EFFECTS OF BROOD-SIZE MANIPULATIONS ON PARENTAL INVESTMENT, BREEDING SUCCESS, AND REPRODUCTIVE ENDOCRINOLOGY OF HOUSE SPARROWS

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ABSTRACT.—Brood sizes of House Sparrows (*Passer domesticus*) were altered experimentally by adding or subtracting 2 nestlings. Unaltered broods served as controls, and experimental brood sizes were within the normal range found under natural conditions. Feeding rates of both parents increased with brood size, and although nestling mass decreased with brood size, most pairs were able to fledge the extra young added to their broods. Males rearing larger broods invested less in nest-site defense and mate-guarding activities, and females rearing larger broods took longer to initiate subsequent broods and produced smaller subsequent clutches. However, the productivity of the subsequent broods did not decrease. Adult survivorship was not affected by the brood manipulations.

In males, circulating levels of dihydrotestosterone increased significantly with brood size. Levels of other hormones, including luteinizing hormone (LH), testosterone, estradiol-17β, and corticosterone (B), were not related to brood size in either sex, although in females LH and B titers tended to increase with brood size. Males feeding larger broods tended to have less body fat, but otherwise there was no relationship between brood size and body condition. These results suggest that adults tending larger broods were not unduly stressed by their extra efforts, at least when feeding nestlings. However, the increased interbrood interval and decreased subsequent clutch size associated with rearing larger broods may have resulted either from the increased energetic and nutrient demand on females after the young fledged or simply from the extra time required to rear the additional fledglings to independence. *Received 10 July 1986, accepted 1 March 1987.*

IMPLICIT in many discussions of life-history phenomena is the assumption that organisms trade off two or more conflicting activities in a manner that maximizes their overall reproductive output (e.g. Williams 1966, Charnov and Krebs 1974). For example, most iteroparous organisms are assumed to forgo maximum annual productivity to increase subsequent survivorship, thereby maximizing lifetime fecundity (e.g. Kluyver 1963, Williams 1966, Charnov and Krebs 1974). Moreover, even within a given breeding season, other trade-offs may occur (e.g. McGillivray 1983). For males, Trivers (1972) proposed a fundamental trade-off between competing with other males to fertilize the ova of females and providing parental care to the offspring they produce. Ecological restrictions on these two options have been used to explain mating systems (e.g. Emlen and Oring 1977). We have suggested that endocrine and associ-

ated behavioral changes of monogamous male House Sparrows (*Passer domesticus*) during the breeding season reflect a compromise between these two options (Hegner and Wingfield 1986a).

In our study area, a given pair of House Sparrows may attempt from 3 to 5 broods within a nesting season. In adults, circulating levels of reproductive hormones vary considerably during different stages of nesting. Plasma concentrations of luteinizing hormone (LH), androgens, and estrogens are maximum during the egg-laying stage of each brood, decline rapidly during incubation, remain low after the young hatch, and rise again as the young approach fledging. In females, rising levels of LH and estradiol (E2) following fledging are indications of physiological preparation for laying the next clutch (Hegner and Wingfield 1986b). In males, levels of LH and testosterone rise rapidly to maximum concentrations when nestlings reach 9–10 days of age, well before the young fledge (typically when 14–15 days old). This reflects a transition between a state of high investment in parental care, when testosterone levels are

low, to one of high investment in male-male competition, when testosterone levels are high (Hegner and Wingfield 1986a).

We examined the physiological and reproductive effects of altering the demand for parental care on free-living House Sparrows. For some pairs we increased the demand for parental care by adding two young to the nest, for others we decreased that demand by removing two young from the nest, and for a third group the number of nestlings was unchanged. We subsequently determined the effects of these manipulations on investment in parental care, investment by males in male-male competition, circulating levels of reproductive hormones, body condition, breeding success in the experimental and subsequent broods, and adult survival to the next year.

METHODS

Experiments were conducted in June and July 1984 at several farms in Dutchess Co., New York (42°N). All nests were located in nest boxes that had been present in the study areas since early 1982. Nest inspections at 2–3-day intervals enabled us to determine dates of laying, hatching, and fledging, clutch and brood sizes, fledging success, and the growth curves of each nestling. All nestlings were weighed when 10–12 days old, when mass typically is greatest (Dawson 1972).

All subjects were marked individually with U.S. Fish and Wildlife Service bands and a unique combination of color bands. Twenty-five pairs were tending their second brood of the season, and the remaining three were renesting following the loss of their first brood. The second brood normally is the most productive of each season (Murphy 1978, McGillivray 1983, Hegner and Wingfield unpubl. data). All manipulations were conducted when the young were 4–6 days of age. Ideally, we wished to manipulate only nests in which all eggs had hatched and no brood reduction had occurred, but these were rare in 1984. Instead, we manipulated the sizes of existing broods in the nests, controlling for initial clutch size and size of the brood at the time of manipulation (see Table 1). To control for differences among local sites, we attempted to have equal numbers of each manipulation group at a given farm. Date of laying within a local site also was controlled among manipulation groups.

In 9 nests brood size was decreased by 2 nestlings. In 8 nests brood size was enlarged by 2 nestlings removed from other nests. All enlarged broods were within the normal range of brood sizes (1–7) in this study area (Hegner and Wingfield unpubl. data). All

nestlings were marked individually with subcutaneous ink tattoos; parents showed no indication of discrimination between the foster young and their own offspring. As a control, nestlings from 11 nests were removed for weighing and replaced. House Sparrow eggs hatch asynchronously, and there often is considerable variance in the nestling mass within a brood (Hegner and Wingfield unpubl. data). We therefore controlled for age and mass of the switched nestlings as far as possible.

Activities of adults at nest boxes were monitored using a focal-nest observation protocol. Data reported are from 49 h of diurnal observations conducted when nestlings were 4–14 days old. From continuous observations during 1–2-h sessions, two measures of adult parental investment were determined: rate of feeding visits and proportion of observation time adults were inside the box (and presumably brooding young). For males, two measures of investment in male-male competition were determined: relative amount of nest-site defense and relative amount of mate-guarding activity. Nest-site defense included the proportion of observation time males were at or near the nest site plus the frequency of aggressive response (e.g. threats, chases, fights) to intrusions by other adult males at the nest box. Mate guarding combined two measures of spatial association between the breeding male and female: the proportion of time both were present at the nest simultaneously and the proportion of arrivals at, or departures from, the nest box together. These measures first were normalized to range between 0 and 1 by dividing each value by the maximum recorded value, then summed to make both aggregate scales. Each aggregate measure thus could range between 0 and 2. The measures making up each aggregate scale were highly correlated, both during this study and in observations at untreated nests, and their frequencies covaried with endocrine changes associated with each stage of nesting (Hegner and Wingfield 1986a, b).

When nestlings were 10–14 days old, the adults were captured at the nest boxes. A small sample of blood (400 μl) was collected within 4 min, body mass was determined to the nearest 0.1 g, and fat levels in the furculum and abdomen were estimated with a scale ranging from 0 (no fat) to 5 (gross bulging fat bodies). From blood samples, plasma concentrations of luteinizing hormone were measured using the radioimmunoassay developed by Follett et al. (1972, 1975). Plasma concentrations of the following steroid hormones were measured by radioimmunoassay after separation and partial purification on diatomaceous earth:glycol microcolumns: 17β-hydroxy-5α-androstan-3-one (dihydrotestosterone, DHT), testosterone (T), estradiol-17β (E2) (females only), and corticosterone (B). The chromatography procedure and radioimmunoassay have been described in detail by Wingfield and Farner (1975) and Wingfield et al. (1982a). Typical values of intra-assay accuracy and
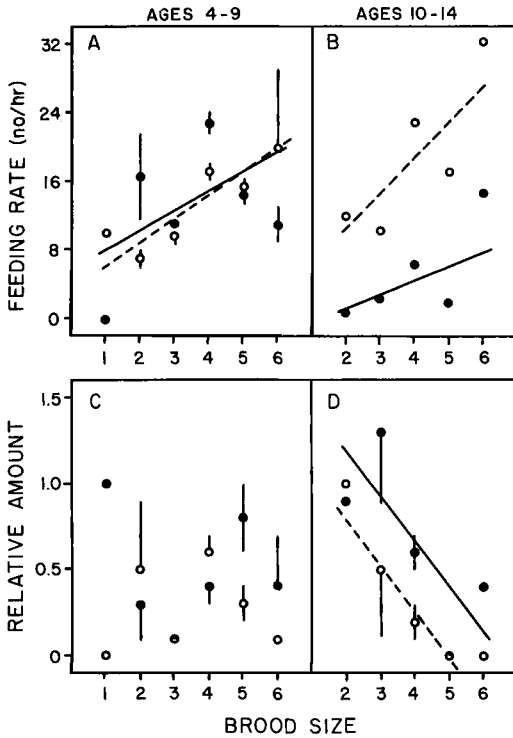
Fig. 1. Relationship between brood size, parental effort, and investment in male-male competition. In the upper portion are rates of feeding visits by males (closed circles) and females (open circles) feeding young aged 4–9 days (A) and 10–14 days (B). Feeding rates by males (solid lines) tended to increase with brood size. At ages 4–9, rate = 5.8 + 2.3(no. young), $r = 0.269$, $P = 0.061$; at ages 10–14, rate = -2.3 + 1.7(no. young), $r = 0.298$, $P = 0.080$. Feeding rates by females (broken lines) increased significantly with brood size. At ages 4–9, rate = 3.4 + 2.7(no. young), $r = 0.432$, $P = 0.009$; at ages 10–14, rate = 2.6 + 4.0· (no. young), $r = 0.487$, $P = 0.020$. In the lower portion are relative amounts of nest-site defense (closed circles) and mate-guarding activity (open circles) by males when young were aged 4–9 days (C) and 10–14 days (D). At ages 10–14, investment in male-male competition declined significantly with brood size: defense = 1.7 − 0.3(brood size), $r = -0.485$, $P = 0.051$; mate guarding = 1.3 − 0.3(brood size), $r = -0.567$, $P = 0.028$. Values are means ± 1 SE. Sample sizes for broods are 1, 3, 6, 9, 8, and 2 (ages 4–9) and 2, 4, 7, 4, and 1 (ages 10–14). Units of nest-site defense and mate guarding are given on scales of 0–2 (see text).

variation were reported by Hegner and Wingfield (1986a).

In most analyses, data were grouped according to age of the oldest nestling as 4–9 days (before the normal rise of T in males) and 10–14 days (during

and after the rise in T). These represent the two portions of the nestling stage in which the parental contribution of males typically differs markedly (Hegner and Wingfield 1986a). Most comparisons examined the effects of increasing parental demands (reduced > control > enlarged broods) on various physiological and reproductive measures by regressing each measure against brood size following the manipulation. As we were specifically interested in the directional effects of the manipulations, one-tailed levels of significance for all correlation coefficients are presented. Other comparisons (two-tailed) among experimental groups were made using nonparametric Kruskal-Wallis and Mann-Whitney U-tests, or the G-test corrected for small sample sizes (Sokal and Rohlf 1981).

RESULTS

Patterns of investment.—Birds adjusted their parental effort to brood size. When nestlings were 4–9 days old, feeding rates of both males ($r = 0.269$, $P = 0.061$) and females ($r = 0.432$, $P = 0.009$) were related to brood size (Fig. 1), and males brought food at a rate equal to that of their mates ($W = 187.5$, $P > 0.50$, Wilcoxon signed-ranks test). Males also spent less time brooding chicks than did females ($W = 0$, $P < 0.001$), although time spent brooding was not related to brood size (data not shown). When feeding older nestlings (aged 10–14 days), feeding rates of females again were related to brood size ($r = 0.487$, $P = 0.020$; Fig. 1), but those of males were not ($r = 0.298$, $P = 0.080$). During this portion of the nestling stage, feeding rates of males relative to their mates declined ($W = 2$, $P < 0.001$), reflecting the typical pattern associated with rising levels of T (Hegner and Wingfield 1986a).

When young were 4–9 days of age, there was no relationship between brood size and investment in male-male competition (Fig. 1C). When nestlings were older, however, males with more nestlings invested less in male-male competition. Both nest defense ($r = -0.485$, $P = 0.051$) and mate guarding ($r = -0.567$, $P = 0.028$) decreased with brood size (Fig. 1D). The frequencies of these activities increased moderately, but not significantly, from levels during the earlier portions of the nestling stage. This was expected because these activities generally peak only after young leave the nest (Hegner and Wingfield 1986a).

Physiological effects.—All hormone levels were within the typical range for free-living House Sparrows at this stage of nesting (see Hegner
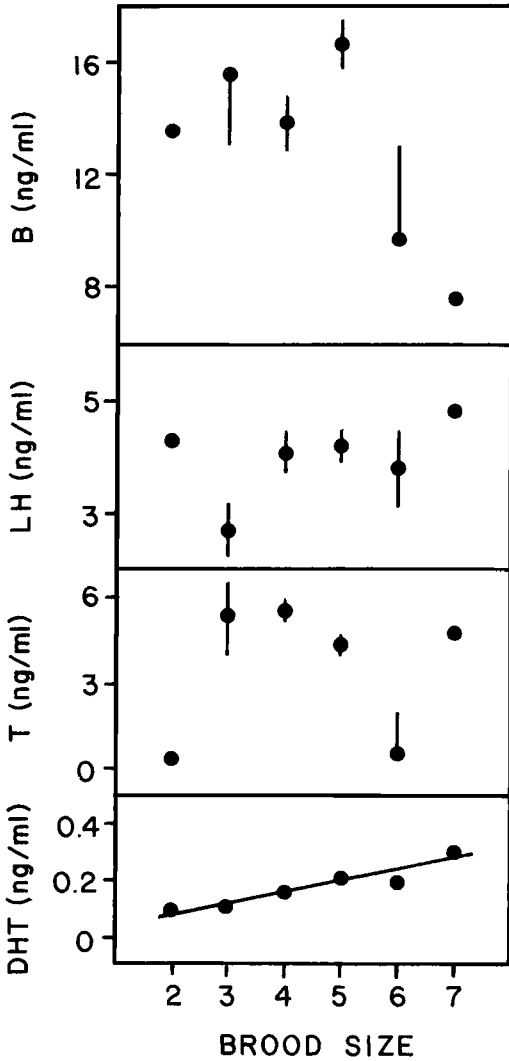
Fig. 2. Relationship between brood size and circulating levels of corticosterone (B), luteinizing hormone (LH), testosterone (T), and dihydrotestosterone (DHT) in males. Levels of DHT increased significantly with brood size: DHT (pg/ml) = 6 + 40(no. young), $r = 0.538$, $P = 0.009$. Values are means ± 1 SE. Sample sizes for broods are 2, 2, 5, 7, 2, and 1.

Fig. 3. Relationship between brood size and circulating levels of B, LH, estradiol (E$_2$), T, and DHT in females. Levels of B tended to increase with brood size: B (ng/ml) = 5.9 + 0.9(no. young), $r = 0.321$, $P = 0.060$; as did levels of LH: LH (ng/ml) = 3.1 + 0.5(no. young), $r = 0.282$, $P = 0.073$. Values are means ± 1 SE. Sample sizes for broods are 2, 2, 5, 3, 4, 4, and 2.

and Wingfield 1986a, b). In males, DHT levels increased significantly with brood size ($r = 0.538$, $P = 0.009$; Fig. 2), but otherwise there were no effects of brood manipulations on hormone levels. In females, there was a tendency for both LH ($r = 0.225$, $P = 0.056$) and B ($r = 0.278$, $P = 0.074$) to increase with brood size, but these were not quite significant (Fig. 3). Levels of other reproductive hormones were not corre-
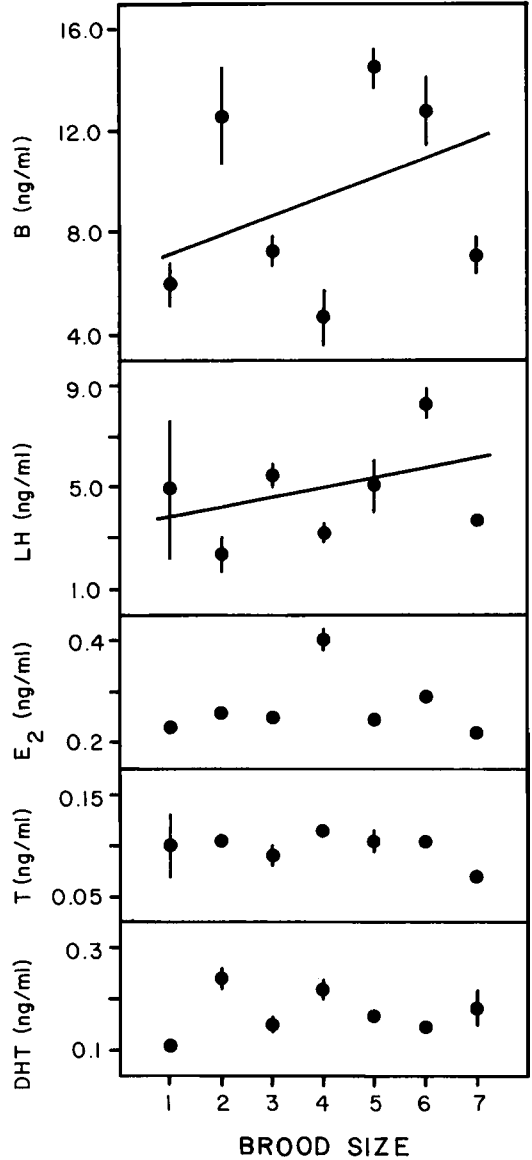
lated with brood size. Similarly, fat levels in males with larger broods tended to be lower ($r = -0.285$, $P = 0.080$), but otherwise there were no effects of brood manipulations on body condition (Fig. 4).

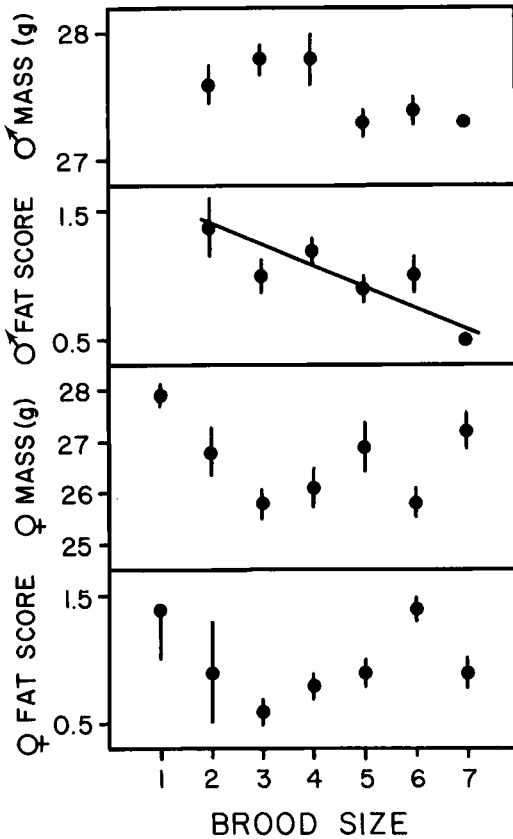*Effects on breeding success.*—There were no dif-

Fig. 4. Relationship between brood size, body mass, and fat score for males and females. Fat scores for males tended to decline with brood size: fat score = $1.7 - 0.2$(no. young), $r = -0.285$, $P = 0.080$. Values are means ± 1 SE. Sample sizes for males are given in Fig. 2 and for females in Fig. 3.

ferences in original clutch or brood sizes among the experimental groups (Table 1), but there was a significant difference among groups in the number of young fledged (Kruskal-Wallis $H = 16.748$, $P < 0.005$), indicating that House Sparrows were able to successfully rear the extra young added to their broods. In fact, there was no difference in the amount of brood reduction following the manipulation across all groups. More importantly, adults tending enlarged broods fledged significantly more young than did adults tending control nests (Mann-Whitney $U = 7.5$, $P < 0.01$). There was an inverse relationship, however, between brood size and the maximum mass attained by surviving nestlings ($r = -0.328$, $P < 0.001$; Fig. 5). Dawson (1972) found that young House Sparrows known to have died within 10 days of fledging were significantly lighter as nestlings (averaging <20.1 g at age 11 days) than were those that survived this period. In the first brood there was a tendency, not significant, for a greater proportion of young in larger broods to fall below this threshold ($r = 0.585$, $P = 0.08$), but when this mortality was taken into account there still was a difference among groups in young produced ($H = 8.183$, $P < 0.025$; Table 1), with adults tending enlarged broods producing more young than those tending control nests ($U = 22.5$, $P < 0.05$).

Brood manipulations also had consequences for the success of the following brood. Some pairs failed to initiate a subsequent brood (Table 1), but these were least frequent among pairs tending enlarged nests ($G = 56.337$, df $= 2$, $P <$

TABLE 1. Effects of brood manipulations on breeding success. Values are means ± 1 SD.

	Reduced broods	Control broods	Enlarged broods	Kruskal-Wallis test
Experimental broods	$(n = 9)$	$(n = 11)$	$(n = 8)$	
Clutch size	5.2 ± 0.7	5.0 ± 0.6	5.0 ± 0.5	$H = 0.846$, $P > 0.50$
Initial brood size	4.6 ± 0.9	4.2 ± 1.2	4.6 ± 0.7	$H = 1.016$, $P > 0.50$
Brood size at manipulation	4.2 ± 1.1	3.7 ± 1.1	4.3 ± 0.7	$H = 1.242$, $P > 0.50$
% manipulated brood starve	0.0 ± 0.0	6.8 ± 16.2	7.9 ± 16.1	$H = 2.369$, $P > 0.25$
No. young fledged	2.2 ± 1.1	3.5 ± 1.3	5.7 ± 1.1	$H = 16.748$, $P < 0.005$
No. young survive[a]	1.9 ± 0.9	3.1 ± 1.1	4.3 ± 2.2	$H = 8.183$, $P < 0.025$
Subsequent broods	$(n = 5)$	$(n = 7)$	$(n = 7)$	
Interbrood interval (days)	7.0 ± 2.3	7.1 ± 2.7	11.3 ± 4.4	$H = 4.355$, $P > 0.10$
Clutch size	5.4 ± 1.1	4.3 ± 1.1	3.6 ± 1.0	$H = 6.582$, $P < 0.05$
Brood size	5.0 ± 1.0	3.3 ± 2.1	2.9 ± 1.5	$H = 4.139$, $P > 0.10$
% brood starve	41.3 ± 8.4	14.2 ± 0.4	4.2 ± 10.2	$H = 11.618$, $P < 0.005$
No. young fledged	3.0 ± 1.0	2.7 ± 1.6	2.7 ± 1.4	$H = 0.067$, $P > 0.90$
No. young survive[a]	3.0 ± 1.0	2.6 ± 1.5	2.4 ± 1.4	$H = 0.435$, $P > 0.75$

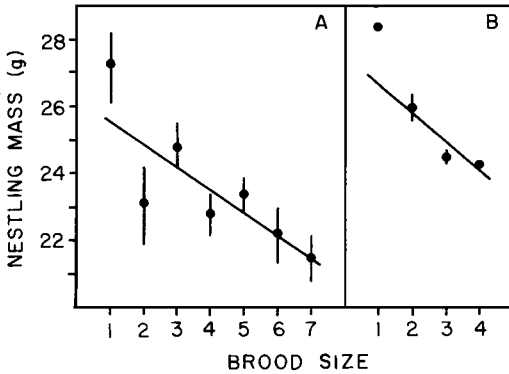[a] Maximum mass ≥ 20.1 g (see text).

Fig. 5. Relationship between brood size and maximum mass of surviving nestlings. Mass declined significantly with brood size during the experimental brood (A): mass (g) = 26.2 − 0.7(no. young), $r = -0.328$, $P < 0.001$; and during the subsequent brood (B): mass (g) = 27.4 − 0.8(no. young), $r = -0.232$, $P = 0.040$. Sample sizes for broods are 4, 6, 18, 24, 20, 24, and 7 (A), and 1, 6, 18, and 28 (B).

0.005). Among renesting pairs, there was a significant increase in interbrood interval with fledgling number ($r = 0.552$, $n = 19$, $P = 0.014$) and a significant decrease in the size of the following clutch with fledgling number ($r = -0.511$, $P = 0.026$) (Fig. 6). Females tending reduced broods had larger than average subsequent clutches, while those tending enlarged broods had smaller than average subsequent clutches ($H = 6.582$, $P < 0.05$; Table 1). Moreover, nearly all pairs tending enlarged broods had a smaller subsequent clutch, while all pairs tending reduced broods had a subsequent clutch the same size or larger ($G = 9.590$, df = 2, $P < 0.05$; Table 2).

Curiously, there was differential brood reduction in the subsequent nesting effort, being higher in pairs that had tended reduced broods ($H = 11.618$, $P < 0.005$), so that there was no difference in fledgling number of the subsequent brood among the experimental groups (Table 1). There also was no relationship between fledgling number in the subsequent brood and either brood size or fledgling number of the experimental brood. This was not due to overall nesting failure: one nest in each group failed to fledge any young, and the analysis was similar when these were eliminated ($H = 10.004$, $P < 0.01$). As in the experimental broods, there was an inverse relationship between brood size and maximum nestling mass during the sub-
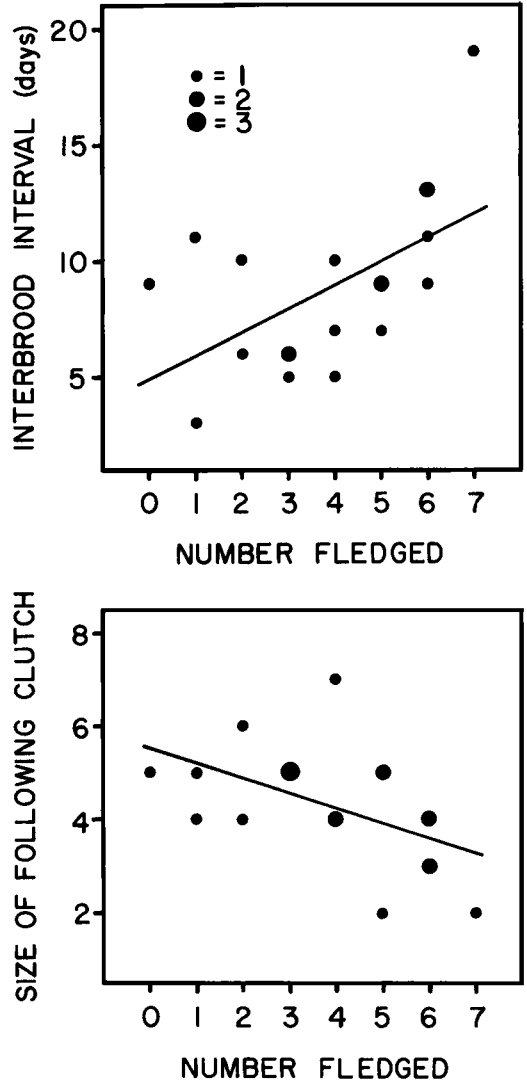

Fig. 6. Relationship between number of young fledged from manipulated broods and length of the interbrood interval (top) and size of the following clutch (bottom). Interbrood interval increased significantly with number fledged: interval (days) = 5.0 + 1.0(no. fledged), $r = 0.552$, $P = 0.014$. Clutch size decreased significantly with number fledged: size = 5.5 − 0.3(no. fledged), $r = -0.511$, $P = 0.026$.

sequent brood ($r = -0.232$, $P = 0.040$; Fig. 5). Nonetheless, nearly all of these young weighed more than 20.1 g and hence were likely to survive the early postfledging period (see Table 1).

There was little indication that adult survivorship was affected by the brood manipulations. In 1985 extensive observations were con-

TABLE 2. Effect of manipulation on size of subsequent clutch vs. previous clutch.

Size of subsequent clutch	Reduced broods	Control broods	Enlarged broods	Total
Smaller	0	2	6	8
Same size	4	5	1	10
Larger	1	0	0	1
Total	5	7	7	19

TABLE 3. Effects of manipulation on adult survivorship. Entries are number of adults seen in 1985 at 3 sites. Values in parentheses are percentages of nests.

	Reduced broods	Control broods	Enlarged broods	Total
Males	4 (67%)	4 (50%)	1 (20%)	9 (47%)
Females	3 (50%)	3 (38%)	2 (40%)	8 (47%)
No. nests	6	8	5	19

ducted at three of the local sites used for these experiments. These sites contained 19 of the 26 experimental nests. The number of adults from these 19 nests seen again in 1985 is given in Table 3. All bred successfully that year. Although sample sizes are small, adults that reared a greater number of young in 1984 were as likely to be seen again in 1985 as were those that reared fewer young (males: $G = 2.301$, df = 2, $P > 0.25$; females: $G = 0.207$, df = 2, $P > 0.90$). Males seen again in 1985 tended to be lighter in 1984, however, weighing 26.9 ± 0.8 g (mean ± SD), than were males not seen again, which weighed 28.1 ± 1.0 g in 1984 ($U = 11$, $0.05 < P < 0.10$).

DISCUSSION

Patterns of investment.—We examined the effects of varying levels of demand for parental care on the allocation of investment in the current vs. subsequent brood by House Sparrows. Investment in the current brood was indicated by the contributions of both sexes to feeding nestlings, while investment in the subsequent brood was indicated for males by rates of nest-site defense and male-male competition and for females by the timing and size of the subsequent brood.

There was considerable evidence for a trade-off between investing in current vs. future reproduction. Adults of both sexes adjusted feeding rates to brood size and successfully reared nearly all of their nestlings, and males feeding larger broods invested less time defending the nest site and mate guarding as the young neared fledging. The consequences of fledging a larger number of young were an increased interbrood interval and a smaller subsequent clutch.

In male House Sparrows, correlational evidence suggests that one mechanism regulating

the allocation of effort between current and future broods is the seasonal variation in circulating levels of the gonadal steroid testosterone. Low levels of testosterone (during incubation and the early portion of the nestling stage) are associated with high investment in parental care of the current brood. Males at this time provide about 25% of diurnal incubation duties and feed young at a rate equal to that of females. High levels of testosterone in males (during the late portion of the nestling stage, the interbrood interval, and the subsequent egg-laying stage) are associated with high investment in future reproduction. Rates of feeding nestlings decline precipitously, and levels of nest-site defense and mate-guarding activity are elevated (Hegner and Wingfield 1986a). Experimental evidence also suggests that high testosterone levels inhibit the expression of parental care in male birds, including House Sparrows (Silverin 1980, Hegner and Wingfield 1987).

We have suggested that the ultimate factors responsible for this shifting pattern of investment by males are high levels of competition for safe nesting sites and a high potential for loss of paternity to other adult males. Moreover, the abundance of easily obtained, high-quality food in our study area allows nestlings to develop at an extremely rapid rate, so that females are able to rear the brood alone once the young reach 9–10 days of age (Hegner and Wingfield 1986a, b). Indeed, once reaching this age most House Sparrow nestlings successfully fledge (Dawson 1972, Hegner and Wingfield unpubl. data).

Reproductive consequences.—Lack (1947, 1968) proposed that the ultimate determinant of clutch size is the maximum number of young for which parents can find food. As a consequence, he predicted that the modal clutch size should be the most productive. This hypothesis has been

extended by others (e.g. Kluyver 1963, Williams 1966, Charnov and Krebs 1974) to include other aspects of life history. Based on assumptions of an inverse relationship between fecundity and survivorship, and selection for maximum lifetime rather than annual fecundity, modal clutch size should be slightly smaller than the most productive. This modification of Lack's hypothesis predicts that parents tending artificially enlarged broods either will produce fewer young than they would have produced from their normal brood, or will suffer increased mortality as a result of their extra effort.

A number of studies have examined the effects of experimental brood enlargement on altricial species. In some the parents were unable to rear the additional nestlings (Perrins 1964, Perrins and Moss 1965, Ward 1965). In the majority of such studies, however, at least some pairs were able to rear one or more additional nestlings (Crossner 1977, Schifferli 1978, Askenmo 1979, Cronmiller and Thompson 1980, De Steven 1980, Silverin 1982, Slagsvold 1982, Bryant and Westerterp 1983, Murphy 1983, Nur 1984b, Røskaft 1985, this study). In some investigations, fledging mass of young from enlarged broods was reduced, suggesting decreased survivorship of postfledging young (Lack 1966, von Haartman 1971, Dawson 1972, this study), but there are exceptions (De Steven 1980, Slagsvold 1982). Moreover, fledging mass does not always correlate with survivorship (Nur 1984b). As a consequence of these results, attention has focused on other negative effects of brood enlargement.

Parental survivorship may be reduced, at least in some years (Askenmo 1979, Nur 1984a), although this is not universal (De Steven 1980, Högstedt 1981, Røskaft 1985, this study). Pairs tending enlarged broods may take longer to renest following loss of the brood to a predator, and the success of the subsequent brood may be lower than average (Slagsvold 1984). Pairs tending enlarged broods also may have a longer interbrood interval within the same year (this study) or may initiate nesting later the following year (Røskaft 1985). Several studies of natural broods also have found an inverse relationship between the number of young fledged and the interbrood interval within a season (Kluyver 1963, Kluyver et al. 1977, McGillivray 1983). Most authors have attributed the relationship between productivity and survival, or interbrood interval, to greater physiological stress on adults caused by rearing the extra young. The evidence for this, however, should be evaluated with caution.

One measure used to estimate stress is a change in adult body mass. In our study there was no relationship between brood size and adult body mass. Several other studies have found a significant negative correlation between brood size and mass of adult females (Hussell 1972, Winkel and Winkel 1976, Askenmo 1977, Bryant 1979, Silverin 1982, Nur 1984a). In Blue Tits (*Parus caeruleus*) this correlated with reduced survival in at least some years (Nur 1984a). Other studies have found a similar, nonsignificant trend (De Steven 1980, Freed 1981), perhaps because sample sizes were low (Nur 1984a). These same studies, however, found no relationship between brood size and mass of adult males, even when the males were feeding the young at a rate equal to that of the females (Winkel and Winkel 1976, Freed 1981, Nur 1984a). Moreover, most mass loss may occur during incubation, suggesting it is an adaptation to reduce the metabolic cost of flying during the nestling stage rather than an indication of stress (Freed 1981, Norberg 1981).

Another measure used to estimate stress is an increased daily energy expenditure (DEE) by adults feeding larger broods. Larger broods require more feeding trips, both in House Sparrows (Seel 1969, this study) and in many other species (reviewed by Nur 1984c). Studies of the House Martin (*Delichon urbica*) revealed a relationship between brood size and DEE that correlated with feeding rate (Hails and Bryant 1979, Bryant and Westerterp 1983). In the European Starling (*Sturnus vulgaris*), however, Ricklefs and Williams (1984) found no relationship between CO_2 production and brood size, brood mass, or change in brood mass. Perhaps these results reflect the differences in feeding ecology between an aerial insectivore and a species that feeds on the ground, but more studies are needed to clarify this relationship.

The above results suggest strongly that larger broods require more work for successful rearing, but is this really stress? In birds, periods of stress normally are characterized by elevated levels of corticosterone and depressed levels of LH and gonadal steroids (Assenmacher 1973, Siegel 1980, Wingfield et al. 1982b). During the breeding season, however, free-living birds, in-

cluding House Sparrows, often exhibit elevated levels of corticosterone without depressed levels of reproductive hormones. Elevated levels of corticosterone at these times thus may represent a response to elevated metabolic demands rather than stress *per se* (Wingfield et al. 1982b; Hegner and Wingfield 1986a, b).

To our knowledge only one previous investigation involving brood manipulations has incorporated endocrine measurements, and the results were similar to ours. Adult Pied Flycatchers (*Ficedula hypoleuca*) tending larger broods had higher circulating levels of corticosterone, but levels of DHT and testosterone in males were not related to brood size (Silverin 1982). Unfortunately, gonadal regression occurs at the time of hatching in this population of Pied Flycatchers (Silverin 1975, 1980), and levels of reproductive hormones fall rapidly to basal (Silverin and Wingfield 1982), so the actual level of stress cannot be determined easily. In our study there was no significant increase in levels of corticosterone in females associated with larger broods (although a trend was apparent), and decreased titers of reproductive hormones were not associated with larger broods. Furthermore, body mass and fat levels of females were not related to brood size. From these data we conclude that adults in this study were not unduly stressed at the time the blood samples were collected (during the later portion of the nestling stage).

Females tending enlarged broods may have been more stressed once young fledged from the nest. In our study area males provide little, if any, postfledging care; instead, they remain near the nest site most of the day (Hegner and Wingfield 1986a). Young House Sparrows are dependent on adults for up to 10 days after fledging (Dawson 1972), and the average interbrood interval is 1 week (Hegner and Wingfield unpubl. data). In that week, females must replenish fat reserves, and 4 days are required for an ovarian follicle to attain maturity (Schifferli 1980, Krementz and Ankney 1986). Hence, females must assume primary care of fledglings at the same time they prepare physiologically for the ensuing brood (Hegner and Wingfield 1986b).

Few studies have compared the work loads of breeding birds during the postfledging stage. Adult Song Sparrows (*Melospiza melodia*) feed fledglings at a higher rate than nestlings (Smith

1978). Moreno (1984) reported similar results for Northern Wheatears (*Oenanthe oenanthe*). These data, however, must be evaluated with caution. Young can move nearer to food resources following fledging, thereby reducing commuting costs for parents (e.g. Moreno 1984). Moreover, when commuting distances are short, parents may provide more food to their young by bringing smaller loads of food at a rapid rate than by bringing a maximum load less frequently (Orians and Pearson 1979). Hence, a higher feeding rate by itself is not necessarily indicative of a higher work load. Quantitative measurements of metabolic rates or energy budgets, or both, are required to make this determination.

In the absence of strong indications to the contrary, we must consider the possibility that females were not unduly stressed by rearing enlarged broods, either when the young were in the nest or in the postfledging stage. What factors might then account for the increased interbrood interval and decreased subsequent clutch size exhibited by these females? Perhaps the increased interbrood interval resulted simply from the extra time required to raise larger broods to independence. Although not unduly stressed, females nonetheless may not have had sufficient time both to care for nestlings and to gather sufficient additional food for themselves to replenish fat and protein reserves required for egg formation (Pinowska 1979, Schifferli 1980, Hegner and Wingfield 1986b). Although this is possible, it fails to explain the decrease in clutch size, which in House Sparrows seems to be correlated with fat reserves (Pinowska 1979). Perhaps this resulted from a compromise between delaying clutch initiation even longer (thus rebuilding greater reserves) and producing a smaller clutch a day or two earlier. The observed differences in interbrood interval thus may have resulted from a proximate effect on females, while differences in the size of the subsequent clutch may have resulted from an ultimate within-season trade-off between the timing and size of that brood (e.g. McGillivray 1983). While these suggestions are speculative, they are at least plausible alternatives to the hypothesis that females tending enlarged broods were "stressed."

We have no satisfactory explanation for the relatively higher levels of brood reduction in the subsequent broods of pairs that had tended

reduced or control broods, particularly in light of the conflicting results reported by Mc-Gillivray (1983) in a study of successive nests in Alberta. In his study, subsequent clutch size did not decrease with fledgling number, but the subsequent number of young fledged did. Environmental conditions during the third brood of this season may have been particularly unfavorable, resulting in more brood reduction in larger broods. This suggests that, at least in some seasons, the productivity of a subsequent nesting attempt depends more on additional factors than on the size of the previous clutch.

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