# INTRASEASONAL REPRODUCTIVE COSTS FOR THE HOUSE SPARROW (PASSER DOMESTICUS)

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ABSTRACT.—House Sparrows (Passer domesticus) near Calgary, Alberta begin breeding in early spring and continue through to late summer. High productivity from previous broods is negatively correlated with fledgling production from second and third broods. Although fat reserves may limit the ability of females to raise young, there is no concomitant drop in clutch size or in the probability of renesting. Pairs that fledge many young in a year space fledgling production evenly over the breeding season but are most productive in mid-season. The interval between fledging and the initiation of the next clutch increases with the number fledged. This delay, an indication of the physiological strain involved in rearing young, is greater for later broods and for females nesting in trees. Measures of reproductive effort (clutch size, number fledged, length of the nestling period) vary seasonally but give no indication of peaking for last broods. Thus, reproductive effort is not adjusted to parallel changes in the probability of surviving to the next breeding attempt. Received 3 November 1981, accepted 24 April 1982.

A COMMON assumption underlying theoretical discussions of life-history phenomena is that trade-offs in life-history characteristics occur (Williams 1966, Charnov and Krebs 1974, Stearns 1976, Snell and King 1977). For example, Pianka and Parker (1975) partition the reproductive value of an individual of age $X$ in a stable nongrowing population into fecundity at age $X$ and expected fecundity conditioned by survival to ages $X + 1$, $X + 2$, . . . , $X + N$. Clearly if survivorship is lowered by current reproduction, future fecundity is reduced.

Many researchers of life-history phenomena in birds have investigated whether or not the modal clutch size is the most productive, as predicted by Lack (1947, 1966). If productivity is measured as the number of young fledged from a brood, then clutch sizes larger than modal appear to be optimal (Klomp 1970, von Haartman 1971, Jones and Ward 1976, Murphy 1978). If parental survivorship is reduced by the effort of raising a large brood, however, then the optimal clutch size might be lower than the most productive (Fisher 1930, Charnov and Krebs 1974). Studies testing the relationship between brood size and parental survivorship show equivocal results. Bryant (1979) found a reduction in the overwinter survivorship of double-brooded female House Martins (Delichon urbica), and male Pied Flycatchers (Ficedula hypoleuca) feeding many young were less likely to return to the study area than those feeding fewer young (Askenmo 1979). Lack (1966) and Kluyver (1970) present evidence suggesting an inverse relationship between brood size and parental survivorship. De Steven (1980), however, did not find a reduction in the survivorship of female Tree Swallows (Iridoprocne bicolor) as a result of brood enlargement. Smith (1981), after demonstrating a positive association between reproductive effort and survivorship, concluded that a trade-off between fecundity and survivorship should not be assumed for passerine birds.

The longevity and mobility of birds usually prevents a precise determination of mortality rates for individuals with a known reproductive history. If dispersers are a nonrandom sample of the population (Lowther 1979), then estimates of survivorship based on individuals staying at or returning to the study area will be biased. As a consequence, the effect of reproduction on survivorship is often estimated from physiological evidence. Weight losses for females through the breeding season suggest a physiological strain that may reduce survivorship (Newton 1966, Hussell 1972, Bryant 1979). For female House Sparrows (Passer domesticus), Pinowska (1979) has shown that levels of fat influence clutch size, while lean dry weight (an indicator of protein level) may determine the number of broods raised in a season. Norberg

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(1981) presented the hypothesis that adult weight losses during breeding may be adaptive. This would be true if the reduced cost of collecting food for the nestlings increases fledgling numbers more than it reduces survivorship and future fecundity.

Birds that raise more than one brood in a season may be expected to show differential reproductive effort and productivity through the breeding season. There is a higher probability of surviving from one brood to the next during the breeding season than from the last brood of one season to the following spring. An increase in the level of reproductive effort would be expected as the probability of surviving to the next breeding attempt decreases. There is some evidence that high levels of reproductive effort lower the ability of females to invest in a subsequent brood. For Great Tits (*Parus major*), Kluyver (1963) found a lesser probability of a second brood if the first was large. Pinkowski (1977) noted a drop in the clutch size of second broods for Eastern Bluebirds (*Sialia sialis*) that raised a large first brood, and Smith and Roff (1980) found that an increase in the interbrood interval was associated with a large first brood for Song Sparrows (*Melospiza melodia*).

In this study I look at the productivity of multibrooded House Sparrows through the breeding season and address two questions. First, is there variation in the productivity of successive broods within the breeding season associated with brood size in earlier broods (is there a demonstrable within-season cost associated with reproduction)? Second, do adults modify their reproductive effort in accordance with seasonal changes in the probability of renesting and surviving?

## METHODS AND MATERIALS

*Study site.*—In 1977, the study areas were six farms near Conrich, Alberta, 5 km east of Calgary. For 1978, all data were collected at one of these farms, 8 km east of Calgary. At each of the farms, about 20 nest boxes were erected in fall 1974 (see Murphy 1978 for details). As well as nesting in boxes, the sparrows used buildings, machinery, and trees. At the farm studied both years, nests built in trees were monitored in addition to those in nest boxes.

*Data collection.*—Nests were inspected at 3–5 day intervals from 2 May to 15 August 1977 and from 20 April to 13 August 1978. If weather conditions permitted, a 3-day interval was maintained. Eggs were counted and numbered. Nestlings 5–6 days old were banded with a U.S. Fish and Wildlife Service aluminum leg band and color marked with leg bands after reaching a 20-g weight.

*Data analysis.*—Because the nests were not checked every day, exact clutch-initiation data and nestling ages were not known for all nests. For these cases, estimates were used. Nestling age when first found was estimated by comparing the weight of the largest nestling in a brood to average values obtained from broods of known age. Clutch-initiation date was estimated by assuming an average incubation period of 11 days and a laying rate of one egg per day (McGillivray 1978). This estimate was needed only for clutches begun before my arrival at the study area.

In this study I investigated the productivity from multiple broods of a pair; hence, I made the general assumption that broods raised at a single nest through the breeding season were raised by the same pair. House Sparrows usually remain at the same site unless one of the pair dies (Summers-Smith 1963). To reduce the importance of this potential source of error, I imposed some residency conditions. If a tree nest was extensively modified following a nesting attempt, I assumed that a new pair was nesting. The average interval between successive clutch initiations for first through third clutches for each brood size was determined. Ninety five percent prediction intervals were calculated for each clutch-interval, brood-size combination. Nests where the interclutch interval fell outside these limits were excluded from further analyses.

The interval between the departure of the last nestling and the initiation of the next clutch is called the interbrood interval. The date of fledgling departure was considered to be the midpoint of the interval between the last observation of the nestlings and the first nest check after departure. Fledging is a gradual process, so a departure date is only an approximate measure. Paired comparison *t*-tests were used to compare the mean interbrood interval of successive broods and different nest types.

For the investigation of the effects of one brood on the next breeding attempt, data for the two years were pooled. Pooling requires trends to be consistent over the two years in order for the trends to be detected, and productivity for both years was similar except for the first broods. The strength of trends associated with brood size was measured by Pearson's product-moment correlation coefficient, *r*. Although significance levels were determined for *r*, paired variables were not tested for bivariate normality. Nonetheless, *r* is a useful indicator of trend.

This analysis assumes that fledglings of equal weight contribute equally to parental fitness. This assumption may not be valid for a species with a long breeding season. Dyer et al. (1977) published the following survivorship equation for juvenile House Sparrows (from Summers-Smith 1963); $Y =$

TABLE 1.  Seasonal variation in productivity: comparison between years; yearly means with standard error.

| Variable | Clutch | | | | | | | |
| --- | --- | --- | --- | --- | --- | --- | --- | --- |
| | First | | Second | | Third | | Fourth | |
| | 1977 | 1978 | 1977 | 1978 | 1977 | 1978 | 1977 | 1978 |
| Sample size | 276 | 210 | 227 | 157 | 162 | 87 | 40 | 15 |
| Clutch initiation date[a] | 131.8 | 133.8 | 157.1 | 162.5 | 183.1 | 191.2 | 198.6 | 206.2 |
| Clutch size | 4.8 (0.06) | 4.8 (0.06) | 5.2 (0.06) | 5.0 (0.07) | 4.8 (0.07) | 4.8 (0.11) | 4.3 (0.17) | 4.5 (0.13) |
| Number hatching[b] | 3.0 (0.10) | 2.8 (0.14) | 3.0 (0.12) | 3.2 (0.14) | 2.5 (0.15) | 3.1 (0.19) | 2.1 (0.26) | 2.4 (0.40) |
| Number fledging[b] | 1.8 (0.10) | 1.0 (0.10) | 1.9 (0.08) | 1.8 (0.13) | 1.5 (0.14) | 1.5 (0.18) | 0.8 (0.19) | 0.8 (0.34) |
| Fledging weight (g)[c] | 24.1 (0.20) | 26.1 (0.30) | 25.3 (0.27) | 26.6 (0.25) | 26.1 (0.28) | 27.1 (0.36) | 27.0 (0.56) | 24.0 (0.98) |

[a] Date measured from the beginning of the year.
[b] Significantly different between years for first broods ($P < 0.05$, t-test).
[c] Significantly different between years for all broods ($P < 0.05$, t-test).

TABLE 2.  Interbrood interval (days).

| Number of fledglings | 1978 | 1977-box nests[a] | 1977-tree nests[a] |
| --- | --- | --- | --- |
| | | **First to second** | |
| 0 | 11.4 | 6.0** | 8.1* |
| 1 | 6.4 | 6.3 | 8.0 |
| 2 | 7.4 | 7.3 | 8.3 |
| 3 | 10.8 | 8.0 | 9.4 |
| 4 | 9.5 | 9.1 | 11.0 |
| 5 | 11.0 | 8.3 | — |
| | | **Second to third** | |
| 0 | 10.7 | 6.9** | 7.2 |
| 1 | 10.0 | 7.4 | 9.2 |
| 2 | 10.9 | 7.9 | 9.4 |
| 3 | 11.7 | 8.7 | 10.0 |
| 4 | 10.2 | 8.1 | 9.2 |
| 5 | 12.0 | 10.6 | 9.5 |

[a] * = correlation with number of fledglings is significant at $P < 0.05$.
** = correlation with number of fledglings is significant at $P < 0.01$.
Paired comparison t-test for differences between first to second and second to third intervals: $d = 0.694$, $t = 1.92$, 16 df, $0.05 < P < 0.10$.
Paired comparison t-test for differences between tree and box nests for 1977: $d = 1.18$, $t = 4.32$, 10 df, $P < 0.01$.

$102.9X^{-0.688}$, where $Y =$ percentage of juveniles surviving and $X =$ month after fledging. If this equation accurately describes juvenile survivorship, then late-fledging young are more likely to be recruited into the population, and reproductive effort should be concentrated toward the end of the breeding season. In a seasonal environment such as that at Calgary, however, late-fledging young experience cold temperatures, snowcover, and food shortages at a younger age than do early-fledging young. Thus, a late-fledging cohort might suffer greater overwinter mortality (McGillivray 1981a).

Predation on eggs and nestlings was rare at this site. Few entire clutches or broods disappeared, and most nesting mortality can be attributed to starvation.

## RESULTS

For species that raise a single brood each season, the breeding season would be that period of the year during which parents have the highest probability of successfully fledging young. The same is true for a multibrooded species, but conditions are unlikely to be constant through the season. The average House Sparrow productivity for clutch initiations 1 through 4 is displayed in Table 1. If one considers only the average number fledged, the second brood is the most productive, the third slightly less, the fourth relatively unproductive, and the first quite different between years.

TABLE 3. Relationship between fledgling production and measures of reproductive effort (and standard error) for each brood.

| Number fledged | Clutch size[a] | | Fledgling weight | Nestling period length (days)[a] | | Breeding attempt length (days)[a,b] | |
|---|---|---|---|---|---|---|---|
| | | | **Brood 1** | | | | |
| 0 | 4.68** | (0.06) | — | 2.82* | (0.25) | 26.32** | (0.60) |
| 1 | 4.81 | (0.17) | 24.52 (0.48) | 13.03 | (0.50) | 33.32 | (0.55) |
| 2 | 4.50 | (0.13) | 25.47 (0.35) | 13.56 | (0.41) | 35.73 | (0.31) |
| 3 | 4.87 | (0.10) | 25.21 (0.36) | 13.58 | (0.28) | 36.65 | (0.52) |
| 4 | 5.29 | (0.11) | 24.30 (0.39) | 13.77 | (0.36) | 37.23 | (0.55) |
| 5 | 5.58 | (0.15) | 23.74 (0.45) | 13.91 | (0.72) | 37.80 | (1.08) |
| 6 | 6.00 | (0.00) | 27.84 (0.00) | 15.00 | (0.00) | 39.00 | (0.00) |
| | | | **Brood 2** | | | | |
| 0 | 4.95** | (0.08) | — | 2.28* | (0.27) | 24.00** | (0.88) |
| 1 | 4.96 | (0.19) | 25.78 (0.64) | 12.41 | (0.55) | 33.94 | (0.84) |
| 2 | 5.13 | (0.11) | 26.57 (0.36) | 12.31 | (0.30) | 35.72 | (0.66) |
| 3 | 5.20 | (0.09) | 26.17 (0.35) | 12.90 | (0.26) | 37.46 | (0.56) |
| 4 | 5.37 | (0.10) | 25.07 (0.38) | 12.76 | (0.52) | 36.03 | (0.51) |
| 5 | 5.45 | (0.11) | 24.96 (0.63) | 13.23 | (0.50) | 39.03 | (0.98) |
| 6 | 6.00 | (0.00) | 25.75 (3.50) | 14.50 | (2.50) | 43.00 | (0.00) |
| | | | **Brood 3** | | | | |
| 0 | 4.59* | (0.10) | — | 2.06 | (0.27) | 23.44 | (1.03) |
| 1 | 5.00 | (0.25) | 26.20 (0.83) | 12.08 | (0.57) | 37.00 | (3.50) |
| 2 | 4.50 | (0.19) | 26.64 (0.52) | 11.74 | (0.51) | —[c] | |
| 3 | 4.89 | (0.14) | 26.80 (0.42) | 11.97 | (0.32) | 37.25 | (1.70) |
| 4 | 5.19 | (0.09) | 26.77 (0.41) | 12.67 | (0.32) | 35.80 | (1.96) |
| 5 | 5.25 | (0.11) | 26.05 (0.58) | 12.57 | (0.80) | 33.60 | (0.68) |
| 6 | 6.00 | (0.00) | 25.42 (0.00) | 13.00 | (0.00) | —[c] | |
| | | | **Brood 4** | | | | |
| 0 | 4.22 | (0.17) | — | 1.87 | (0.50) | —[c] | |
| 1 | 4.67 | (0.42) | 26.65 (0.83) | 10.67 | (1.10) | — | |
| 2 | 4.20 | (0.26) | 24.76 (1.74) | 10.50 | (0.87) | — | |
| 3 | 4.80 | (0.37) | 27.60 (0.72) | 11.80 | (0.58) | — | |
| 4 | 5.00 | (0.00) | 24.31 (1.31) | 13.50 | (1.50) | — | |

[a] * = correlation with the number of fledglings significant at $P < 0.05$.
** = correlation with the number of fledglings significant at $P < 0.01$.
[b] Interval between successive clutch initiations.
[c] No subsequent clutch initiated.

High fledgling output from first broods is unusual for House Sparrows in this area (Murphy 1977), because cold weather, rain and snow are common throughout May (McGillivray 1981b).

That the interval between the fledging of a brood and the initiation of the next clutch (interbrood interval) increases as the number fledging increases is shown in Table 2. The longer interval between second and third broods compared to the interval between first and second broods implies that the physiological costs of breeding are cumulative. Sample sizes for the third to fourth brood interval are too small to consider (<5), except for box nests in 1977 that fledged no young in the third brood (interbrood interval = 7.6 days, $n = 17$), where

an increase over the second to third interval is observed. The longer interbrood interval for pairs nesting in trees suggests that daily energy requirements are lower for box-nesting females.

Why the physiological cost of nesting might increase with the number of young fledged from a brood is shown in Table 3. On the average, females must expend energy laying additional eggs, and the pair must spend a longer time feeding the young in large broods. As brood size increases, adult House Sparrows increase the rate of feeding trips to the nestlings (Summers-Smith 1963, Seel 1969, Sappington 1975, McGillivray 1981a), and, at least for these two years, average fledging weight does not change

TABLE 4. Relationship between the number of fledglings produced and productivity in the subsequent breeding attempt.

| Number fledged | $n$ | Clutch size | Number fledged | Probability of starting next clutch |
|---|---|---|---|---|
| **Brood 1** | | | **Brood 2** | |
| 0 | 234 | 5.10 | 1.69 | 0.70 |
| 1 | 38 | 5.48 | 2.36 | 0.82 |
| 2 | 61 | 5.21 | 2.23 | 0.77 |
| 3 | 81 | 5.06 | 2.07 | 0.84 |
| 4 | 56 | 5.10 | 1.88 | 0.73 |
| 5 | 14 | 5.40 | 1.60 | 0.71 |
| 6 | 1 | 4.00 | 0.00 | 1.00 |
| **Brood 1 and Brood 2** | | | **Brood 3** | |
| 0 | 41 | 4.63 | 1.22 | 0.60 |
| 1 | 13 | 5.08 | 1.69 | 0.81 |
| 2–3 | 75 | 4.84 | 1.83 | 0.75 |
| 4–5 | 65 | 4.83 | 1.54 | 0.69 |
| 6–7 | 37 | 4.51 | 1.46 | 0.51 |
| 8–9 | 12 | 5.00 | 0.50 | 0.75 |
| >9 | 1 | 5.00 | 0.00 | 1.00 |
| **Broods 1, 2, and 3** | | | **Brood 4** | |
| 0 | 7 | 4.00 | 1.14 | 0.22 |
| 1–3 | 18 | 4.78 | 0.50 | 0.41 |
| 4–6 | 20 | 4.20 | 1.00 | 0.22 |
| 7–9 | 8 | 4.25 | 0.62 | 0.15 |
| 10–12 | 2 | 4.00 | 0.50 | 0.15 |

TABLE 5. Modal number fledged in each brood for pairs grouped by seasonal total fledgling production.

| Brood | Seasonal total fledgling production | | | | | |
|---|---|---|---|---|---|---|
| | 1–2 | 3–4 | 5–6 | 7–8 | 9–10 | >10 |
| 1 | 2.0 | 3.0 | 3.0 | 3.5 | 3.0 | 3.0 |
| 2 | 2.0 | 3.0 | 3.0 | 4.0 | 5.0 | 4.5 |
| 3 | 0.0 | 0.0 | 0.0 | 0.0 | 4.5 | 4.0 |
| 4 | 0.0 | 0.0 | 0.0 | 0.0 | 1.5 | 1.5 |

with brood size. Although thermoregulatory costs should be lower for nestlings in larger broods, these are unlikely to offset the extra feeding demands on parents created by more nestlings.

For the combined breeding seasons 1977 and 1978, pairs that showed higher productivity from the first clutch tended to have lower output from the second clutch (Table 4). For pairs that fledged at least one young from the first brood, there is a negative correlation between the number fledged in brood 1 and the number fledged in brood 2 ($r = -0.85$, 4 df, $P < 0.05$). The class containing pairs fledging no young was excluded from analyses because of its heterogeneity. It includes a range from pairs raising young to near fledging to others losing clutches before hatching. The probability of starting a second clutch and the size of second clutches are uncorrelated with the number of fledglings from brood one.

Because the interbrood interval data suggested that physiological strain is additive over

broods, I compared third and fourth brood productivity with summed fledgling totals from all previous broods. For pairs fledging at least one young, the summed fledgling production from broods 1 and 2 is negatively correlated with the number fledging in brood 3 (Table 4, $r = -0.81$, 4 df, $0.05 < P < 0.10$). Again, the probability of renesting and the average clutch size are not related to productivity earlier in the season.

There is a nonsignificant, negative relationship between total productivity in broods 1, 2, and 3 and the average number fledging in brood 4 (Table 4). The probability of initiating a subsequent brood has dropped from the previous two comparisons and is lowest for pairs with the highest fledgling numbers from the previous three broods.

When the fledgling data from the three comparisons (broods 1 vs. 2; 1 and 2 vs. 3; and 1, 2, and 3 vs. 4) are combined and standardized by transformation to $Z$-scores, previous productivity is shown to be negatively correlated with future productivity ($r = -0.63$, 14 df, $P < 0.05$).

The strong negative relationship between first and second brood productivity is reflected in the distribution of fledgling production over the breeding season. Table 5 demonstrates that the highest fledgling totals were achieved by pairs with high post-first-brood productivity.

A prediction from life-history theory is that, unless the raising of last broods lowers adult survivorship, reproductive effort should be higher for that brood than for broods earlier in the season. Last broods, as defined here, include fourth broods and third broods after which no fourth clutch was initiated. Because no physiological measures were made, only indirect estimates of effort can be used. Table 6 demonstrates that, for four possible indicators

TABLE 6. Measures of reproductive effort (and standard error) by pairs for broods after which fourth clutches were initiated, third broods that were last broods and fourth broods.

| Variable | Third broods | | Fourth broods |
|---|---|---|---|
| | Not last | Last | |
| Clutch size | 4.83 (0.10) | 4.74 (0.07) | 4.36 (0.13) |
| Number fledged | 2.93 (0.18) | 2.78 (0.13) | 2.11 (0.23) |
| Fledgling weight (g) | 26.54 (0.40) | 26.48 (0.25) | 26.01 (0.65) |
| Nestling period (days) | 12.36 (0.37) | 11.70 (0.25) | 11.22 (0.48) |

of reproductive effort, average values for third broods that are also last broods are not significantly different from those of third broods after which a fourth clutch was laid. There is also no evidence of enhanced effort for fourth broods.

## Discussion

These data suggest that the trade-offs and the theory required to account for them are different for single and multibrooded species. An inverse relationship between present and future fecundity is suggested but not as a function of reduced survivorship. Rather, high productivity delays the initiation of the following clutch and is negatively correlated with productivity from future clutches.

Two studies (Schifferli 1976, Pinowska 1979) have monitored the physiological condition of adult House Sparrows through the breeding season. For females, fat level drops during egg laying, is partially replaced during incubation, drops again during the nestling period, and presumably is restored in the interbrood interval. Protein level drops gradually through the breeding season. Pinowska (1979) found that clutch size was correlated with fat level and the number of clutches initiated in a season was limited by protein level. For males, fat level drops during the nestling period and is replenished in the interbrood interval.

These two studies suggest that, after completing a brood, both sexes of a pair fledging many young would have lower fat levels than those of a pair fledging few young. The lower fat level should result in either a smaller clutch size or a longer delay in the initiation of the subsequent clutch. My observations show that clutch size is not affected by previous productivity but subsequent clutch initiations are delayed. The longer interval between second and third broods compared to that between first and

second broods indicates a cumulative physiological effect of the first two broods. This effect is suggested by Pinowska's observations (1979) of protein levels and by the reduced survivorship of double-brooded House Martins found by Bryant (1979).

The longer interbrood interval for pairs using tree nests supports other observations (Murphy 1978, McGillivray 1981b) showing that box nests are superior nest sites. A warmer microclimate (Mertens 1977) would reduce nestling thermoregulatory costs, and a reduction in the need for nest maintenance would facilitate renesting in boxes.

While the tree-versus box-nest comparisons provide appealing evidence for physiological correlates of reproductive costs, they point out a problem in the evaluation of reproductive effort. If nest-site selection can modify the cost of raising young, then other factors such as weather, distance to food sources, time of clutch initiation, and parental age and size are also likely to modify the reproductive effort associated with raising a brood of fixed size. The importance of factors other than productivity may provide a partial explanation for the contradictory results obtained in previous studies of the trade-off between reproductive effort and survivorship in passerines (Bryant 1979, Askenmo 1979, De Steven 1980, Smith 1981).

There is no simple physiological hypothesis to account for reduced productivity from pairs fledging many young. Because clutch size and the probability of renesting are generally unrelated to previous productivity, the cost of reproduction is felt by parents during the incubation and nestling period. While the nestling period is considered highly demanding (Ricklefs 1973), much of the evidence (particularly weight losses for adults) is now questionable (Norberg 1981).

There is no evidence from the data that re-

productive effort increases as the probability of surviving to the next breeding attempt decreases. As mentioned earlier, however, only partial estimates of reproductive effort are possible. Pinowska (1979) felt that breeding in House Sparrows followed a cyclical pattern in which a pool of resources is alternatively tapped and partially replenished until depleted below a critical point and breeding ceases. Hence, second, third, and fourth broods are initiated only by females that possess sufficient resources. Last broods, which should show enhanced reproductive effort according to life-history theory, might, in fact, show evidence of physiological strain. Seasonal differences make comparisons among broods difficult to interpret, but the comparison between third broods that were last broods and third broods after which a fourth clutch was initiated is revealing. Table 6 indicates that, while none of the chosen measures of effort is different between groups, the direction of difference always suggests lower resource levels for pairs raising last broods.

A reviewer pointed out that life-history theorists consider ultimate causes, but field workers are forced to explain proximate reasons for phenomena such as clutch size, number of breeding attempts per season, and survivorship. The lack of concordance between theory and field observations (Smith 1981, this study), while perhaps an indictment of the theory, is equally likely to be the result of failure to control and account for proximate variation.

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