hand, males in Alaska may have greater pressure to reduce costs of reproduction to maximize survival. However, if indeed survivorship is lower, life-history theory predicts that individuals should show greater effort relative to higher surviving individuals. More work is needed to determine experimentally the conditions that cause males to differ from females in response to brood-size manipulation.

As predicted, increased parental care in offspring led to increases in offspring quality, but with male and female provisioning behaviour affecting nestlings differently. Female feeding effort was correlated with nestling growth rate, while male feeding was linked with residual body mass, contrary to results reported in willow warblers (*Phylloscopus trochilus* (L., 1758)) where male feeding effort increased growth rates (Bjornstad and Lifjeld 1996). Feeding visits in tree swallows reflect prey delivery (McCarty 2002), so differences among parents in feeding visits may not indicate differences in the mass of food delivered. Interestingly, there is no direct effect of brood size on offspring quality (Ardia 2005*a*, 2005*b*), as also reported here. Additional work has

shown that sites differ in nestling development strategies, with Alaskan nestlings showing higher levels of residual body mass, while New York nestlings tend to grow faster; however, there is no difference between sites in rates of growth between body measures (Ardia 2006). A main cause of differences between sexes in their effect on nestlings may reflect differences in diet quality (Johnston 1993; Dawson and Bidwell 2005); the next step in this line of inquiry would be to compare quality of prey across season and among sites. It is possible that males may bring different kinds of food and thus may influence nestlings in different ways, such as seen in blue tits (Banbura et al. 2001), or that males respond to different cues than do females, such as seen in common canaries (Kilner 2002). Because female feeding effort varies less, perhaps female effort contributes to the most important initial component of nestling survival, growth. Larger tree swallow nestlings, especially those with longer wing feathers, may be at a selective advantage, particularly relative to timing of fledging. Residual body mass, an indication of resource stores, may be secondary and thus increased male feeding effort may enhance this second priority of offspring quality. That males increased effort at levels similar to females in enlarged broods is contrary to predictions may reflect a need to maintain a minimum level of offspring quality. My results are contrary to those of Dunn and Robertson (1992) who found that male parental care was less valuable when food availability was high. Here, I report that male care influences offspring quality similarly at both sites.

The direct mechanism by which males and females within a pair assess and respond to each other's level of effort is not clear. Some have suggested that individuals have a set level of effort they exert, a so-called "sealed bid", that is invariant regardless of how their mate changes effort in a variety of species (McNamara et al. 1999; Schwagmeyer et al. 2002), although other experiments have shown the opposite (e.g., Wright and Cuthill 1990; Whittingham et al. 1994). Whittingham et al. (1994) found that female tree swallows only partly compensated for their mate and increased feeding more following mate removal than when male feeding was reduced through handicapping. It is not clear whether males decreased feeding effort in reduced broods in Alaska because of how females responded or vice versa. In this experiment, the brood swap was conducted on nestling day 3, while feeding rates were recorded beginning on nestling day 8, the period of peak demand. Therefore, assessment of the response of mates could have occurred by this time, as models suggest that individuals will make multiple assessments of a mate's response (Houston et al. 2005). Although the results reported here suggest that individuals may be responding more to cues from nestlings rather than a direct assessment of their mate's behaviour, a next step would be to compare parental responses over the course of a breeding attempt.

Acknowledgements

References

Ardia, D.R. 2005a. Individual quality mediates tradeoffs between reproductive effort and immune function in tree swallows. J. Anim. Ecol. **74**: 517–524.

Ardia, D.R. 2005b. Tree swallows tradeoff immune function and reproductive effort differently across their range. Ecology, **86**: 2040–2046. doi:10.1890/04-1619.

Ardia, D.R. 2006. Geographic variation in the tradeoff between nestling growth rate and body condition in the Tree Swallow. Condor, **108**: 601–611. doi:10.1650/0010-5422(2006)108[601: GVITTB]2.0.CO;2.

Banbura, J., Perret, P., Blondel, J., Sauvages, A., Galan, M.J., and Lambrechts, M.M. 2001. Sex differences in parental care in a Corsican Blue Tit *Parus caeruleus* population. Ardea, **89**: 517–526.

Bjornstad, G., and Lifjeld, J.T. 1996. Male parental care promotes early fledging in an open-nester, the willow warbler *Phylloscopus trochilus*. Ibis, **138**: 229–235.

Bryant, D.M., and Westerterp, K.R. 1983. Time and energy limits to brood size in house martins (*Delichon urbica*). J. Anim. Ecol. **52**: 905–925. doi:10.2307/4463.

Burness, G.P., McClelland, G.B., Wardrop, S.L., and Hochachka, P.W. 2000. Effect of brood size manipulation on offspring physiology: an experiment with passerine birds. J. Exp. Biol. **203**: 3513–3520. PMID:11044389.

Chase, I.D. 1980. Cooperative and noncooperative behavior in animals. Am. Nat. **115**: 827–857. doi:10.1086/283603.

Dawson, R.D., and Bidwell, M.T. 2005. Dietary calcium limits size and growth of nestling tree swallows *Tachycineta bicolor* in a non-acidified landscape. J. Avian Biol. **36**: 127–134. doi:10. 1111/j.0908-8857.2005.03406.x.

Dunn, P.O., and Robertson, R.J. 1992. Geographic variation in the importance of male parental care and mating systems in tree swallows. Behav. Ecol. **3**: 291–299. doi:10.1093/beheco/3.4.291.

Hinde, C.A., and Kilner, R.M. 2007. Negotiations within the family over the supply of parental care. Proc. R. Soc. Lond. B Biol. Sci. **274**: 53–60. doi:10.1098/rspb.2006.3692.

Houston, A.I., and Davies, N.B. 1985. The evolution of cooperation and life history in the dunnock, *Prunella modularis*. *In* Behavioural ecology: the ecological consequences of adaptive behaviour. *Edited by* R. Sibly and R. Smith. Blackwell Scientific Publications, Oxford. pp. 471–487.

Houston, A.I., Szekely, T., and McNamara, J.M. 2005. Conflict between parents over care. Trends Ecol. Evol. **20**: 33–38. doi:10.1016/j.tree.2004.10.008. PMID:16701338.

Johnston, R.D. 1993. Effects of diet quality on the nestling growth of a wild insectivorous passerine, the house martin *Delichon urbica*. Funct. Ecol. **7**: 255–266. doi:10.2307/2390203.

Kempenaers, B., Lanctot, R.B., and Robertson, R.J. 1998. Certainty of paternity and paternal investment in eastern bluebirds and tree swallows. Anim. Behav. **55**: 845–860. doi:10.1006/anbe. 1997.0667. PMID:9632472.

Kilner, R.M. 2002. Sex differences in canary (*Serinus canaria*) provisioning rules. Behav. Ecol. Sociobiol. **52**: 400–407. doi:10. 1007/s00265-002-0533-8.

Leffelaar, D., and Robertson, R.J. 1986. Equality of feeding roles and the maintenance of monogamy in tree swallows. Behav. Ecol. Sociobiol. **18**: 199–206. doi:10.1007/BF00290823.

Lombardo, M.P. 1991. Sexual differences in parental effort during the nestling period in tree swallows (*Tachycineta bicolor*). Auk, **108**: 393–404.

McCarty, J.P. 2001. Variation in growth of tree swallows across multiple temporal and spatial scales. Auk, **118**: 176–190. doi: 10.1642/0004-8038(2001)118[0176:VIGONT]2.0.CO;2.

McCarty, J.P. 2002. The number of visits to the nest by parents is an accurate measure of food delivered to nestlings in Tree Swallows. J. Field Ornithol. **73**: 9–14.

McCarty, J.P., and Winkler, D.W. 1999. Foraging ecology and diet selectivity of tree swallows feeding nestlings. Condor, **101**: 246–254. doi:10.2307/1369987.

McNamara, J.M., Gasson, G.E., and Houston, A.I. 1999. Incorporating rules for responding into evolutionary games. Nature (London), **401**: 368–371. PMID:10517633.

Murphy, M.T., Armbrecth, B., Vlamis, E., and Pierce, A. 2000. Is reproduction by Tree Swallows cost free? Auk, **117**: 902–912. doi:10.1642/0004-8038(2000)117[0902:IRBTSC]2.0.CO;2.

Neter, J., Kutner, M.H., Nachtsheim, C.J., and Wasserman, W. 1996. Applied linear statistical models. Irwin, Chicago.

Queller, D. 1997. Why do females care more than males? Proc. R. Soc. Lond. B Biol. Sci. **264**: 1555–1557. doi:10.1098/rspb.1997. 0216.

Robertson, R.J., Stutchbury, B.J., and Cohen, R.R. 1992. Tree swallow. *In* The birds of North America. No. 11. *Edited by* A. Poole, P. Stettenheim, and F. Gill. Academy of Natural Sciences, Philadelphia, Pa., and The American Ornithologists' Union, Washington, D.C. p. 27.

Sanz, J.J., Kranenbarg, S., and Tinbergen, J.M. 2000. Differential response by males and females to manipulation of partner contribution in the great tit (*Parus major*). J. Anim. Ecol. **69**: 74–84. doi:10.1046/j.1365-2656.2000.00373.x.

SAS Institute Inc. 1988. SAS/STAT® user's guide. SAS Institute Inc., Cary, N.C.

Schwagmeyer, P.L., Mock, D.W., and Parker, G.A. 2002. Biparental care in house sparrows: negotiation or sealed bid? Behav. Ecol. **13**: 713–721. doi:10.1093/beheco/13.5.713.

Starck, J.M., and Ricklefs, R.E. (*Editors*). 1998. Variation, constraint, and phylogeny: comparative analysis of growth. *In* Avian growth and development. Evolution within the altricial–precocial spectrum. Oxford University Press, New York. pp. 247–265.

Stearns, S.C. 1992. The evolution of life histories. Oxford University Press, Oxford.

Tremblay, I., Thomas, D.W., Lambrechts, M.M., Blondel, J., and Perret, P. 2003. Variation in Blue Tit breeding performance across gradients in habitat richness. Ecology, **84**: 3033–3043. doi:10.1890/02-0663.

Tremblay, I., Thomas, D.W., Blondel, J., Perret, P., and Lambrechts, M.M. 2005. The effect of habitat quality on foraging patterns, provisioning rate and nestling growth in Corsican Blue Tits *Parus caeruleus*. Ibis, **147**: 17–24. doi:10.1111/j.1474-919x. 2004.00312.x.

Trivers, R.L. 1972. Parental investment and sexual selection. *In* Sexual selection and the descent of man. *Edited by* B. Campbell. Aldine, Chicago. pp. 136–179.

Whittingham, L.A., Dunn, P.O., and Robertson, R.J. 1993. Confidence of paternity and male paternal care: an experimental study

in tree swallows. Anim. Behav. **46**: 139–147. doi:10.1006/anbe. 1993.1169.

Whittingham, L.A., Dunn, P.O., and Robertson, R.J. 1994. Female response to reduced male parental care in birds: an experiment in tree swallows. Ethology, **96**: 260–269.

Winkler, D.W. 1987. A general model for parental care. Am. Nat. **130**: 526–543. doi:10.1086/284729.

Wright, J., and Cuthill, I. 1990. Biparental care: short-term manipulations of partner contribution and brood size in the starling, *Sturnus vulgaris.* Behav. Ecol. **1**: 116–124. doi:10.1093/beheco/ 1.2.116.

Zach, R., and Mayoh, K.R. 1982. Weight and feather growth of nestling Tree Swallows. Can. J. Zool. **60**: 1080–1090.