

Brood size and body condition in the House Sparrow *Passer domesticus*: the influence of brooding behaviour

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In many bird species, females undergo a marked decline in body condition during the first days of the nestling period. This decline may be because brooding young chicks reduces the time available for foraging. Alternatively, it might be viewed as an adaptive way to reduce flight costs when the food demand of the brood is highest. To test these hypotheses we modified the brooding commitment of House Sparrows *Passer domesticus* by manipulating brood size to see if changes in time spent brooding affects adult body condition. During the nestling period, females provided on average three times as much brooding as males. Reduced broods received 14% more brooding than large broods and time spent brooding declined with brood size and chick age according to an exponential decay function. Male body condition was unaffected by brood size and remained stable throughout the reproductive period. Body condition of females with enlarged broods decreased gradually during the nestling period, whereas that of females tending reduced broods dropped abruptly and significantly upon hatching. This resulted in females with reduced broods having lower body condition during the first half of the nestling period than those with enlarged broods. The sharp drop in body condition of females with reduced broods coincided with the period that brooding was most intensive. Indeed, female body condition at the end of the nestling period was negatively correlated with the proportion of time they spent brooding during the first half of the nestling period. Thus, the probable lower homeothermic capacities of reduced broods implies a higher brooding commitment for female House Sparrows that, in turn, may reduce their opportunity to forage and consequently also their body condition.

Parental effort, the extra energy expenditure devoted to the care of offspring, is thought to incur fitness costs such as a reduced survival or lower future fecundity (Williams 1966). In birds, several studies have tested such predictions by experimentally manipulating brood size (Lindén & Møller 1989); parental effort has been measured by recording nest provisioning rate and change in adult condition (Bryant 1988). Thus, a decline in adult condition is interpreted as the physiological stress imposed on parents by feeding young (Drent & Daan 1980, Yom-Tov & Hilborn 1981, Gosler 1991). This

'stress hypothesis' predicts that adult body condition is negatively correlated with brood size and with the frequency of feeding visits to the chicks. However, in several studies conducted on passerine birds (Lindén & Møller 1989, Wolf *et al.* 1991, Verhulst 1995, Winkler & Allen 1995, Deerenberg *et al.* 1996, Orell & Koivula 1996) there was no negative effect of increased brood size on adult condition. Furthermore, several authors (Freed 1981, Pettifor *et al.* 1988, Gosler 1991, Sanz & Tinbergen 1999) have predicted the absence of a link between feeding effort and a decline in adult condition.

In most brood manipulation experiments, adult body condition has been measured at the end of the chick-rearing period. However, in many species,

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females undergo a marked decline in body condition during the first days of the nestling period (Moreno 1989a). This post-hatching decline is unlikely to be caused directly by the effort of provisioning young chicks because feeding rates are known to peak during the latter part of the nestling period (Ricklefs 1974). However, small chicks, which are not yet thermally independent, require regular brooding which may place another type of stress on parents (Ricklefs & Hussell 1984, Curlee & Beissinger 1995). Because brooding and feeding are incompatible, brooding parents are unable to feed for themselves, and this may result in mass loss. The brooding of young chicks can be especially stressful because females must either rely on males to bring them food (e.g. owls and parrots; Korpimäki 1986, Curlee & Beissinger 1995) or draw upon their own body reserves (e.g. many passerines; Jones & Ward 1976, Ricklefs & Hussell 1984). Unfortunately, few studies have measured the impact of time spent brooding on adult condition (Curlee & Beissinger 1995, Sanz & Moreno 1995) or relationships between brood size, time spent brooding and body condition (Moreno 1989b).

The time spent brooding has been shown to decrease with brood size (Dunn 1976, Moreno 1989b). This may be because the total heat produced by the brood increases proportionally to brood size (Clark 1984). Alternatively, parents rearing large broods have to spend more time foraging to provision the nestlings and therefore may allocate less time to brooding. Either way, if brooding is costly, females raising small broods should be more stressed and should therefore exhibit a greater decline in body condition during the first part of the chick-rearing period than those raising a large brood. The 'cost of brooding hypothesis' predicts that brood size and body condition should be positively correlated during the first part of the chick-rearing period.

An alternative hypothesis has been proposed to explain the decline in body condition observed in brooding birds. Freed (1981) suggested that a decline in adult condition is an adaptive adjustment of body reserves to reduce flight costs when food requirements of chicks are highest. Several observational and experimental studies support this 'adaptive hypothesis' (House Wren *Troglodytes aedon*, Freed 1981; Barn Swallow *Hirundo rustica*, Jones 1987; Pied Flycatcher *Ficedula hypoleuca*, Sanz & Moreno 1995; Mountain Bluebird *Siala currucoides*, Merkle & Barclay 1996). This 'adaptive hypothesis' predicts that a decline in adult condition should

occur during the first part of the chick rearing and should be either independent (Freed 1981) or negatively correlated (Merila & Wiggins 1997) with brood size, to attain the optimal body condition required for the high food provisioning effort demanded at the end of the nestling period.

To test predictions from the 'cost of brooding hypothesis' and the 'adaptive hypothesis', we conducted a study on the House Sparrow *Passer domesticus*, a species in which parental care is provided by both parents. House Sparrow nestlings are regularly brooded until they become thermally independent at 10 days of age (Seel 1969). Consequently, both parents potentially face the problem of allocating time between brooding and feeding. We studied the impact of brooding behaviour in relation to brood size on parental body condition in male and female House Sparrows. In order to manipulate the levels of parental effort observed, chicks were switched between nests to create enlarged or reduced broods to test whether changes in the time spent brooding would affect adult body condition.

METHODS

The fieldwork was carried out during the breeding season of 1997 (late April to early July) in a population of House Sparrows breeding in nestboxes at the Centre d'Etudes Biologiques de Chizé, western France (46°09'N, 0°24'W). From early April onwards, nestbox contents were checked every 2 days to determine laying, hatching, fledging dates and brood survival.

From the end of April to early July, adult House Sparrows were captured at random with traps and mist-nets dispersed over the study area. At first capture, birds were marked with a numbered aluminium ring and a unique combination of plastic colour rings to enable identification in the field. We measured the length of tarsus, sternum, and head + culmen with callipers (± 0.1 mm). Wing length was measured with a steel rule (± 1 mm) and body mass with an electronic balance (± 0.1 g). When birds were recaptured later in the season, we measured only body mass. Most birds (72%, $n = 228$) were measured by O.C. ($n = 164$) and measurements of birds made by M.K. ($n = 64$) did not differ significantly (one-way ANOVAS, all $P > 0.05$ for the four morphometric variables). An index of body size was calculated using the first factor (PCI) from a principal component analysis (Rising & Somers 1989) on the four body size measurements. The first factor explained 45.1% of the size variance in males

($n = 124$) and 45.6% in females ($n = 104$). Body mass was positively correlated with PCI in both males (MASS = 1.058 PCI + 27.78, $r^2 = 0.41$, $n = 152$, $P \leq 0.001$) and females (MASS = 1.105 PCI + 27.47, $r^2 = 0.30$, $n = 115$, $P \leq 0.001$). As the two equations relating body mass to body size were similar for males and females, data were combined and body condition was expressed as the residual mass from a linear regression relating body mass to body size (MASS = 1.093 PCI + 27.65, $r^2 = 0.35$, $n = 267$, $P \leq 0.001$). Thus defined, body condition is expressed as a size-corrected body mass in grams.

We systematically tried to capture each parent with an electronic trap installed at the entrance of the nestbox when the nestlings were 10–11 days old, that is 1–3 days before fledging. Although this method was highly effective, it was impossible to use earlier in the breeding cycle because House Sparrows were sensitive to disturbance and easily abandoned eggs or small chicks when captured at the nest. Thus, to measure the body condition of birds incubating eggs or tending young chicks, we had to rely on random catches (mist-nets).

In this House Sparrow population, brood size at hatching was four or five chicks (average: 3.91 chicks; range 2–6, $n = 55$). To create reduced broods (2–4 chicks) and enlarged broods (5–7 chicks), we manipulated brood size within 2 days of hatching by switching two chicks between nestboxes. We thus created two experimental groups of pairs having either a reduced brood or an enlarged brood. To measure the effect of brood size on nestling condition, 10-day-old chicks were weighed with an electronic balance (± 0.1 g).

We measured the time spent brooding, and feeding rates, during continuous morning observations lasting 3–6 h from 06:00 to 12:00 h (06 April–26 June). Because we could not see inside the nestbox, parents were assumed to be brooding when they stayed for longer than 30 s in the nestbox (maximum time required to transfer the food and to remove a faecal sac). Feeding rates of adults were recorded by measuring the numbers of feeding visits per hour to the nest. To assess the effect of ambient temperatures on brooding activity, external temperature was recorded and stored in a data logger (Hamster, ELPRO-BUCHS).

Statistical analysis was performed using SYSTAT 7.0 (Wilkinson 1997). All statistical tests are two-tailed, and probability levels < 0.05 were considered significant. Values are presented as means \pm standard deviation unless otherwise indicated.

RESULTS

Brooding and feeding the chicks

Since male and female House Sparrows alternate brooding, the total time that the chicks are brooded equals the sum of the contribution by each partner. During the observation period, the percentage of time that chicks were brooded was unaffected by ambient temperature (GLM, t -test = 1.02, $P = 0.31$). The percentage of time that chicks were brooded declined with chick age according to an exponential decay function (Fig. 1). Reduced broods were brooded 7.9% more than predicted (se $\pm 2.8\%$, $n = 21$), while enlarged broods were brooded 6.1% less than predicted (se $\pm 1.8\%$, $n = 20$). Thus, reduced broods received 14% more brooding than enlarged broods; this difference was statistically significant (t -test = 4.28, $df = 39$, $P = 0.0001$). The percentage of time that chicks were brooded declined linearly with the number of chicks in the nest and this negative trend persisted until the end of the nestling period (Fig. 2). Across the nestling period, females provided on average three times as much brooding as males (Fig. 3). The female's contribution appeared slightly greater in reduced broods ($81.9\% \pm 16.6\%$, $n = 21$) than in enlarged broods ($72.2\% \pm 14.4\%$, $n = 20$, Student t -test: $t = 1.99$, $df = 39$, $P = 0.053$). The proportional contribution of females increased

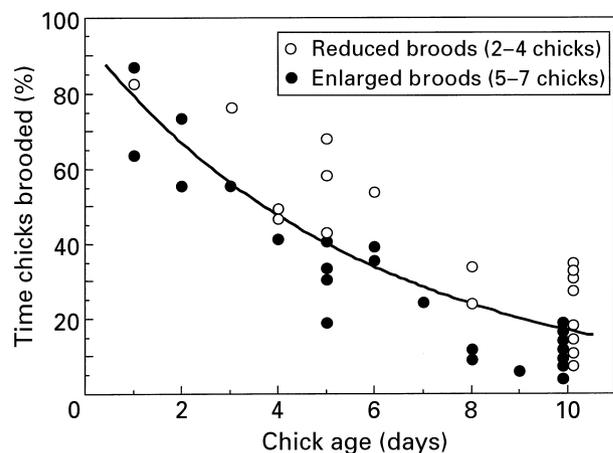


Figure 1. Percentage of time spent brooding by parent House Sparrows (male and female combined) in relation to the age of the chicks and brood size. Time spent brooding decreased with chick age according to an exponential decay function: $Y = 94.2 * \exp(-0.17 * X)$, $r^2 = 0.74$, $n = 42$. Open circles refer to reduced broods (2–4 chicks); dots refer to enlarged broods (5–7 chicks). Reduced broods: $Y = 102.8 * \exp(-0.148 * X)$, $r^2 = 0.79$, $n = 19$; Enlarged broods: $Y = 96.6 * \exp(-0.214 * X)$, $r^2 = 0.89$, $n = 23$.

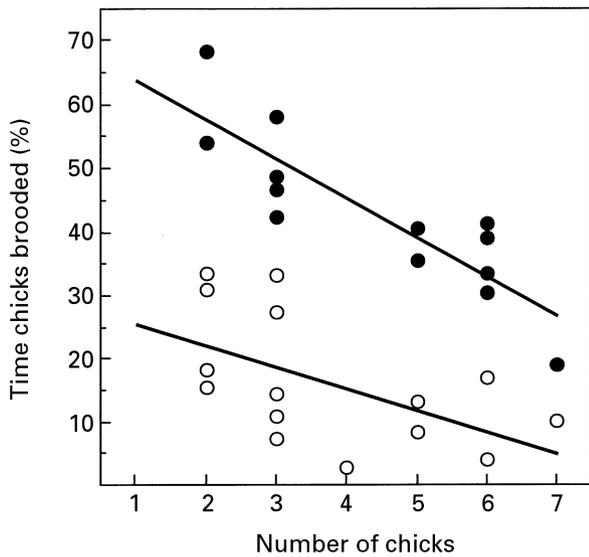


Figure 2. Time spent brooding by parent House Sparrows (male and female combined) in relation to the number of chicks in the brood. Ten-day-old chicks (open circles): $Y = 29.0 - 3.4 \times X$, $r^2 = 0.30$, $t = 2.36$, $df = 13$, $P = 0.035$; 4–6-day-old chicks (dots): $Y = 70.3 - 6.2 \times X$, $r^2 = 0.75$, $t = 5.75$, $df = 11$, $P = 0.0001$.

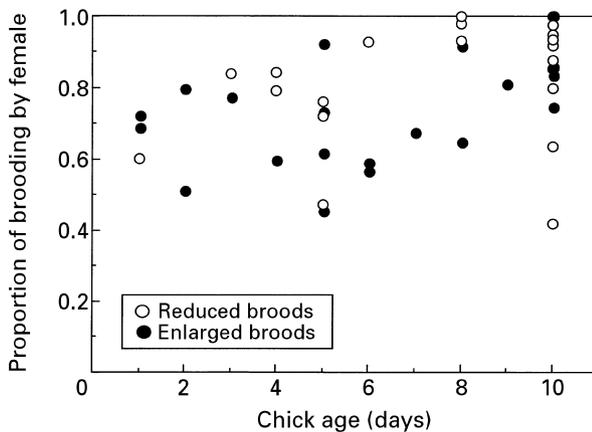


Figure 3. The proportion of total brooding time provided by female House Sparrows in relation to the age of the chicks and brood size. Open circles refer to females with reduced broods (2–4 chicks), dots refer to females with enlarged broods (5–7 chicks).

slightly, but significantly, with nestling age (Student t -test: $t = 2.62$, $df = 39$, $P = 0.014$).

Brood age had a significant effect on the frequency of feeding visits made by female House Sparrows (Table 1, reduced broods: Student t -test: $t = 3.86$, $df = 17$, $P = 0.013$; enlarged broods: Student t -test: $t = 6.82$, $df = 12$, $P < 0.0001$). In males, the same trend was observed but differences were not statistically significant. Females raising enlarged broods fed their offspring at a significantly higher rate than females with reduced broods (Table 1). In males, the same trend was observed but differences were not statistically significant.

Adult body condition

Among parents tending unmanipulated broods, male body condition remained stable throughout the reproductive period (ANOVA, $F_{4,33} = 0.67$, $P = 0.62$; Fig. 4). In contrast, female body condition peaked during egg-laying (probably in relation to the mass of eggs and ovaries) and declined gradually from clutch completion until fledging (ANOVA, $F_{4,28} = 11.71$, $P < 0.0001$; Fig. 4).

Brood size did not seem to affect male body condition, which remained constant throughout the nestling period, whereas female body condition decreased between incubation and the end of the nestling period (Fig. 5). The body condition of females with enlarged broods decreased gradually between incubation and the end of the nestling period, while that of females with reduced broods dropped abruptly, and significantly upon hatching of the brood (Student t -test: $t = 2.86$, $df = 9$, $P = 0.019$). Consequently, the body condition of females with reduced broods was significantly lower than that of females with enlarged broods during the first half of the nestling period (Student t -test: $t = 3.89$, $df = 7$, $P = 0.006$). At the end of the nestling period, this difference was still present but had diminished and was no longer statistically significant (Student t -test: $t = 1.86$, $df = 27$, $P = 0.073$).

Table 1. Number of feeding visits per hour in female and male House Sparrows with respect to brood size (reduced or enlarged) and to age of the chicks. Given are means \pm sd, with sample sizes (number of broods) in parentheses.

	1–7-day-old chicks				10–11-day-old chicks			
	Reduced	Enlarged	t -test	P	Reduced	Enlarged	t -test	P
Males	5.28 \pm 2.48 (6)	8.46 \pm 0.48 (7)	2.31	0.04	16.33 \pm 6.72 (13)	27.24 \pm 7.27 (7)	3.29	0.007
Females	4.51 \pm 3.69 (6)	8.61 \pm 4.73 (7)	1.76	0.11	7.16 \pm 5.62 (13)	11.74 \pm 4.60 (7)	1.96	0.07

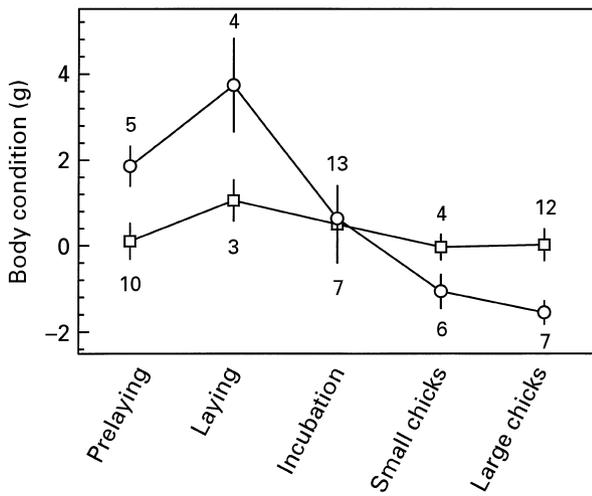


Figure 4. Body condition of adult male (squares) and female (circles) House Sparrows. Shown are average values of birds with unmanipulated brood sizes at different stages of the breeding cycle. Shown are average values representing from left to right: prelaying birds, parents incubating a clutch, birds tending 1–6-day-old chicks (small chicks) and birds tending 10–12-day-old chicks (large chicks). Sample sizes are indicated at the end of error bars which represent one standard error of the mean at either side of the average.

In females with reduced broods, the sharp drop in body condition between incubation and the first half of the nestling period coincided with the period during which most brooding occurred. This suggests that brooding may be responsible for some of the changes in body condition over the breeding cycle. Indeed, female body condition at the end of the nestling period was negatively correlated with the percentage of time spent brooding during the first half of the nestling period (Student *t*-test: $t = 2.76$, $df = 6$, $P = 0.033$, Fig. 6).

At the age of 10 days, chicks in reduced broods were significantly heavier than chicks from enlarged broods (Table 2). There was a significant effect of brood size on nestling survival, enlarged broods experiencing a higher mortality from day 2 to day 11 after hatching (Table 2).

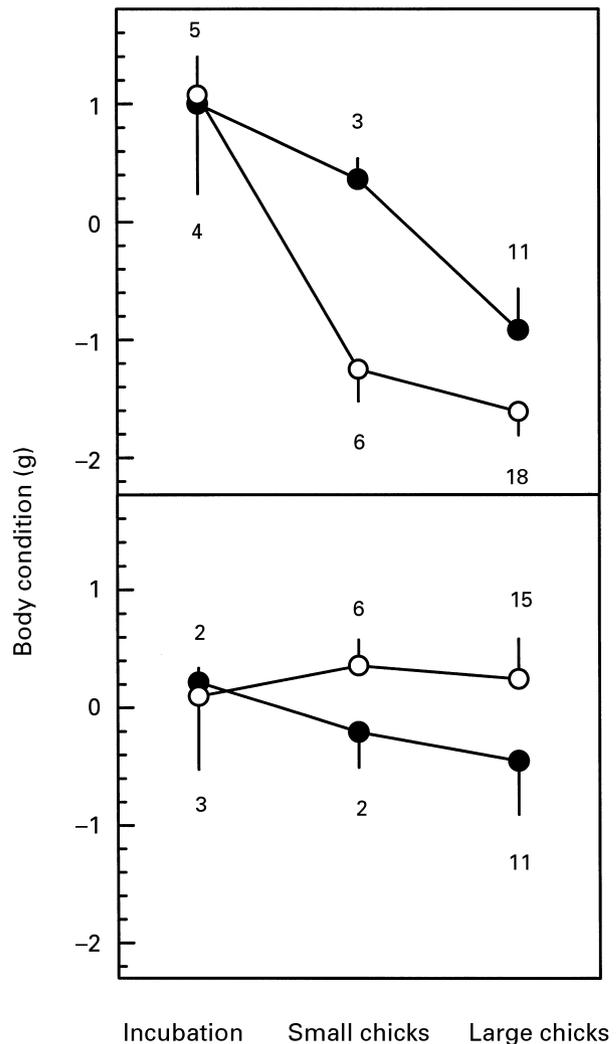


Figure 5. Body condition of female (upper) and male (lower) House Sparrows during the reproductive cycle. Shown are average values representing from left to right: parents incubating a clutch, birds tending 1–6-day-old chicks (small chicks) and birds tending 10–12-day-old chicks (large chicks). Open circles refer to parents with reduced broods (2–4 chicks), dots refer to parents with enlarged broods (5–7 chicks). Sample sizes are indicated at the end of error bars which denote one standard error.

Table 2. Body mass on day 10 and survival from day 2 to day 11 after hatching of House Sparrow nestlings with respect to brood size (reduced or enlarged). Given are means \pm sd, with sample sizes in parentheses (sample sizes for nestling survival indicate the number of broods).

	Reduced	Enlarged	<i>t</i> -test	<i>P</i>
Nestling mass (g)	23.01 \pm 2.40 (62)	21.05 \pm 4.08 (85)	3.38	0.0009
Nestling survival (%)	94.8 \pm 0.11 (16)	80.0 \pm 0.24 (15)	2.19	0.037

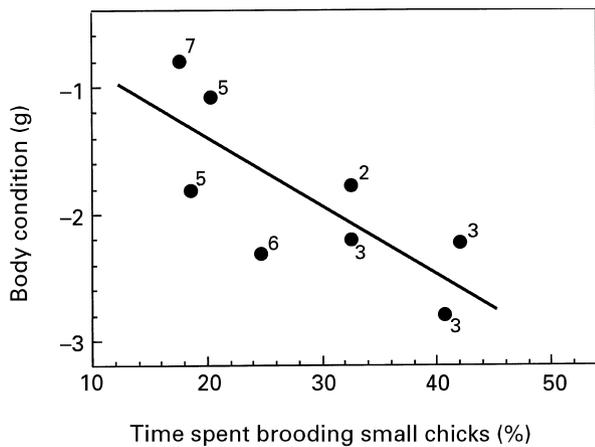


Figure 6. Female body condition towards the end of the nesting period (chick age: 10–12 days) in relation to the percentage of time spent brooding 4–6-day-old chicks. Body condition at fledging decreased linearly with time spent brooding according to the relation: $Y = -0.311 - 0.054 * X$, $r^2 = 0.56$, $n = 8$. Figures next to the datapoints indicate the number of chicks in a brood.

DISCUSSION

As reported in other species (Pied Flycatcher *Ficedula hypoleuca*, Sanz & Moreno 1995; Starling *Sturnus vulgaris*, Westerterp *et al.* 1982, Clark 1984; Northern Wheatear *Oenanthe oenanthe*, Moreno 1987; Great Tit *Parus major*, Sanz & Tinbergen 1999), House Sparrow parents reduced their brooding commitment as their nestlings grew older. In our study, reduced broods required more brooding, especially early in the nestling period. Two hypotheses might explain this (Dunn 1976, Moreno 1989b). First, the lower brooding commitment of parents tending enlarged broods may result from the better insulation afforded by large broods (Clark 1984). Secondly, during the first part of the chick-rearing period, female House Sparrows tending enlarged broods fed their young more often than those rearing reduced broods (Hegner & Wingfield 1987, this study). Thus, females rearing enlarged broods might have allocated less time to brooding because they had to spend more time foraging to provision the nestlings. In this case the lower brooding commitment of females rearing enlarged broods would not have been guided solely by the better thermoregulatory properties of large broods.

In our study, male body condition remained constant over the reproductive cycle, while in females, body mass peaked during egg production, dropped after hatching and stayed low until the chicks fledged. This is consistent with data obtained in

other species rearing altricial young (House Wren *Troglodytes aedon*, Freed 1981; Pied Flycatcher, Sanz & Moreno 1995; Barn Swallow *Hirundo rustica*, Jones 1987; Northern Wheatear *Oenanthe oenanthe*, Moreno 1989a; Green-rumped Parrotlet *Forpus passerinus*, Curlee & Beissinger 1995; Mountain Bluebird *Sialia currucoides*, Merkle & Barclay 1996). According to Moreno (1989a), male House Sparrows neither store nor mobilize body reserves while breeding, but females store reserves that are used during laying and incubation. Female body reserves are depleted during the first days of the nestling period. Females will continue to rear their chicks even if they are, themselves, in poor condition.

In our study, brooding represented a significant part of the female time budget (up to 40 min/h). In the House Sparrow, as in most passerines (Moreno 1989a), females perform all or most of the brooding. Consequently, females may have less time for self-maintenance, and the difference in brooding commitment between parents may explain the difference in body condition dynamics between the sexes. During the first part of the nestling period the frequency of feeding visits by females rearing enlarged broods was higher than those rearing reduced broods. However, early in the nestling period, those females that expended the greatest effort (enlarged broods) were apparently in better condition than those working less hard (reduced broods). Furthermore, male and female House Sparrows provisioned their offspring equally at this time, but only females experienced a decline in their condition. Thus, the frequency of feeding visits does not seem to be the major factor responsible for the decline in female body condition.

The body condition of females tending reduced broods dropped significantly during the early nestling period. This resulted in females with reduced broods being in poorer condition than females rearing enlarged broods. Such a positive effect of brood size on female condition suggests that brooding is costly, and supports the 'cost of brooding hypothesis'. Furthermore, we found that females, which spent more time brooding young nestlings, were in poorer condition at the end of the chick-rearing period. This suggests that the brooding of small chicks is probably a significant factor responsible for the decline in body condition observed in female House Sparrows. Interestingly, Moreno (1989b) reported a similar positive effect of brood size in female Northern Wheatears and proposed that 'females raising large broods experience less stress or are subjected to smaller costs than those rearing smaller broods'.

Similarly, although not significant, female Great Tits raising experimentally reduced broods tended to have a lower body condition index than those with control or enlarged broods (Sanz & Tinbergen 1999).

In our study, the finding that females raising reduced broods can incur a reduction in condition is unlikely to support the 'adaptive hypothesis' (Freed 1981). If a drop in body condition represents an adaptive way to reach an optimal weight to reduce flight costs, then the observed decline in body condition should be independent of brood size, or negatively correlated with it. Accordingly, the body condition of females tending reduced broods should be similar to, or slightly better than, that of females with enlarged broods. Thus, the poorer homeothermic capabilities of reduced broods (Clark 1984) imply a higher brooding commitment for female House Sparrows that, in turn, may reduce their opportunity to forage for themselves (Moreno 1989a). This must eventually result in a loss of body condition. This may be reinforced by the fact that, contrary to some other passerine species, male House Sparrows do not provision the female when she is brooding. Sanz and Moreno (1995) tested the 'cost of brooding hypothesis' in the Pied Flycatcher. These authors experimentally manipulated the length of the brooding period to test whether females experiencing a longer brooding period would lose body condition. Their results did not support the 'cost of brooding hypothesis' as females that experienced a longer brooding duration were in better condition than control females at day 8 after hatching. Such a finding, interpreted by Sanz and Moreno (1995) as evidence for the 'adaptive hypothesis', differs from our findings that brooding activity is likely to incur a decline in female's body condition. However, as the manipulation performed (duration of the brooding period) was different, the two studies are difficult to compare.

Maintaining a low body mass has been interpreted as an adaptive way to reduce the risk of predation through a reduced wing loading (Lima 1986, Slagsvold & Johansen 1998). It has been shown that birds can afford this when food is abundant and predictable (Ekman & Hake 1990, Gosler 1996). When food becomes scarce temporarily (e.g. bad weather), the lower food requirement of a reduced brood would present a lesser problem than that of an enlarged brood. Hence, an alternative explanation is that females tending reduced broods should be better able to keep a low body mass to reduce the risk of predation (T. Slagsvold pers. comm.).

Unlike females, the body condition of male House Sparrows remained constant throughout breeding. As they do not seem to accumulate body reserves, males have little scope for a significant decline in body condition (Moreno 1989b), and furthermore, their small involvement in brooding should leave them enough time for self-foraging.

During the first part of the nestling period, females tending enlarged broods were in better condition than those rearing fewer offspring. By spending less time brooding enlarged broods, these females may have saved reserves during the early nestling period. However, at the end of the nestling period, the body condition of all females was similar. It is unlikely that the high provisioning effort of these females was responsible for this gradual decline in body condition (Freed 1981, Sanz & Moreno 1995). By the end of the nestling period, House Sparrow chicks still need regular brooding (Seel 1969, this study). It may be that females with enlarged broods convert some of the body reserves saved from the early nestling stage to sustain them while brooding later on.

In Passerines, out of 12 studies where the effect of brood size on adult condition has been measured (reviewed by Lindén & Møller 1989 and Golet *et al.* 1998), only four (Pied Flycatcher, Askenmo 1977, 1979; Blue Tit *Parus caeruleus*, Nur 1984, 1988; Great Tit, Smith *et al.* 1987, Källander & Smith 1990; Snow Bunting *Plectrophenax nivalis*, Hussell 1972) reported a negative effect (i.e. parents rearing enlarged broods were in poorer condition). In our study, brood size had a positive effect on condition early in the nestling period, but around fledging all females were in a similar condition resulting in a null effect of brood size. Similarly, in another study of the House Sparrow, brood size manipulation had no effect on the body condition of females at the end of the nestling period (Hegner & Wingfield 1987). It may be that the overall null effect of brood size found in most of the experimental studies of passerines is the consequence of two processes: (1) in females tending reduced broods, a decline in body condition early in the nestling period due to a high brooding commitment and (2) in females tending enlarged broods, the use of the body reserves saved early in the nestling period to sustain brooding or provisioning effort later in the nestling period.

Our data on the effect of brood size on body condition suggest that a high brooding commitment is probably responsible for the decline in body condition observed in female House Sparrows. We suggest that the poorer lower thermal conductivity of reduced

broods requires that they receive more brooding from females, and that this results in a greater depletion of the female's body reserves. What might be the fitness consequences of this for the brood and for adults raising reduced or enlarged broods? As found in other studies (Lindén & Møller 1989), chicks from reduced broods were in better condition around fledging and suffered less mortality in the nest. Further experiments are needed to measure the consequences of brooding effort on adult survival or on the ability of females to initiate subsequent broods during the breeding season (De Laet & Dhondt 1987, Smith *et al.* 1987, Lindén & Møller 1989).

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REFERENCES

- Askenmo, C.** 1977. Effects of addition and removal of nestlings on weight, nestling survival and female weight loss in the Pied Flycatcher *Ficedula hypoleuca*. *Ornis Scand.* **8**: 1–8.
- Askenmo, C.** 1979. Reproductive effort and return rate of male Pied Flycatcher. *Am. Nat.* **114**: 748–753.
- Bryant, D.M.** 1988. Energy expenditure and body mass changes as a measure of reproductive costs in birds. *Funct. Ecol.* **2**: 23–24.
- Clark, L.** 1984. Consequences of homeothermic capacity of nestlings on parental care in the European Starling. *Oecologia* **65**: 387–393.
- Curlee, A.P. & Beissinger, S.R.** 1995. Experimental analysis of mass change in female Green-rumped Parrotlets (*Forpus passerinus*): the role of male cooperation. *Behav. Ecol.* **2**: 192–198.
- De Laet, J.F. & Dhondt, A.A.** 1987. Weight loss of the female during the first brood as a factor influencing second brood initiation in Great Tits *Parus major* and Blue Tits *P. caeruleus*. *Ibis* **131**: 281–289.
- Deerenberg, C., de Kogel, C.H. & Overkamp, G.J.F.** 1996. Costs of reproduction in the Zebra Finch *Taeniopygia guttata*: manipulation of brood size in the laboratory. *J. Avian Biol.* **27**: 321–326.
- Drent, R.H. & Daan, S.** 1980. The prudent parent: energetic adjustments in avian breeding. *Ardea* **68**: 225–252.
- Dunn, E.H.** 1976. The relationship between brood size and age of effective homeothermy in nestling House Wrens. *Wilson Bull.* **88**: 478–482.
- Ekman, J.B. & Hake, M.K.** 1990. Monitoring starvation risk: adjustments of body reserves in Greenfinches (*Carduelis chloris* L.) during periods of unpredictable foraging success. *Behav. Ecol.* **1**: 62–67.
- Freed, L.A.** 1981. Loss of mass in breeding wrens: stress or adaptation. *Ecology* **62**: 1179–1186.
- Golet, G.H., Irons, D.B. & Estes, J.A.** 1998. Survival costs of chick rearing in Black-legged Kittiwakes. *J. Anim. Ecol.* **67**: 827–841.
- Gosler, A.G.** 1991. On the use of greater covert moult and pectoral muscle as measures of condition in passerines with data for the Great Tit *Parus major*. *Bird Study* **38**: 1–9.
- Gosler, A.G.** 1996. Environmental and social determinants of winter fat storage in the Great Tit *Parus major*. *J. Anim. Ecol.* **65**: 1–17.
- Hegner, R.E. & Wingfield, J.C.** 1987. Effects of brood size manipulations on parental investment, breeding success and reproductive endocrinology of House Sparrows. *Auk* **104**: 470–480.
- Hussell, D.J.T.** 1972. Factors affecting clutch size in arctic passerines. *Ecol. Monogr.* **42**: 317–364.
- Jones, G.** 1987. Parent-offspring resource allocation in Swallows during nestling rearing: an experimental study. *Ardea* **75**: 145–168.
- Jones, P.J. & Ward, P.** 1976. The level of reserve protein as the proximate factor controlling the timing of breeding and clutch size in the Red-billed Quelea *Quelea quelea*. *Ibis* **118**: 547–574.
- Källander, H. & Smith, H.G.** 1990. Manipulation of the brood size of Pied Flycatchers. In Blondel, J., Gosler, A.D., Lebreton, J.D. & McCleery, R. (eds) *Population Biology of Passerine Birds. An Integrated Approach*, Vol. 24: 257–268. Berlin: Springer-Verlag.
- Korpimäki, E.** 1986. A test of the starvation hypothesis. *Ornis Scand.* **17**: 326–332.
- Lima, S.** 1986. Predation risk and unpredictable feeding conditions: determinants of body mass in birds. *Ecology* **67**: 377–385.
- Lindén, M. & Møller, A.P.** 1989. Cost of reproduction and covariation of life history traits in birds. *Trends Ecol. Evol.* **4**: 367–371.
- Merilä, J. & Wiggins, D.A.** 1997. Mass loss in breeding blue tits: the role of energetic stress. *J. Anim. Ecol.* **66**: 452–460.
- Merkle, M.S. & Barclay, R.M.R.** 1996. Body mass variation in breeding bluebirds *Sialia currucoides*: evidence of stress or adaptation for flight? *J. Anim. Ecol.* **65**: 401–413.
- Moreno, J.** 1987. Parental care in the Wheatear *Oenanthe oenanthe*: effects of nestling age and brood size. *Ornis Scand.* **18**: 291–301.
- Moreno, J.** 1989a. Strategies of mass change in breeding birds. *Biol. J. Linn. Soc.* **37**: 297–310.
- Moreno, J.** 1989b. Body-mass variation in breeding Northern Wheatears: a field experiment with supplementary food. *Condor* **91**: 178–186.
- Nur, N.** 1984. The consequences of brood size for breeding blue tits. I. Adult survival, weight change and cost of reproduction. *J. Anim. Ecol.* **53**: 479–496.
- Nur, N.** 1988. The consequences of brood size for breeding blue tits. III. Measuring the cost of reproduction: survival, future fecundity, and differential dispersal. *Evolution* **42**: 351–362.
- Orell, M. & Koivula, K.** 1996. Brood size manipulations within the natural range did not reveal intragenerational cost of reproduction in the Willow Tit *Parus montanus*. *Ibis* **138**: 630–637.

- Pettifor, R.A., Perrins, C.M. & McCleery, R.H.** 1988. Variation in clutch-size in Great Tits: evidence for individual optimisation hypothesis. *Nature* **336**: 160–162.
- Ricklefs, R.E.** 1974. Energetics of reproduction in birds. In Paynter, R.A. Jr (ed.) *Avian Energetics*: 152–297. Cambridge, MA: Nuttall Ornithological Club.
- Ricklefs, R.E. & Hussell, D.J.T.** 1984. Changes in adult mass associated with the nestling cycle in the European Starling. *Ornis Scand.* **15**: 155–161.
- Rising, J.D. & Somers, D.J.T.** 1989. The measurement of overall body size in birds. *Auk* **106**: 666–674.
- Sanz, J.J. & Moreno, J.** 1995. Mass loss in brooding female Pied Flycatcher *Ficedula hypoleuca*: no evidence for reproductive stress. *J. Avian Biol.* **26**: 313–320.
- Sanz, J.J. & Tinbergen, J.M.** 1999. Energy expenditure, nestling age, and brood size: an experimental study of parental behavior in the Great Tit *Parus major*. *Behav. Ecol.* **10**: 598–606.
- Seel, D.C.** 1969. Food, feeding rates and body temperature in the nestling House Sparrow *Passer domesticus* at Oxford. *Ibis* **111**: 36–47.
- Slagsvold, T. & Johansen, M.A.** 1998. Mass loss in female Pied Flycatchers *Ficedula hypoleuca* during late incubation: supplementation fails to support the reproductive stress hypothesis. *Ardea* **86**: 203–211.
- Smith, H.G., Källander, H. & Nilsson, J.A.** 1987. Effect of experimentally altered brood size on frequency and timing of second clutches in the Great Tit. *Auk* **104**: 700–706.
- Verhulst, S.** 1995. *Clutch size and parental effort. Reproductive decisions in Great Tits*. PhD Thesis, University of Groningen, The Netherlands.
- Westerterp, K., Gortmaker, W. & Wijngaarden, H.** 1982. An energetic optimum in brood-raising in the Starling *Sturnus vulgaris*: An experimental study. *Ardea* **70**: 153–162.
- Wilkinson, L.** 1997. *SYSTAT 7.0 for Windows: Statistics*. Chicago: SPSS Inc.
- Williams, G.C.** 1966. Natural selection, the cost of reproduction, and a refinement of Lack's principle. *Am. Nat.* **100**: 687–690.
- Winkler, D.W. & Allen, P.E.** 1995. Effects of handicapping on female condition and reproduction in Tree Swallows *Tachycineta bicolor*. *Auk* **112**: 737–747.
- Wolf, L., Ketterson, E.D. & Nolan, V.** 1991. Female condition and delayed benefits to males that provide parental care: a removal study. *Auk* **108**: 371–380.
- Yom-Tov, Y. & Hilborn, R.** 1981. Energetic constraints on clutch size and time of breeding in temperate zone birds. *Oecologia* **48**: 234–243.

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