

Parental investment and brood value in tree swallows, *Tachycineta bicolor*

Meagan H. Hainstock^{1,2)}, Melissa C. Smith^{1,3)}, Julia Carr^{1,4)}
& Dave Shutler^{1,5)}

(¹ Department of Biology, Acadia University, Wolfville, Nova Scotia, Canada B4P 2R6)

(Accepted: 7 November 2009)

Summary

Parent birds are predicted to provide greater care to broods with greater value. Begging vocalizations may provide proximate cues of brood value. Finally, parental quality may also affect care. We assessed parental care in nestling tree swallows (*Tachycineta bicolor*) relative to brood value in both natural broods, and in those where brood size and flea loads (*Ceratophyllus idius*) were manipulated. We also quantified parental quality (based on their size and mass), nestling sex and age (natural broods only), and begging vocalizations (manipulated broods only). Feeding rates were not related to brood value in natural brood sizes (range 2–6), but were positively related over the range (1–8) of manipulated brood sizes. Defence intensity was greater for larger and heavier nestlings, independent of age, in natural broods, but not in manipulated broods. Although measures of parental investment were not significantly related to flea load, flea manipulations did not result in higher flea loads when measured following fledging. Parental feeding rates were not associated with variation in parental morphology, but defence intensity was higher by females with longer tails and by heavier males. In our population of tree swallows, only a few of the predicted relationships from parental investment theory were supported.

Keywords: begging, brood value, parental investment, sex ratios, *Tachycineta bicolor*, tree swallows.

²⁾ Present address: 51 Arlington Street, Winnipeg, MB, Canada R3G 1Y2

³⁾ Present address: 1109 Albert St. W., Moose Jaw, SK, Canada S6H 2Y3

⁴⁾ Present address: 3119 Point Grey Road, Vancouver, BC, Canada V6K 1B3

⁵⁾ Corresponding author's email address: dave.shutler@acadiau.ca

Introduction

Trivers (1972) defined parental investment as care that increases offspring survival at a cost to parents in terms of either reduced survival or reduced ability to invest in other offspring. Hence, parents are predicted to increase investment to offspring that have greater potential fitness benefits (Trivers, 1972); we refer collectively to these traits as brood value. Factors that can increase brood value include the number of young, their size and mass, their age, their sex, and their intensity of parasitism (Trivers & Willard, 1973; Curio, 1987; Clutton-Brock, 1991; Magrath, 1991; Brown & Brown, 1996). Parents may assess brood value based on honest signals such as begging vocalizations (Trivers, 1974; Godfray, 1991). Also, parents that are of higher quality are expected to invest more in their offspring, and to produce higher quality offspring. We tested whether parental investment in tree swallow (*Tachycineta bicolor*) broods varied relative to brood value, begging vocalizations and parental quality, and whether parental quality was associated with brood quality.

Two important components of avian parental investment are feeding and nest defence. Feeding offspring is energetically demanding. To provision nestlings optimally, parents must balance risks of predation and fatigue against foraging abilities and local food supply (Drent & Daan, 1980; Yom Tov & Hilborn, 1981; Wright et al., 1998). Parents may also invest substantially in defence of their offspring, because nest predation is one of the most important factors affecting nesting success in birds (Montgomerie & Weatherhead, 1988). Higher defence intensities can be associated with decreased predation (Andersson et al., 1980; Greig-Smith, 1980; Blancher & Robertson, 1982). However, nest defence may be costly in terms of either risk of injury or death to parents, or in terms of time and energy that could be spent on other activities, such as nestling provisioning.

Broods with more young will be more valuable to parents if they result in a greater contribution of parental genes to subsequent generations (Trivers, 1972; Clutton-Brock, 1991). Parents may favour larger or heavier nestlings because they often have increased chances of survival (Shutler et al., 2006), perhaps because these offspring have better nutrient stores or advantages in aggressive interactions with conspecifics (Garnett, 1981; Tinbergen & Boerlijst, 1990; Magrath, 1991). Thus, there is a tradeoff between number and quality of young that parents can produce. Older broods closer to fledging

may have reduced instantaneous rates of mortality and, in general, higher probabilities of survival (Nur, 1984b; Tinbergen & Boerlijst, 1990; Magrath, 1991). Hence, older offspring are more valuable than younger ones (Andersson et al., 1980). Brood sex ratios may also affect parental investment if fitness benefits of producing sons and daughters differ (e.g., Trivers & Willard, 1973; Komdeur et al., 1997).

Parasites can significantly reduce nestling survival (Lehmann, 1993; Richner et al., 1993) and development (Dufva & Allander, 1996; Heeb et al., 1999; Nilsson, 2003), which could in turn lower brood value and, thus, optimal parental investment. If parents partition investment between current and future reproductive success, they might reduce effort in current, parasitized broods and conserve energy for future breeding attempts (Forbes, 1993). However, in single-brooded species with low adult survivorship rates, such as tree swallows, parents may not have the option of reducing parental investment (Shutler et al., 2006). Thus, if there is no tradeoff between current and future broods, parents may increase investment in current broods to compensate for the negative effects of parasites (Tripet & Richner, 1997; Tripet et al., 2002).

Parental investment may respond to honest signals of nestling need (Trivers, 1974; Godfray, 1991). Previous studies of tree swallows have demonstrated that begging rates honestly convey such information, and that parents respond to begging behaviours related to short-term needs, such as hunger (Leonard & Horn, 1996, 1998, 2001).

Parental investment may also be related to the quality of the parents themselves. High-quality, experienced parents with sufficient resources may provide more care per offspring than low-quality, inexperienced parents (e.g., Tolonen & Korpimäki, 1995). Similarly, if sons are more costly to produce than daughters, which usually occurs when payoffs for larger sons are enhanced from sexual selection, parents in good condition should invest more in sons (Trivers & Willard, 1973; Clutton-Brock, 1986; Sutherland, 2002). Parents' ability to skew avian offspring sex ratios appears limited in most species, but several studies have reported skews that are surprising for vertebrates (Ligon & Ligon, 1990; Heinsohn et al., 1997; Komdeur et al., 1997; West & Sheldon, 2002), given the constraints of chromosomal sex determination (Williams, 1979).

Tree swallows are secondary cavity nesters that are well-studied because they nest readily in artificial boxes and tolerate a variety of manipulations

(Robertson et al., 1992). They are socially monogamous passerines, in which both parents provide care to nestlings. Adult male tree swallows are approximately 4% larger than females (Whittingham & Dunn, 2000), which is comparable to sexual dimorphism of great tits (*Parus major*), a species in which body size is heritable (Garnett, 1981) and where larger males can have greater reproductive success (Kölliker et al., 1999). Tree swallows have one of the highest known levels of extra-pair paternity among birds, so that genetic monogamy is the exception (Lifjeld et al., 1993; Dunn et al., 1994; Barber & Robertson, 1999). Hence, parents in good condition might favour sons if those sons were more likely to be successful in gaining extra-pair fertilizations (Whittingham & Dunn, 2000). Tree swallow nests are commonly infested with fleas (*Ceratophyllus idius*) that breed during the nesting season when swallow nestlings and adults are available for regular blood meals (Benton, 1980; Pilgrim & Galloway, 2000).

We investigated parental investment (feeding rates and experimentally-provoked nest defence) relative to brood value, in both natural broods and in those in which brood size and flea loads were manipulated. We predicted that parental investment would be greater for broods of greater value, indexed by number, size, mass, age, and sex ratio of nestlings, and intensity of flea parasitism. We also tested for effects of begging rates on parental investment in experimentally manipulated broods, and investigated whether parental quality (size and mass) influenced parental investment and quality of broods produced in natural broods. In addition, we investigated whether feeding and defence were correlated, to test for a trade-off between these two forms of parental investment.

Methods

General methods

All procedures were approved by the Acadia Animal Care Committee, and abided by accepted guidelines (Canadian Council on Animal Care, 1993; Gaunt & Oring, 1997). Permits were provided by the Canadian Wildlife Service.

Data were collected from May to July in 2001, 2003 and 2004. Our tree swallows occupied nestboxes that had been erected in spring 2000, a minimum of 25 m apart and facing south to minimize microclimatic variation,

within seven grids near Wolfville, Nova Scotia (45°06'N–64°18'W; see Shutler et al., 2004a). All nestboxes were visited at the same rate to record nest initiation date (day of first egg), clutch size, hatching date (day first egg hatched), and number of young fledged (number of nestlings banded at day 12, where hatching date is designated as day 1, less any dead found in boxes on day 22). We avoided disturbing birds in inclement weather.

In 2001, we tested parental investment theory using observational data. In 2003 and 2004, we modified our foci and methods, and experimentally manipulated flea intensity and brood size to evaluate parental investment.

Parental investment

In tree swallows, the number of parental visits to the nest is an accurate measure of food delivery (McCarty, 2002). Feeding rate is maximal by day 8 and remains so until after day 16, and it does not vary relative to time of day or time of year (McCarty, 2002; Shutler et al., 2006; this study). In 2001, observations of feeding rate occurred in both the morning and afternoon on each of days 8, 12 and 16, except in inclement weather. A concealed observer, located ≥ 30 m from the nestbox and using binoculars or a spotting scope, recorded the number of feeding visits made by both male and female parents during 20-min observation sessions. In 2003 and 2004, recordings were made using a lapel microphone concealed in the nest box and a portable cassette recorder concealed in vegetation below the box. These 45-min recordings were taken in both the morning and afternoon on each of days 8, 10 and 12. Recordings were digitized and used to determine the number of feeding trips over 20-min observation periods.

In all years, to control for disturbance from observers, observation periods commenced when the first feeding trip occurred. After the first trip, feeding rates were evenly spaced within observation periods (unpubl. data). We pooled feeding observations for each box and converted them to a rate per hour. However, when analyzing relationships between nestling ages and feeding in 2001, we pooled feeding rates within days 8, 12 and 16.

To assess parental defence intensity in 2001, we used a variety of predator models because we were uncertain as to which one would elicit measurable responses. Aggressive behaviours toward a home-made plasticine weasel, a commercially-purchased plastic owl, and a human intruder were quantified for 5 min. To control for the possibility that tree swallows reacted to any

foreign objects around their nests, a museum mount of a dark-eyed junco (*Junco hyemalis*) was also used as a control. Model nest predators and the control junco were placed directly on top of nestboxes, whereas the human intruder stood 0.5 m away from the nestbox, facing the entrance hole, but not watching the adults (Knight & Temple, 1986a). Parents at each nest were presented only once with each predator. Presentations were made on days 6, 8, 10 and 12, and only after feeding rates had been monitored. Order of presentation was randomized for each nest. A 30-s period was allowed for observers to retreat to ≥ 30 m from the nestbox prior to recording. As measures of defence intensity, we recorded the number of dives made by adult birds (Greig-Smith, 1980; Blancher & Robertson, 1982; Knight & Temple, 1986b), and the number of parental alarm calls (recorded with a cassette player placed on the ground under the box). Parents flew too quickly to allow us to distinguish females from males. Moreover, extra birds sometimes joined in attacks on predators. These individuals could not be distinguished from the pair associated with the box, so observers counted adults during presentations.

Because all three simulated predators provoked defence responses in 2001, we used only a human intruder in 2003 and 2004, on days 10 and 12 after afternoon feeding observations. In addition to counting dives, a simultaneous 5-min recording was also taken, and later digitized to quantify alarm calls, raspy aggression calls and ticking aggression calls (Robertson et al., 1992), viewed in a spectral display in Adobe Audition[®].

Brood value

In all years, nestlings were given uniquely numbered Canadian Wildlife Service aluminum bands at day 12. At this time, nestling head length was measured to the nearest 0.1 mm using callipers, and tail and first primary feather length were measured to the nearest 0.1 mm using a wing ruler. Nestlings were also weighed to the nearest 0.1 g using spring balances. By day 12, nestling tail and wing lengths have reached approximately 60% of their adult size (Zach & Mayoh, 1982) and their body mass is slightly greater than adult mass, but is significantly correlated with mass at fledging.

In 2001, for 31 nests, blood was taken from the brachial vein of each adult and the metatarsal vein of all 147 offspring that reached 6 days of age. Using 25 or 28 gauge needles and microhaematocrit capillary tubes,

50–150 μ l blood was drawn (Barber et al., 1998) and stored in 600 μ l lysis buffer (Seutin et al., 1991). Samples were refrigerated at 4°C until molecular sexing was done (blind with respect to behavioural observations). DNA was isolated from blood samples using DNeasy tissue kits (Qiagen). Amplifications were carried out using the P2/P8 primer pair of Griffiths et al. (1998). PCR reaction mixtures (25 μ l) consisted of 20 mM Tris-HCl (pH 8.4) and 50 mM KCl (both in the 10 \times reaction buffer), 2.5 mM MgCl₂, 1.6 μ M P₈ primer, 0.8 μ M P₂ primer (Griffiths et al., 1998), 200 μ M of each dNTP and 1 U Platinum *Taq* DNA polymerase (Gibco BRL). Amplification conditions were as follows: 94°C/120 s, 45 \times (94°C/30 s, 55°C/45 s, 72°C/45 s), 72°C/300 s. PCR products were digested following manufacturers' instructions with *Hae*III (MBI Fermentas) to differentiate male and female products (Whittingham et al., 2000). Digested products were electrophoresed at 100 V for approximately 60 min on 2% agarose gels, stained with ethidium bromide, and visualised on a Gel Doc UV light system (Bio-Rad). A set of known sex adult tree swallows (12 males and 10 females) was tested prior to using the method on nestlings. In all cases, molecular sexing matched field sexing of adults.

In 2003, as each nest was initiated, it was sequentially assigned to one of five treatments (+fleas/–2 eggs, +fleas/+2 eggs, –2 eggs, +2 eggs, and control). When 2–4 eggs had been laid, 40 fleas were added to +fleas treatments, whereas other nests were visited but left unmanipulated. When clutches were complete, two eggs were transferred from –2 eggs to +2 eggs treatments, and eggs in control nests were handled but not moved. In 2004, nests were not sequentially assigned to treatments until clutches were complete. This ensured that nestling development in nests paired for clutch manipulations was more synchronous. Although methods of clutch manipulation were the same as in 2003, a later assignment to treatment made it necessary to delay flea manipulations until after clutches were complete. The number of fleas added to +flea nests was also doubled in 2004 (40 adults added at each experimental nest within 48 h of clutch completion and 40 adults added at each experimental nest within 48 h of hatch).

Begging vocalizations

In 2003 and 2004, begging behaviours were measured using the same digitized recordings described above for feeding observations. To measure begging rate, a 5-s begging sequence was digitized from the beginning of each

feeding trip. Sequence lengths were based on the average length of parental visits in 2003, to ensure that adults were present. Using Adobe Audition®, begging sequences were viewed as 0.5-s frames in a spectral display and begging rate was the number of begging syllables visible for the entire 5-s sequence.

Parental quality

In all years, adults were trapped inside nestboxes, banded between nestling day 3 and 5, and measured as described above for nestlings. Adult sex was determined based on brood patches (present for females and absent for males). Female age, either second-year or after-second-year, was determined based on plumage (Stutchbury & Robertson, 1985). Adult sex and age were often verified by multiple captures during the breeding season. We retained second-year females in our analyses (3 in 2001, 3 in 2003 and 8 in 2004) because their exclusion did not qualitatively change results. In 2001 only, adults were given unique color combinations on their chests, wings, or tails using non-toxic acrylic paints or felt markers.

Analyses

Nests were the unit of analysis, and we used average size and mass measures for each brood. Nestling size measures and mass were considered separately because mass is not structural or related to feather growth in tree swallows (Zach & Mayoh, 1982), and because it is a significant predictor of subsequent recruitment (Shutler et al., 2006).

Sample sizes varied among analyses because it was not always possible to measure every variable for each brood. Statistical analyses were performed using SAS (SAS Institute, Cary, NC, USA). We normalized variable distributions (assessed with Shapiro–Wilks tests) as much as possible using transformations (square root for owl defence, human defence, diving rate, raspy aggression calls and flea load; $\log(x + 1)$ for alarm calls and ticking aggression calls; none for remaining variables).

We used Principle Components Analysis (PCA) on the correlation matrix of closely related variables to reduce the number of analyses we ran. Using the broken stick model, only PCs (variable names in capital letters) that explained more variation than expected by chance were retained for analysis (Jackson, 1993). In all cases, a maximum of one PC was retained (Table 1). In PCAs of adult morphology from 2001 (head length, tail length,

Table 1. Principle component variables (PCs) used in statistical analysis.

Composite variables	PC	First eigenvalue	% of variation explained
Weasel calls, weasel dives, owl calls, owl dives, human calls, human dives	DEFENCE 2001	3.2	54
Weasel calls, weasel dives	WEASEL DEFENCE 2001	1.6	79
Owl calls, owl dives	OWL DEFENCE 2001	1.8	90
Human calls, human dives	HUMAN DEFENCE 2001	1.7	86
Human calls, human dives	HUMAN DEFENCE 2003-04	2.6	64
Head length, tail length, wing length	DAY-12 SIZE 2001	2.3	78
Head length, tail length, wing length	DAY-12 SIZE 2003-04	2.6	64

and wing length), PC1 explained less variation than expected by chance for both females (first eigenvalue 1.4, 47% of variation explained) and males (first eigenvalue 1.2, 40% of variation explained). This suggested that adult morphological measures were independent, so they were treated as separate variables.

We used general linear models (GLMs) to simultaneously test for significant effects of explanatory variables; those with the largest *p* values were sequentially dropped until only significant associations remained (Sorci et al., 1996). To control for multicollinearity in GLMs with measures of brood value as predictors, those measures that were significantly correlated with brood size (2003–2004 nestling mass, begging rate and flea load) were replaced by residuals from regressions on brood size.

Knight & Temple (1986a,b) proposed that parents would react to repeated perceived success in driving off simulated predators with increasingly aggressive defensive behaviours, leading to a spurious correlation between defence intensity and nestling age. Because we presented the weasel and owl only once to each nest, a positive correlation between intensity of defence and nestling age should only be explained by brood value. However, because humans visited nests repeatedly, we could not reliably distinguish between brood value and acclimatization as explanations for more intense swallow responses to humans. We, thus, tested whether swallow defence varied relative to brood age separately for weasels and owls. In this case, we used PCA to create single response variables for each predator (Table 1).

In univariate analyses involving proportion sons, we used logistic regression rather than GLMs (Wilson & Hardy, 2002). When GLMs were repeated so that the explanatory variables brood size and flea load were replaced with egg treatment (+2, 0 or -2) and flea load per nestling, respectively, results were essentially unchanged.

Results

General observations

The total number of nests initiated was 52 in 2001, 43 in 2003 and 53 in 2004. The number of nests that survived long enough to produce data for analyses was 32 in 2001, 30 in 2003 and 20 in 2004. Mean \pm SD brood size was 4.7 ± 0.8 (range 2–6) in 2001 and 4.5 ± 1.7 (range 1–8) after experimental manipulations in 2003 and 2004. Nestling and parental morphology, and parental feeding rates were comparable to data reported elsewhere (Robertson et al., 1992) for all years.

Over the course of this study, nestlings died in 10 nests when they were between 6 and 12 days of age (1 nestling in each of 6 nests in 2001; 1 nestling in each of 3 nests and 4 nestlings in 1 nest in 2003–2004). Because we did not count nestlings between these ages, we cannot be certain of when mortality occurred. However, excluding these nests from analyses did not qualitatively affect results.

In 2001, at 17 of 29 nests, there were no calls or dives in response to the junco control predator, although no calls or dives occurred at least once in response to each of the other predators. Responses to the junco that did occur were minimal (median calls 0, maximum 69; median dives 0, maximum 7). As further evidence that the junco was not perceived as a threat, parents entered nestboxes at 7 trials, sometimes more than once, presumably to feed young. In contrast, calls and dives were both more frequent for experimental predators (median calls 2.5, 96 and 29, maxima 234, 609 and 523; median dives 0.5, 18.5 and 7.5; maxima 91, 162 and 123, for weasel, owl and human, respectively). This suggests that tree swallows usually treated each of the simulated predators as genuine.

In 2003–2004, duration of incubation, hatching success, duration of nestling period, and fledging success did not differ among clutch size manipulations (Kruskal–Wallis tests: all $p > 0.390$) or flea load manipulations

(Kruskal–Wallis tests: all $p > 0.070$). Number of young fledged was significantly correlated with manipulated clutch size ($r = 0.86$, $p < 0.001$).

Parental investment, brood value and begging rate

In 2001, there were no significant relationships between maternal or paternal feeding rates and our first four indices of brood value (Table 2; also, no significant relationship remained after sequential variable removal). Feeding rate did not change significantly over this range in brood ages (age nested within box; box $F_{30,59} = 1.8$, $p = 0.03$; age $F_{1,59} < 0.1$, $p = 0.97$). In fact, slopes of feeding rates were negative at 15 boxes, positive at 15 boxes and flat at 1 box.

In 2003–2004, larger broods were fed more often than small broods, but each nestling in larger broods received less food (final model of feeding rate per brood: $R^2 = 0.16$, $F_{4,35} = 6.0$, $p = 0.02$; final model of feeding rate per nestling: $R^2 = 0.44$, $F_{4,35} = 25.8$, $p < 0.001$; also see Shutler et al., 2006) and weighed less (final model: $R^2 = 0.34$, $F_{1,34} = 16.8$, $p < 0.001$).

Greater DEFENCE-2001 was associated with greater brood value (Table 2). Brood size and proportion sons were not significantly associated with DEFENCE-2001. Because DAY-12 SIZE 2001 and day-12-mass 2001 were

Table 2. Associations between parental investment and brood value.

Explanatory variable	Maternal feeding 2001		Paternal feeding 2001		Parental feeding 2003–2004		DEFENCE 2001		HUMAN DEFENCE 2003–2004	
Number in brood	0.1	0.76	0.1	0.68	3.4	0.07	0.3	0.57	0.2	0.69
DAY-12 SIZE	0.1	0.80	2.9	0.10	0.1	0.75	2.7	0.12	0.1	0.83
Day-12-mass	0.4	0.56	0.7	0.43	0.1	0.72	4.1	0.06	2.0	0.17
Proportion sons	2.9	0.10	2.2	0.15			<0.1	0.91		
Begging rate					1.3	0.27			<0.1	0.99
Flea load					2.4	0.13			0.1	0.83
Overall model										
<i>N</i>		29		29		35		25		27
<i>R</i> ²		0.12		0.16		0.25		0.39		0.15
<i>F</i>		0.8		1.1		1.9		3.2		0.5
<i>p</i>		0.54		0.37		0.13		0.03		0.74

Shown are results of general linear models with each of the explanatory variables entered simultaneously (different variables were measure in different years). Some associations became significant in final models (see text).

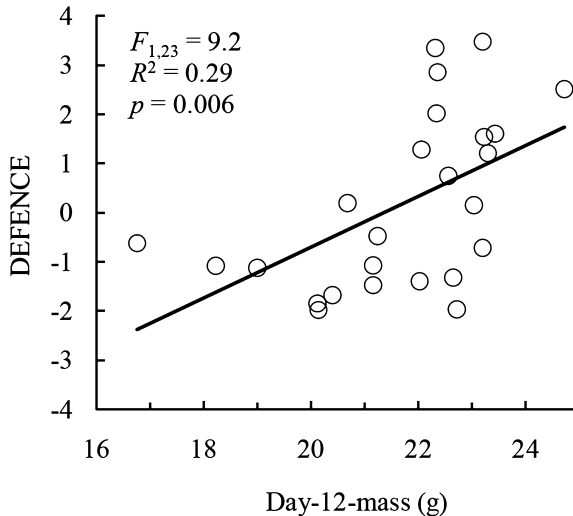


Figure 1. In 2001, DEFENCE (the first principal component from a principal components analysis of calls and dives for weasel, owl, and human predator presentations) was greater for broods with greater day-12 masses (total brood mass/number in brood).

correlated ($r = 0.48$, $p = 0.006$), we ran separate univariate analyses on these variables; DEFENCE-2001 was strongly associated with both DAY-12 SIZE 2001 ($F_{1,23} = 8.8$, $p = 0.007$) and day-12-mass 2001 (Figure 1). Although more neighbours were likely to be present when we recorded vigorous DEFENCE-2001 ($r = 0.62$, $p = 0.001$), separate GLMs, that simultaneously considered the number of birds present, confirmed that DEFENCE-2001 was still predicted by DAY-12 SIZE 2001 ($F_{1,22} = 4.2$, $p = 0.05$) and day-12-mass 2001 ($F_{1,22} = 6.1$, $p = 0.02$). Note that day-12-mass 2001 did not vary with brood size ($R^2 = 0.006$, $p = 0.68$). There were no significant relationships between nestling age and WEASEL ($r = -0.18$, $p = 0.34$, $N = 29$), OWL ($r = 0.09$, $p = 0.63$, $N = 28$), or HUMAN 2001 ($r = 0.26$, $p = 0.17$, $N = 29$) DEFENCE. In GLMs of HUMAN DEFENCE 2003-04, no predictors relating to brood value were significant (Table 2).

Our measures of parental investment were not significantly related to intensity of flea parasitism in manipulated broods. Although we found a positive relationship between flea load and brood size ($R^2 = 0.17$, $F_{1,34} = 6.7$, $p = 0.014$), flea loads were lower than expected (range 0–7, mean 1.5; cf., Shutler et al., 2004b; Shutler & Campbell, 2007, who found as many as 1700 fleas in unmanipulated nests).

Neither feeding rate nor HUMAN DEFENCE 2003-04 was significantly associated with residual begging rate in manipulated broods.

Parental quality and parental investment

Variation in feeding rate was not associated with morphology of female (saturated model $R^2 = 0.13$, $F_{4,22} = 0.8$, $p = 0.52$) or male (saturated model $R^2 = 0.15$, $F_{4,22} = 1.0$, $p = 0.45$) parents in 2001, even after the least significant variables were sequentially removed from the model. In contrast, defence intensity was greater at nests associated with females with longer tails (final model $R^2 = 0.22$, $F_{1,23} = 6.7$, $p = 0.02$) and at nests associated with males of greater mass (final model $R^2 = 0.21$, $F_{1,23} = 5.4$, $p = 0.03$).

Parental quality and brood value

Because parents' morphological measurements were independent (see above), we had to relate each of four measures of parental quality with four measures of brood value, requiring 8 separate analyses (Table 3). For females, the only significant result was a negative relationship between proportion sons and female head length (Wald $\chi^2 = 4.8$, $p = 0.03$). For males, number in brood was positively related to male head length ($F_{1,28} = 5.7$, $p = 0.02$) and negatively related to male tail length ($F_{1,28} = 5.3$, $p = 0.03$; final model $R^2 = 0.27$, $F_{2,28} = 5.3$, $p = 0.01$). In addition, heavier nestlings were associated with heavier males (final model $R^2 = 0.18$, $F_{1,28} = 5.9$, $p = 0.02$) (Table 3).

Feeding rate was independent of DEFENCE in 2001 ($N = 24$, $r = 0.12$, $p = 0.58$) and 2003–2004 ($N = 22$, $r = 0.22$, $p = 0.33$).

Discussion

General findings

Parental feeding rate was not associated with any of four measures of brood value in natural nests. However, feeding rates increased, while per capita feeding rates decreased, with brood size in manipulated nests. Parental defence was greater for broods that were structurally larger and heavier in natural nests, but was unrelated to any measure of brood value in manipulated

Table 3. Associations between parent morphology and measures of brood value in 2001.

Explanatory variable (1 df each)	Response variable			
	Number in brood	DAY-12 SIZE 2001	Day-12 mass 2001	Proportion sons
Female parent				
Head length	0.5	1.6	3.0	3.8*
Tail length	0.3	3.5	1.9	2.3
Wing length	0.2	2.2	0.3	0.4
Mass	0.2	2.3	3.5	0.6
Overall model				
R^2	0.03	0.22	0.28	
F	2.30	1.70	2.30	
p	0.09	0.19	0.09	
Male parent				
Head length	5.9*	0.9	0.4	0.4
Tail length	6.3*	0.1	0.7	0.4
Wing length	0.7	0.3	0.8	1.0
Mass	0.0	2.2	6.2*	1.0
Overall model				
R^2	0.33	0.16	0.23	
F	3.00	1.20	1.80	
p	0.04*	0.34	0.16	

For the first three response variables, shown are F values from general linear models before non-significant associations were removed. For proportion sons, shown are Wald χ^2 values. Directions of significant relationships (indicated with asterisks; $p < 0.05$) are reported in the text.

nests. In manipulated nests, parents did not appear to base feeding rate or defence on nestling begging rates or intensity of parasitism.

In natural nests, feeding rate was not associated with any of four morphological measures of female or male parents, but greater defence was associated with female parents that had longer tails and with male parents that had greater mass.

Of four measures of brood value, only proportion of sons was associated with measures of maternal quality; females with larger heads produced fewer sons.

We cannot distinguish between spuriousness and legitimate significance among the many tests we conducted (Rothman, 1990; Nakagawa, 2004), so

we suggest caution in ascribing too much weight to individual results (data to calculate effect sizes available upon request).

Parental investment and brood value

Feeding can be the most energetically demanding kind of parental investment, but it may, at least in the short term, impose fewer risks than defending against predators. Generally, larger broods receive more food on average than smaller ones, but each nestling in a large brood receives less (Nur, 1984a; Leffelaar & Robertson, 1986; Rytönen et al., 1990), as was observed in our manipulated broods. Accordingly, nestlings in our experimentally enlarged broods were significantly lighter than those in small broods.

Feeding rate can be influenced by nestling age (e.g., Yom-Tov & Hilborn, 1981). However, this variation is primarily limited to bottlenecks in food intake that occur early in life before linear growth begins (e.g., Ricklefs, 1973), which would be before we began monitoring. Previous studies have not found consistent relationships between offspring sex ratios and feeding rates (Leonard et al., 1994; Nishiumi et al., 1996; Lessells et al., 1998; Leech et al., 2001), so it is premature to judge the generality of the non-significant association we found, although our results are consistent with Whittingham et al.'s (2003) tree swallow study.

Most predictions relating defence to brood value were not supported. In contrast to our findings, greater nest defence has been reported for broods with more nestlings (Greig-Smith, 1980; Curio & Regelman, 1987; Curio & Onnebrink, 1994). However, other studies (Regelman & Curio, 1983; Hakkarainen & Korpimäki, 1994; Rytönen et al., 1995), including two of tree swallows (Winkler, 1991, 1992), failed to detect these relationships. In some species, brood size may not be a good predictor of offspring value to parents because the number of offspring that survive to fledging is still constrained by parental ability (and condition). The most valuable brood size could, therefore, be considered relative to individual parental ability and experience, so that a small brood for poor-quality parents may have the same relative value as a large brood for good-quality parents (Rytönen et al., 1995; Tolonen & Korpimäki, 1995). If parents produce brood sizes independent of their defence abilities, only brood manipulations properly test the relationship between brood size and defence. We found no significant relationship between defence and brood value in manipulated brood sizes.

Generally, defence increases with brood age, even after controlling for acclimatization to predators (Montgomerie & Weatherhead, 1988; Forbes et al., 1994). We found no evidence for changes in parent defence or acclimatization. Possibly, parents were more energetically stressed later in the breeding cycle, so that they did not increase feeding rates. Alternatively, we may have observed effects if we monitored defence over a greater age range because brood value may begin to asymptote by 8 days. As is the case for feeding, parental defence is not consistently affected by offspring sex ratio (Nishiumi et al., 1996; Lessells et al., 1998; Radford & Blakey, 2000). Thus, it is difficult to generalize about the importance to parental defence of offspring sex ratios. Nonetheless, conflicting results to date suggest that sex ratio is less important than other aspects of brood value. Another index of brood value that we did not measure, paternity, similarly has no effect on paternal investment in a variety of species, including tree swallows (Whittingham et al., 1993; Dickinson, 2003).

Flea additions did not translate into higher flea populations after fledging, nor was there evidence that flea manipulations significantly affected parental investment. The number of fleas we added was comparable to other studies (e.g., Tripet & Richner, 1999). However, exposure of great tit nestlings to infestations early in the nestling period may actually reduce the reproductive output of fleas (Walker et al., 2003). These results illustrate that the dynamic between nestlings and ectoparasites can shift throughout the nestling period, and may also explain the low flea numbers observed in this study. Flea populations may also be limited by disease, predation, starvation, competition, microclimate, nestling condition and brood mass (Harper et al., 1992; Eeva et al., 1994; Rendell & Verbeek, 1996; Tripet & Richner, 1999).

Parental investment and begging

Although begging rates were significantly associated with potential measures of nestling need and value in this study, begging rate was not a significant predictor of parental feeding rate. This may be because parents base feeding rates on other cues that, whether under nestling control or directly assessed by parents, provide a more accurate measure of brood need or value. For example, previous studies of tree swallows indicate that nestlings closest to parents have a higher probability of being fed, that postural intensity increases with nestling hunger (Leonard & Horn, 1996; Whittingham et al.,

2003), and that parents are more responsive to postural cues, independent of differences in calling rate (Leonard et al., 2003).

Another possibility is that parental ability to assess brood need and value is compromised in enlarged broods. For example, in an experimental manipulation of barn swallow (*Hirundo rustica*) brood size, parents of control and reduced broods based feeding behaviours on nestling need and condition, but parents of enlarged broods did not appear to discriminate (Saino et al., 2000). One interpretation of this is that parents of enlarged broods are working at maximal capacity and are unable to meet nestling needs due to time or energy limits. Similarly, we found that parents defended heavier nestlings more vigorously in natural broods, but not in manipulated broods. However, we did not find a correlation between feeding and defence.

Parental quality and parental investment

Feeding rate was unrelated to parent morphology in 2001. In contrast, defence was greater at nests associated with female parents having longer tails and with male parents that weighed more, despite the potential for these traits to constrain flight. However, parents that defended more intensely did not have extreme physical dimensions, and in particular, higher mass within limits may provide extra energy for greater activity.

Our finding that defence was more vigorous for heavier nestlings suggests that parents that provided their broods with more food were also more aggressive. However, we found no association between feeding rate and defence, in either natural or manipulated broods. This contrasts with two studies where provisioning rates and nest defence were highly correlated (Grieg-Smith, 1980; Rytönen et al., 1995). Some of the flying skills needed for foraging are possibly similar to those needed for reducing risk during defence, but there is also a tradeoff between these investments in terms of time, so that on the whole, parents may not be able to maximize both investments.

Parents in good condition are likely able to invest more in their young without incurring substantial survival costs (Wallin, 1987; Rytönen et al., 1995) and a certain portion of size is heritable (Wiggins, 1989). This is important since nestling mass prior to fledging is a good predictor of subsequent survival in several passerines (Nur, 1984b; Magrath, 1991; Tinbergen & Boerlijst, 1990), including tree swallows (Shutler et al., 2006). However, we found no strong associations in parent-nestling morphology. We could

have considered combined parental morphology, but because rates of extra-pair paternity are so high in this species, we should only expect resemblance between females and their broods, which we did not find.

Parental quality and brood value

In our study, more daughters were produced by females with larger heads. This contrasts with several previous studies (Bradbury & Blakey, 1998; Nager et al., 1999; Aparicio & Cordero, 2001; Whittingham et al., 2002), including two of tree swallows (Whittingham & Dunn, 2000; Whittingham et al., 2005), that found that larger females or females in good condition produced more sons. In any case, it is not known whether sexual size dimorphism in tree swallows is sufficient to make sons significantly more costly to produce than daughters (see Teather & Weatherhead, 1988), or whether larger male tree swallows are more reproductively successful than smaller ones (Peer et al., 2000; Kempenaers et al., 2001). More information is needed regarding lifetime reproductive success of offspring from different broods. However, this information will be difficult to obtain for tree swallows, given that only approximately 5% of locally fledged birds recruit locally, so that the reproductive success of very few young can be determined (Robertson et al., 1992; Shutler & Clark, 2003). Also, male reproductive success may be spread among many nests and it is especially difficult to identify the fathers of extra-pair young if floaters are involved (Barber & Robertson, 1999; Peer et al., 2000; Kempenaers et al., 2001).

Even if sex ratios at conception were not under parental control, biased investment to offspring sexes might occur after hatch (Clutton-Brock, 1991). It is unclear which cues parents could use to detect offspring sex ratios and at what stage (from ova to nestling) detection might occur (Krakow, 1995). Differences between sons and daughters in begging behaviour might facilitate detection by parents (Burley, 1986), although the occurrence of such cues has been noted for only a few species (Stamps et al., 1987; Price et al., 1996). If parents detect offspring sex ratios after hatching, experimental manipulation of brood sex ratios (e.g., Lessells et al., 1998) would be one way to investigate the importance of offspring sex ratios to parental investment. Molecular sexing methods will facilitate such investigations (Ellegren & Sheldon, 1997).

Collectively, our results provided support for only a few of the predictions we tested from parental investment theory. This could be because the

relationships are weak or highly variable, which would mean we had too little statistical power to detect them, particularly for analyses on sex ratios (Ewen et al., 2003). However, many studies cited herein have detected significant associations with comparable sample sizes and experimental designs. Alternatively, the multiple relationships for tree swallows are confounded with each other or with unmeasured variables. Future studies should consider the proportions of adult time- and energy-budgets devoted to all forms of parental investment to experimentally manipulated brood sizes to provide a more comprehensive evaluation of the influence of brood value on parental investment. The discrepancy between our results and other studies, with respect to begging rates and flea loads, also warrants further investigation.

Acknowledgements

Bruce Fuller, Bill and John Kenny, Bert Peters, Jim Keech, Doug Gates, Joe Hickman, and families of the aforementioned tolerated us on their properties. Katie Sparkman, James Windley and Steve Gates provided able field assistance. Don Stewart, Stephen Petersen, members of the Molecular Markers class and molecular lab, Linda Whittingham, Peter Dunn, Colleen Barber, Trina Fitzgerald and Nick Colegrave provided advice and technical assistance. Additional support was provided by Dick Rogers of Wildwood Labs Inc. This manuscript was improved substantially by comments from Marty Leonard, Andy Horn, Tom Herman, Kate Lessells, Adele Mullie, Nathaniel T. Wheelwright and anonymous reviewers. Funding was from NSERC in the form of postgraduate scholarships to the first and second authors, and operating grants to the junior author.

References

- Andersson, M., Wiklund, C.G. & Rundgren, H. (1980). Parental defence of offspring: a model and an example. — *Anim. Behav.* 28: 536-542.
- Aparicio, J.M. & Codero, P.J. (2001). The effects of the minimum threshold condition for breeding on offspring sex-ratio adjustment in the lesser kestrel. — *Evolution* 55: 1188-1197.
- Barber, C.A. & Robertson, R.J. (1999). Floater males engage in extrapair copulations with resident female tree swallows. — *Auk* 116: 264-269.
- Barber, C.A., Robertson, R.J. & Boag, P.T. (1998). Experimental mate replacement does not increase extra-pair paternity in tree swallows. — *Proc. Roy. Soc. Lond. B: Biol.* 265: 2187-2190.
- Benton, A.H. (1980). An atlas of the fleas of the Eastern United States. — *Marginal Media*, Fredonia, NY.
- Blancher, P.J. & Robertson, R.J. (1982). Kingbird aggression: does it deter predation? — *Anim. Behav.* 30: 929-945.

- Bradbury, R.B. & Blakey, J.K. (1998). Diet, maternal condition, and offspring sex ratio in the zebra finch, *Poephila guttata*. — Proc. Roy. Soc. Lond. B: Biol. 265: 895-899.
- Brown, C.R. & Bomberger Brown, M. (1996). Coloniality in the cliff swallow: the effect of group size on social behaviour. — University of Chicago Press, Chicago, IL.
- Burley, N. (1986). Sex ratio manipulation in colour-banded populations of zebra finches. — Evolution 40: 1191-1206.
- Canadian Council on Animal Care (1993). CCAC guide to the care and use of experimental animals, Volume 1, 2nd edition.
- Clutton-Brock, T.H. (1986). Sex ratio variation in birds. — Ibis 128: 317-329.
- Clutton-Brock, T.H. (1991). The evolution of parental care. — Princeton University Press, Princeton, NJ.
- Curio, E. (1987). Brood defence in the great tit: the influence of age, number and quality of young. — Ardea 75: 35-42.
- Curio, E. & Onnebrink, H. (1994). Brood defense and brood size in the great tit (*Parus major*): a test of a model of unshared parental investment. — Behav. Ecol. 6: 235-241.
- Curio, E. & Regelmann, K. (1987). Do great tit, *Parus major*, parents gear their brood defence to the quality of their young? — Ibis 129: 344-352.
- Dickinson, J.L. (2003). Male share of provisioning is not influenced by actual or apparent loss of paternity in western bluebirds. — Behav. Ecol. 14: 360-366.
- Drent, R.H. & Daan, S. (1980). The prudent parent: energetic adjustments in avian breeding. — Ardea 68: 225-252.
- Dufva, R. & Allander, K. (1996). Variable effects of the hen flea *Ceratophyllus gallinae* on the breeding success of the great tit *Parus major* in relation to weather conditions. — Ibis 138: 772-777.
- Dunn, P.O., Robertson, R.J., Michaud-Freeman, D. & Boag, P.T. (1994). Extra-pair paternity in tree swallows: why do females mate with more than one male? — Behav. Ecol. Sociobiol. 35: 273-281.
- Eeva, T., Lehikoinen, E. & Nurmi, J. (1994). Effects of ectoparasites on breeding success of great tits (*Parus major*) and pied flycatchers (*Ficedula hypoleuca*) in an air pollution gradient. — Can. J. Zool. 72: 624-635.
- Ellegren, H. & Sheldon, B. (1997). New tools for sex identification and the study of sex allocation in birds. — Trends Ecol. Evol. 12: 255-259.
- Ewen, J.G., Cassey, P. & King, R.A.R. (2003). Assessment of the randomization test for binomial sex-ratio distributions in birds. — Auk 120: 62-68.
- Forbes, M.R.L. (1993). Parasitism and host reproductive effort. — Oikos 67: 444-450.
- Forbes, M.R.L., Clark, R.G., Weatherhead, P.J. & Armstrong, T. (1994). Risk-taking by female ducks: intra- and interspecific tests of nest defense theory. — Behav. Ecol. Sociobiol. 34: 79-85.
- Garnett, M.C. (1981). Body size, its heritability & influence on juvenile survival among great tits, *Parus major*. — Ibis 123: 31-40.
- Gaunt, A.S. & Oring, L.W. (1997). Guidelines to the use of wild birds in research. — The Ornithological Council special publication, Washington, DC.
- Godfray, H.C.J. (1991). Signalling of need by offspring to their parents. — Nature 352: 328-330.
- Greig-Smith, P.W. (1980). Parental investment in nest defence by stonechats (*Saxicola torquata*). — Anim. Behav. 28: 604-619.

- Griffiths, R., Double, M., Orr, K. & Dawson, R.J. (1998). A DNA test to sex most birds. — *Mol. Ecol.* 7: 1071-1075.
- Hakkarainen, H. & Korpimäki, E. (1994). Nest defence of Tengmalm's owls reflects offspring survival prospects under fluctuating food conditions. — *Anim. Behav.* 48: 843-849.
- Harper, G.H., Marchant, A. & Boddington, D.G. (1992). The ecology of the hen flea *Ceratophyllus gallinae* and the moorhen flea *Dasypsyllus gallinulae* in nestboxes. — *J. Anim. Ecol.* 61: 317-327.
- Heeb, P., Werner, I., Mateman, A.C., Kölliker, M., Brinkhof, M.W.G., Lessells, C.M. & Richner, H. (1999). Ectoparasite infestation and sex-biased local recruitment of hosts. — *Nature* 400: 63-65.
- Heinsohn, R., Legge, S. & Barry, S. (1997). Extreme bias in sex allocation in *Ecliptus* parrots. — *Proc. Roy. Soc. Lond. B: Biol.* 264: 1325-1329.
- Jackson, D.A. (1993). Stopping rules in principal components analysis: a comparison of heuristic and statistical approaches. — *Ecology* 74: 2204-2214.
- Kempnaers, B., Everding, S., Bishop, C., Boag, P. & Roberston, R.J. (2001). Extra-pair paternity and the reproductive role of male floaters in the tree swallow (*Tachycineta bicolor*). — *Behav. Ecol. Sociobiol.* 49: 251-259.
- Knight, R.L. & Temple, S.A. (1986a). Methodological problems in studies of avian nest defence. — *Anim. Behav.* 34: 561-566.
- Knight, R.L. & Temple, S.A. (1986b). Nest defence in the American goldfinch. — *Anim. Behav.* 34: 887-897.
- Kölliker, M., Heeb, P., Werner, I., Matemann, A.C., Lessells, C.M. & Richner, H. (1999). Offspring sex ratio is related to male body size in the great tit (*Parus major*). — *Behav. Ecol.* 10: 68-72.
- Komdeur, J., Daan, S., Tinbergen, J. & Mateman, C. (1997). Extreme adaptive modification in sex ratio of the Seychelles warbler's eggs. — *Nature* 385: 522-525.
- Krakow, S. (1995). Potential mechanisms for sex ratio adjustment in mammals and birds. — *Biol. Rev.* 70: 225-241.
- Leech, D.I., Hartley, I.R., Stewart, I.R.K., Griffith, S.C. & Burke, T. (2001). No effect of parental quality or extrapair paternity on brood sex ratio in the blue tit (*Parus caeruleus*). — *Behav. Ecol.* 12: 674-680.
- Leffelaar, D. & Robertson, R. (1986). Equality of feeding roles and the maintenance of monogamy in tree swallows. — *Behav. Ecol. Sociobiol.* 18: 199-206.
- Lehmann, T. (1993). Ectoparasites: direct impact on host fitness. — *Parasitol. Today* 9: 8-13.
- Leonard, M.L. & Horn, A.G. (1996). Provisioning rules in tree swallows. — *Behav. Ecol. Sociobiol.* 38: 341-347.
- Leonard, M.L. & Horn, A.G. (1998). Need and nestmates affect begging in tree swallows. — *Behav. Ecol. Sociobiol.* 42: 431-436.
- Leonard, M.L. & Horn, A.G. (2001). Begging calls and parental feeding decisions in tree swallows (*Tachycineta bicolor*). — *Behav. Ecol. Sociobiol.* 49: 170-175.
- Leonard, M.L., Horn, A.G. & Parks, E. (2003). The role of posturing and calling in the begging display of nestling birds. — *Behav. Ecol. Sociobiol.* 54: 188-193.
- Leonard, M.L., Teather, K.L., Horn, A.G., Koenig, W.D. & Dickinson, J.L. (1994). Provisioning in western bluebirds is not related to offspring sex. — *Behav. Ecol.* 5: 455-459.
- Lessells, C.M., Oddie, K.R. & Mateman, A.C. (1998). Parental behaviour is unrelated to experimentally manipulated great tit brood sex ratio. — *Anim. Behav.* 56: 385-393.

- Lifjeld, J.T., Dunn, P.O., Robertson, R.J. & Boag, P.T. (1993). Extra-pair paternity in monogamous tree swallows. — *Anim. Behav.* 45: 213-229.
- Ligon, J.D. & Ligon, S.H. (1990). Female-biased sex ratio at hatching in the green woodhoopoe. — *Auk* 107: 765-777.
- Magrath, R.D. (1991). Nestling weight and juvenile survival in the blackbird, *Turdus merula*. — *J. Anim. Ecol.* 60: 335-351.
- McCarty, J.P. (2002). The number of visits to the nest by parents in an accurate measure of food delivered to nestlings in tree swallows. — *J. Field Ornithol.* 73: 9-14.
- Montgomerie, R. & Weatherhead, P.J. (1988). Risks and rewards of nest defence by parent birds. — *Q. Rev. Biol.* 63: 167-186.
- Nager, R.G., Monaghan, P., Griffiths, R., Houston, D.C. & Dawson, R. (1999). Experimental demonstration that offspring sex ratio varies with maternal condition. — *Proc. Natl. Acad. Sci. USA* 96: 570-573.
- Nakagawa, S. (2004). A farewell to Bonferroni: the problems of low statistical power and publication bias. — *Behav. Ecol.* 15: 1044-1045.
- Nilsson, J. (2003). Ectoparasitism in marsh tits: costs and functional explanations. — *Behav. Ecol.* 12: 175-181.
- Nishiumi, I., Yamagishi, S., Maekawa, H. & Shimoda, C. (1996). Paternal expenditure is related to brood sex ratio in polygynous great reed warblers. — *Behav. Ecol. Sociobiol.* 39: 211-217.
- Nur, N. (1984a). Feeding frequencies of nestling blue tits (*Parus caeruleus*): costs, benefits and a model of optimal feeding frequency. — *Oecologia* 65: 125-137.
- Nur, N. (1984b). The consequences of brood size for breeding blue tits II: nestling weight, offspring survival and optimal brood size. — *J. Anim. Ecol.* 53: 497-517.
- Peer, K., Robertson, R.J. & Kempnaers, B. (2000). Reproductive anatomy and indices of quality in male Tree Swallows: the potential reproductive role of floaters. — *Auk* 117: 74-81.
- Pilgrim, R.L.C. & Galloway, T.D. (2000). Descriptions of flea larvae (Siphonaptera: Ceratophyllidae: *Ceratophyllus* spp.) found in the nests of swallows (Aves: Passeriformes: Hirundinidae) in North America, North of Mexico. — *Can. Entomol.* 132: 15-37.
- Price, K., Harvey, H. & Ydenberg, R. (1996). Begging tactics of nestling yellow-headed blackbirds, *Xanthocephalus xanthocephalus*, in relation to need. — *Anim. Behav.* 51: 421-435.
- Radford, A.N. & Blakey, J.K. (2000). Intensity of nest defence is related to offspring sex ratio in the great tit, *Parus major*. — *Proc. Roy. Soc. Lond. B: Biol.* 267: 535-538.
- Regelmann, K. & Curio, E. (1983). Determinants of brood defense in the great tit, *Parus major* L. — *Behav. Ecol. Sociobiol.* 13: 131-145.
- Rendell, W.B. & Verbeek, N.A.M. (1996). Are avian ectoparasites more numerous in nest boxes with old nest material? — *Can. J. Zool.* 74: 1819-1825.
- Richner, H., Oppliger, A. & Christe, P. (1993). Effect of an ectoparasite on reproduction in great tits. — *J. Anim. Ecol.* 62: 703-710.
- Ricklefs, R.E. (1973). Patterns of growth in birds. II. Growth rate and mode of development. — *Ibis* 115: 177-201.
- Robertson, R.J., Stutchbury, B.J. & Cohen, R.R. (1992). Tree Swallow. — In: *The birds of North America*, No. 11. (Poole, A., Stettenheim P. & Gill, F., eds). The Academy of Natural Sciences, Washington, DC.

- Rothman, K.J. (1990). No adjustments are needed for multiple comparisons. — *Epidemiology* 1: 43-46.
- Rytkönen, S., Koivula, K. & Orell, M. (1990). Temporal increase in nest defense intensity of the willow tit (*Parus montanus*): Parental investment or methodological artifact? — *Behav. Ecol. Sociobiol.* 27: 283-286.
- Rytkönen, S., Orell, M., Koivula, K. & Soppela, M. (1995). Correlation between two components of parental investment: nest defense intensity and nestling provisioning effort of willow tits. — *Oecologia* 104: 386-393.
- Saino, N., Ninni, P., Incagli, M., Calza, S., Sacchi, R. & Møller, A.P. (2000). Begging and parental care in relation to offspring need and condition in the barn swallow (*Hirundo rustica*). — *Am. Nat.* 156: 637-649.
- Seutin, G., White, B.N. & Boag, P.T. (1991). Preservation of avian blood and tissue samples for DNA analyses. — *Can. J. Zool.* 69: 82-90.
- Shutler, D. & Campbell, A.A. (2007). Effects on tree swallow nestlings of experimental exposure to yarrow. — *J. Avian Biol.* 38: 7-12.
- Shutler, D. & Clark, R.G. (2003). Causes and consequences of natal and breeding dispersal by Tree Swallows. — *Auk* 120: 619-631.
- Shutler, D., Clark, R.G., Fehr, C. & Diamond, A.W. (2006). Time and recruitment costs as currencies in manipulation studies on the costs of reproduction: evidence from tree swallows. — *Ecology* 87: 2938-2946.
- Shutler, D., Hussell, D.J.T., Horn, A.G., Leonard, M.L., Shutler, R. & Lepage, D. (2004a). Breeding between tree swallows from the same brood. — *J. Field Ornithol.* 74: 353-358.
- Shutler, D., Mullie, A. & Clark, R.G. (2004b). Tree swallow reproductive investment, stress, and parasites. — *Can. J. Zool.* 82: 442-448.
- Sorci, G., Clobert, J. & Michalakakis, Y. (1996). Cost of reproduction and cost of parasitism in the common lizard, *Lacerta vivipara*. — *Oikos* 76: 121-130.
- Stamps, J., Clark, A., Kus, B. & Arrowood, P. (1987). The effects of parent and offspring gender on food allocation in budgerigars. — *Behaviour* 101: 177-199.
- Stutchbury, B.J. & Robertson, R.J. (1985). Floating populations of female Tree Swallows. — *Auk* 102: 651-654.
- Sutherland, W.J. (2002). Science, sex and the kakapo. — *Nature* 419: 265-266.
- Teather, K.L. & Weatherhead, P.J. (1988). Sex-specific energy requirements of great-tailed grackles (*Quiscalus mexicanus*) nestlings. — *J. Anim. Ecol.* 57: 659-668.
- Tinbergen, J.M. & Boerlijst, M.C. (1990). Nestling weight and survival in individual great tits (*Parus major*). — *J. Anim. Ecol.* 59: 1113-1127.
- Tolonen, P. & Korpimäki, E. (1995). Parental effort of kestrels (*Falco tinnunculus*) in nest defense: effects of laying time, brood size and varying survival prospects of offspring. — *Behav. Ecol.* 6: 435-441.
- Tripet, F., Glaser, M. & Richner, H. (2002). Behavioural responses to ectoparasites: time-budget adjustments and what matters to blue tits *Parus caeruleus* infested by fleas. — *Ibis* 144: 461-469.
- Tripet, F. & Richner, H. (1997). Host responses to ectoparasites: food compensation by parent blue tits. — *Oikos* 78: 557-561.
- Tripet, F. & Richner, H. (1999). Density-dependent processes in the population dynamics of a bird ectoparasite *Ceratophyllus gallinae*. — *Ecology* 80: 1267-1277.
- Trivers, R.L. (1972). Parental investment and sexual selection. — In: *Sexual selection and the descent of man* (Campbell, B., ed.). Aldine, Chicago, IL, p. 136-179.

- Trivers, R.L. (1974). Parent-offspring conflict. — *Am. Zool.* 14: 249-264.
- Trivers, R.L. & Willard, D.E. (1973). Natural selection of parental ability to vary the sex ratio of offspring. — *Science* 179: 90-92.
- Walker, M., Steiner, S., Brinkhof, M.W.G. & Richner, H. (2003). Induced responses of nestling great tits reduce hen flea reproduction. — *Oikos* 102: 67-74.
- Wallin, K. (1987). Defence as parental care in tawny owls (*Strix aluco*). — *Behaviour* 102: 213-229.
- West, S.A. & Sheldon, B.C. (2002). Constraints in the evolution of sex ratio adjustment. — *Science* 295: 1685-1688.
- Whittingham, L.A. & Dunn, P.O. (2000). Offspring sex ratios in tree swallows: females in better condition produce more sons. — *Molec. Ecol.* 9: 1123-1129.
- Whittingham, L.A., Dunn, P.O. & Clotfelter, E.D. (2003). Parental allocation of food to nestling tree swallows: the influence of nestling behaviour, sex, and paternity. — *Anim. Behav.* 65: 1203-1210.
- Whittingham, L.A., Dunn, P.O. & Nooker, J.K. (2005). Maternal influences on brood sex ratios: an experimental study in tree swallows. — *Proc. Roy. Soc. Lond. B: Biol.* 272: 1775-1780.
- Whittingham, L.A., Dunn, P.O. & Robertson, R.J. (1993). Confidence of paternity and male parental care: an experimental study in tree swallows. — *Anim. Behav.* 46: 139-147.
- Whittingham, L.A., Valkenaar, S.M., Poirier, N.E. & Dunn, P.O. (2002). Maternal condition and nestling sex ratios in house wrens. — *Auk* 119: 125-131.
- Wiggins, D.A. (1989). Heritability of body size in cross-fostered tree swallow broods. — *Evolution* 43: 1808-1811.
- Williams, G.C. (1979). The question of adaptive sex ratio in outcrossed vertebrates. — *Proc. Roy. Soc. Lond. B: Biol.* 205: 567-580.
- Wilson, K. & Hardy, I.C.W. (2002). Statistical analysis of sex ratios: an introduction. — In: *Sex ratios: concepts and research methods* (Hardy, I.C.W., ed.). Cambridge University Press, Cambridge. p. 48-92.
- Winkler, D.W. (1991). Parental investment decision rules in tree swallows: parental defence, abandonment, and the so-called Concorde Fallacy. — *Behav. Ecol.* 2: 133-142.
- Winkler, D.W. (1992). Causes and consequences of variation in parental defense behaviour by tree swallows. — *Condor* 94: 502-520.
- Wright, J., Both, C., Cotton, P.A. & Bryant, D. (1998). Quality vs. quantity: energetic and nutritional trade-offs in parental provisioning strategies. — *J. Anim. Ecol.* 67: 620-634.
- Yom-Tov, Y. & Hilborn, R. (1981). Energetic constraints on clutch size and time of breeding in temperate zone birds. — *Oecologia* 48: 234-243.
- Zach, R. & Mayoh, K. (1982). Weight and feather growth of nestling tree swallows. — *Can. J. Zool.* 60: 1080-1089.
-