# INTRASEASONAL COSTS OF REPRODUCTION IN STARLINGS[1]

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*Abstract.* I examined intraseasonal reproductive trade-offs in European Starling (*Sturnus vulgaris*) females breeding in central New Jersey in 1984–1988. Among females experimentally forced to rear enlarged broods, one of four treatments reduced the likelihood of initiating a second clutch, but there was no clear relationship between first brood size or reproductive success and likelihood of initiating a second clutch. Females that initiated second clutches laid smaller first clutches, but reared larger first broods relative to their original clutches, than did females that did not initiate second clutches. For females rearing unmanipulated first broods, first brood reproductive effort did not affect the likelihood of initiating a second clutch. Among both experimental and control females, only those individuals that initiated first clutches relatively early laid second clutches.

Neither brood size in manipulated broods nor reproductive success in control nests affected second brood reproductive success, but those females that reared broods larger than their clutches laid smaller second clutches. Clutch size in second broods declined seasonally, but was a poor predictor of the number of second brood fledglings. Since some second broods were successful and intraseasonal costs did not affect second brood success, it is unclear why only 44% of females initiated second broods.

Compared to artificially synchronized broods of the same size, asynchronous hatching increased neither the probability of initiating a second clutch nor the reproductive success of second broods. Thus asynchronous hatching in first broods was not a strategy to increase reproductive success in subsequent broods.

*Key words: Asynchronous hatching; clutch size; costs of reproduction; European Starling; reproductive success; second broods; Sturnus vulgaris.*

## INTRODUCTION

A fundamental assumption of life history theory is that organisms allocate reproductive effort to maximize lifetime reproductive success (Williams 1966a, 1966b; Stearns 1976). In iteroparous organisms, an individual must balance the cost of present reproduction against the potential benefit of future reproduction. The observation that some species of birds can successfully rear more nestlings than their normal clutch size has been interpreted as evidence of decreased present parental investment in an effort to improve future reproductive success (Williams 1966b, Murphy and Haukioja 1986). Alternatively, limiting present fecundity may be a means of maximizing offspring quality (Lack 1954:22; see also Gustafsson and Sutherland 1988).

Experiments are necessary to examine the consequences of present reproductive effort on future reproduction. Individual variation may confound correlative studies because birds phenotypically superior in traits for present reproduction may also be phenotypically superior in traits for survival (e.g., Smith 1981, Clobert et al. 1987). For this reason correlative results are likely to show a positive relationship between present and future reproduction, falsely suggesting a benefit, rather than a cost, to reproduction (see Partridge and Harvey 1985, Den Boer-Hazewinkel 1987). In some experimental studies, increased brood size reduced parental return rates (and presumably survival) in the following season, although sometimes for only one sex (Pied Flycatcher, *Ficedula hypoleuca*, Askenmo 1979; Blue Tit, *Parus caeruleus*, Nur 1984; Glaucous-winged Gull, *Larus glaucescens*, Reid 1987). This relationship was not found in other species (Tree Swallow, *Tachycineta bicolor*, DeSteven 1980; Collared Flycatcher, *Ficedula albicollis*, Gustafsson and Sutherland 1988; Great Tit, *Parus major*, Pettifor et al. 1988). Studies with double-brooded Great Tits (Smith et al. 1987, Tinbergen 1987, Lindén 1988) and House Wrens, *Troglodytes aedon*, (Finke et al. 1987) have shown reduced frequency of second broods or an increase in the time between broods associated with experimentally increased brood size.

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Like reduced clutch size, asynchronous hatching may be a strategy that altricial birds use to reduce present investment in an effort to increase subsequent reproductive success. Asynchronous hatching was proposed to be adaptive because it allows parents to selectively starve offspring to reduce brood size to the number of nestlings that can be fledged given the available food supply (the "brood reduction hypothesis": Lack 1954, Ricklefs 1965). However, some experimental studies suggest that asynchronous hatching is not necessary for brood reduction to occur or that synchronous hatching would produce more fledglings (Haydock and Ligon 1986; Skagen 1987, 1988; Amundsen and Stokland 1988; Stouffer and Power 1991). An alternative hypothesis was proposed by Mock and Ploger (1987): they observed that Cattle Egret (*Bubulcus ibis*) nestlings in control (asynchronous) broods solicited their parents less for food than did nestlings in experimentally synchronized broods. Mock and Ploger (1987) suggested that improved condition of parents rearing asynchronously hatched broods may result in greater future reproductive success in comparison to parents rearing synchronously hatched broods. This hypothesis (here called the 'parental efficiency hypothesis'), which has not been tested, implies that the hatching pattern in a current brood affects future reproductive success. The parental efficiency hypothesis can be considered a special case of the iteroparity effect first proposed by Williams (1966b) in the context of clutch size.

Two predictions can be made from the parental efficiency hypothesis. First, parents rearing asynchronous broods should be more likely to breed again than parents rearing synchronous broods of the same size. Second, among the parents breeding again, those that had previously reared asynchronous broods should have higher reproductive success than parents that previously reared synchronous broods. Confirmation of either prediction would support the parental efficiency hypothesis.

The relationship between present cost and future reproductive success need not be linear or symmetrical (see discussion in Nur 1984). Reduced present cost may not increase future reproductive success, although increased present cost may decrease future reproductive success. The parental efficiency hypothesis requires that an increase in present cost comparable to the cost saved by asynchronous hatching decreases future

reproductive success. Thus the hypothesis is best tested by experimental synchronization. For most birds, asynchronous hatching often reduces brood size by one nestling due to early mortality of the last-hatched nestling (Clark and Wilson 1985, see also Stouffer and Power 1991), so experimentally demonstrating a decrease in future reproductive success after rearing a single additional nestling also provides indirect support for the hypothesis. Simply showing a cost in grossly enlarged broods does not support the hypothesis, although finding no such costs would suggest the hypothesis does not apply.

European Starling (*Sturnus vulgaris*) populations typically initiate first clutches during a period of a few days (Feare 1984:124, see also Results). In the study population, modal clutch size during this period is five eggs (Power et al. 1989). Some females that successfully rear first broods initiate second clutches beginning about 40 days later, but the productivity of second broods is generally lower than in first broods (Kessel 1957, Feare 1984, Chapter 6 and 7). Regardless of clutch size, most clutches hatch over a period of about 24 hr (Stouffer and Power 1990). Last-hatched nestlings are most likely to die, but much of this mortality would be reduced, especially in broods of five or less, by synchronous hatching (Stouffer and Power 1990, 1991). Nestling survival and growth was reduced in experimentally enlarged broods of six and seven (Stouffer and Power 1991).

I manipulated brood size and hatching pattern in starling broods in 1988 to test the predictions of the parental efficiency hypothesis and to evaluate the effect of first brood reproduction on second brood reproductive success. I manipulated broods that were initiated early in the breeding season and quantified first and second brood reproductive success. I also considered the relationship between first brood reproductive success and subsequent second brood success in unmanipulated broods from 1984–1987.

## METHODS

I studied starlings breeding in nest boxes mounted on utility poles on the Kilmer Campus of Rutgers University in Piscataway, New Jersey. The study site is a mosaic of mowed lawns, sports fields, and early secondary growth as well as buildings, roads and parking lots (Romagnano 1987).

In 1984–1987 I followed the fate of unmanipu-

lated broods. In 1988 I experimentally made broods of five, six, and seven nestlings that hatched either within one day (hereafter "synchronous broods"), or over two days with the last eggs hatching a day later than the others (hereafter "asynchronous broods"). Treatment names describe the number of nestlings and the hatching pattern (e.g., treatment 4:1 means 4 eggs hatching synchronously followed by 1 egg a day later, producing an asynchronous brood of 5; 5: 0 means a synchronously hatching brood of 5). I manipulated broods initiated from 16–30 April (see Stouffer and Power [1991] for more details of manipulation). Within the 15-day manipulation period, the treatment assigned to any nest was independent of initiation date. Females that reared successful first broods (i.e., first broods from which at least one nestling fledged) initiated second clutches as early as 25 May. "Initiation date" refers to the day the first egg in a clutch was laid. "Second clutches" and "second broods" refer only to broods following successful first broods. "Interclutch interval" refers to the number of days between hatching of the first egg in the first brood and laying of the first egg in the second brood.

In 1984–1987 I recorded the following: initiation date, clutch size, brood size, and number of fledglings. I recorded the following additional information from broods in 1988: hatching pattern, mean mass at day 19 of nestlings that subsequently fledged ("mean fledgling mass"), and combined mass at day 19 of all surviving nestlings ("brood mass").

During first broods I caught the resident females at treatment nest boxes during the night while the females were brooding four to ten day-old nestlings (see also Romagnano et al. 1989). I caught females rearing second broods at night either during the post-laying incubation period (1988 only) or while brooding nestlings (1984–1987). If a breeding female was not captured, the nest box where she bred was deleted from the sample for that year.

Based on clutch size and number of fledglings, I derived variables that reflected reproductive effort relative to clutch size. These variables controlled for differences among females that laid clutches of different sizes. "Relative brood size" (brood size minus clutch size) measured the extent of brood size manipulation relative to actual clutch size. "Relative number of fledglings" (number of fledglings minus clutch size) mea-

sured parental effort relative to clutch size. As an example of relative measures in comparison to absolute measures, consider the following. A female that laid five eggs but was given six nestlings to rear had a relative brood size of $+1$. If she fledged five nestlings she had a relative number of fledglings of 0, and her absolute number of fledglings was 5. Relative brood size and relative number of fledglings were generally positive in 1988 because of enlarged brood size. These measures were generally negative in unmanipulated broods in 1984–1987 because of non-hatching (Stouffer 1989) and egg removal (Lombardo et al. 1989). Because of these differences among years, the 1988 data were most likely to show the effects of increased parental effort and the 1984–1987 data were most likely to show the effects of decreased parental effort.

I compared frequencies with the log-likelihood ratio test ($G$ test) and report $G$ values when sample sizes were sufficient. I adjusted the error rate in simultaneous comparisons of data subsets following the procedure of Sokal and Rohlf (1981: 728). If $>25\%$ of expected values in any frequency test was $<5$, I used Fisher's exact test and report only the $P$ value. In some cases I analyzed the effects of a continuous independent variable on a discrete dependent variable with a logistic regression analysis for goodness-of-fit (Dobson 1983, Chapter 8). Other analyses are detailed below. All tests are two-tailed.

## RESULTS

### TIMING OF BREEDING

Figure 1 shows timing of clutch initiation for all years combined. Most first clutches were initiated between about 14 and 28 April, although some females initiated first clutches through the entire breeding season. Some of the first clutches after the beginning of May may have been from females that failed in first brood attempts off the colony, or from females that started clutches in nest boxes, failed before they were identified, and switched nest boxes before initiating new clutches. Most second clutches were initiated between 30 May and 10 June. Females usually initiated second broods in the same nest boxes as first broods (64 of 71 females, 90.1%).

### SECOND BROOD INITIATION

Whether a female initiated a second brood was strongly dependent on the time of initiation of
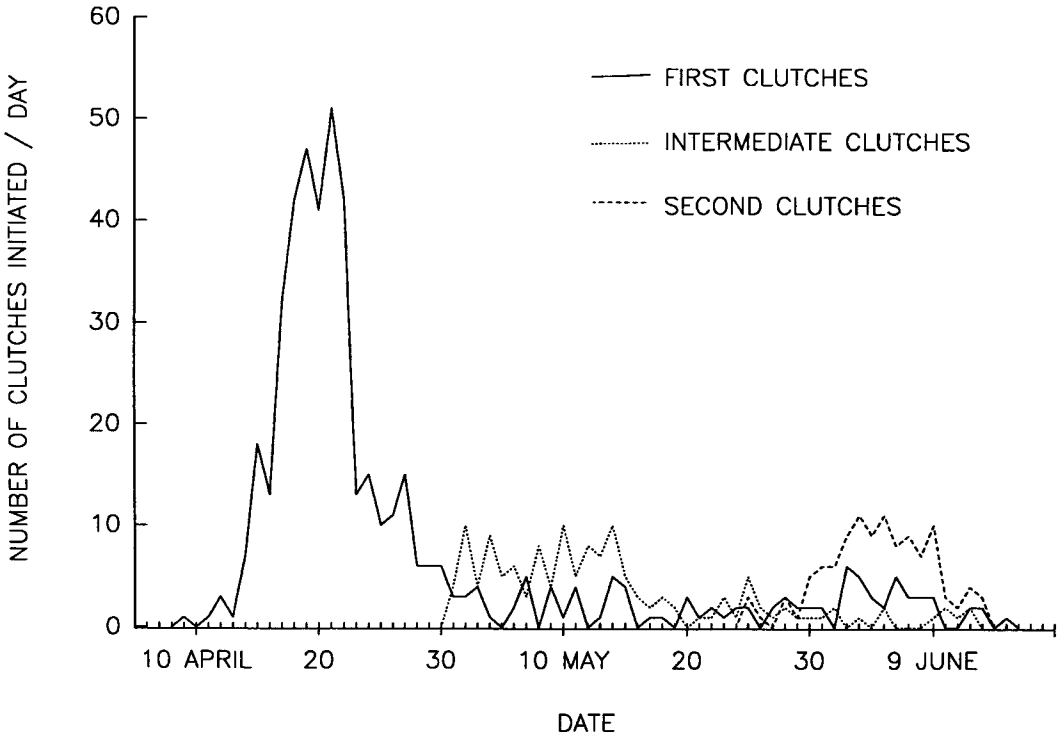
FIGURE 1. Clutch initiation in 1984–1988. "First clutches" include only the first clutch a female is known to have initiated in a year. "Intermediate clutches" include replacement clutches initiated after failed first clutches. "Second clutches" include clutches initiated after successful first broods.

the first brood in 1988 (Table 1A). Females that initiated second broods began their first broods earlier (logistic regression, $P = 0.014$); no female that initiated a first brood after 21 April later initiated a second brood. Considering only those clutches initiated on or before 21 April, there were differences among treatments in second brood attempts (Table 1B). Females in treatment 5:1 were less likely to initiate second broods than were females from any other treatment (all pairwise $P < 0.038$). No other treatments differed (all pairwise $P > 0.608$). The anomalous result for females in treatment 5:1 had no readily apparent basis (Table 1C); log-linear analysis revealed no significant effect of brood size ($P = 0.095$), hatching pattern ($P = 0.106$), or brood size × hatching pattern ($P = 0.170$).

Most measures of first brood reproductive success were unrelated to initiation of second broods in 1988 (Table 2). Analysis of variance revealed no difference between females that initiated second broods and those that did not in first brood size, number of fledglings, mean fledgling mass, or brood mass. Date of first brood initiation was not a significant covariate in these analyses. For clutch size and relative brood size birds that had second broods differed from those that did not; females with second broods laid smaller first clutches but had greater relative brood size. Date of clutch initiation was a significant covariate in analyses of both clutch size and relative brood size; first clutch size increased over the period from 16–21 April. Logistic regression of first brood variables, ignoring possible covariance with initiation date, led to qualitatively similar results.

I compared first brood reproductive effort between females that initiated second broods and those that did not in 1984–1987. As in 1988, females that initiated second broods began their first broods earlier than females that did not have second broods (logistic regression, $P = 0.010$). For more detailed analyses of first brood effects I considered only those first broods initiated dur-

TABLE 1. Initiation of second clutches by females rearing manipulated first broods in 1988. Parts B and C include only broods initiated before 22 April.

A. Frequency of second broods partitioned by date of first clutch initiation.

| | Date (1 April = 1) | | | | | | |
|---|---|---|---|---|---|---|---|
| | 16 | 17 | 18 | 19 | 20 | 21 | 22–30 |
| % second broods | 100 | 72.7 | 60.0 | 45.5 | 22.2 | 25.0 | 0 |
| Total | (1) | (11) | (15) | (11) | (9) | (4) | (6) |

B. Frequency of second broods partitioned by treatment.

| | Treatment | | | | | |
|---|---|---|---|---|---|---|
| | 4:1 | 5:0 | 5:1 | 6:0 | 6:1 | 7:0 |
| % second broods | 57.1 | 54.6 | 8.3 | 66.7 | 75.0 | 75.0 |
| Total | (7) | (11) | (12) | (9) | (8) | (4) |

C. Frequency of second broods partitioned by hatching pattern and brood size.

| | Hatching pattern | | Brood size | | |
|---|---|---|---|---|---|
| | Asynchronous | Synchronous | 5 | 6 | 7 |
| % second broods | 40.1 | 62.5 | 55.6 | 33.3 | 75.0 |
| Total | (27) | (24) | (18) | (21) | (12) |

ing the period each year when some females later initiated second broods (analogous to considering only 16–21 April [Table 1A] in the 1988 analyses). I analyzed two absolute measures: clutch size and number of fledglings. These variables might correlate with female quality. I also analyzed two relative measures of parental investment: relative brood size, and relative number of fledglings. If the parental investment expended in a first brood reduced the likelihood of initiating a second brood, females rearing broods with larger relative size or females fledging relatively more nestlings should have been less likely to have second broods. For no first brood measures

did females with second broods differ from those that did not have second broods (Table 3). The covariate initiation date was significant for clutch size and number of fledglings, indicating a decline in first brood productivity over time. The covariate effect was apparently due to relatively early breeding in 1987; in 1984–1986 the modal date of first clutch initiation was 21 or 22 April, but in 1987 it was 16 April. Using initiation date relative to modal initiation date for the year as the covariate in the analyses in Table 3 (i.e., correcting for differences among years in first brood timing), the covariate for clutch size and number of fledglings was not significant (both $P$

TABLE 2. First brood reproductive effort (mean ± SD) for females that initiated second broods and for those that did not in 1988. Only first broods initiated before 21 April are included (1 April = day 1 for initiation dates). Initiation date was tested with logistic regression. For other variables, the covariate is first brood initiation date. Analyses are by ANCOVA if the covariate effect is significant. If the covariate is not significant, $P$ values are from ANOVA. For no ANCOVA were slopes heterogeneous (all $P > 0.640$).

| Variable | Returning | Non-returning | $P$ means | $P$ covariate |
|---|---|---|---|---|
| Number of females | 26 | 25 | | |
| Initiation date | 18.06 ± 1.16 | 19.04 ± 1.24 | 0.022 | — |
| Clutch size | 4.81 ± 0.63 | 5.04 ± 0.79 | 0.005 | 0.001 |
| Brood size | 5.96 ± 0.87 | 5.80 ± 0.65 | 0.457 | 0.337 |
| Relative brood size | 1.15 ± 1.12 | 0.76 ± 0.97 | 0.008 | 0.001 |
| Number of fledglings | 4.85 ± 0.93 | 4.84 ± 1.11 | 0.983 | 0.771 |
| Relative number of fledglings | 0.038 ± 0.12 | −0.200 ± 1.41 | 0.516 | 0.066 |
| Fledgling mass | 71.44 ± 5.42 | 69.77 ± 4.53 | 0.240 | 0.122 |
| Brood mass | 343.8 ± 57.1 | 337.9 ± 78.4 | 0.760 | 0.382 |

TABLE 3. First brood reproductive effort (mean ± SD) for females that initiated second broods and for those that did not in 1984–1987. For each year the sample includes only those broods initiated on days when at least one female returned (as in Table 2, in which broods initiated after 21 April were deleted). Analyses are as in Table 2. For no ANCOVA were slopes heterogeneous (all $P > 0.447$).

| Variable | Returning | Non-retunring | P means | P covariate |
|---|---|---|---|---|
| Number of females | 45 | 65 | | |
| Initiation date | 19.40 ± 3.44 | 20.15 ± 2.71 | 0.256 | — |
| Clutch size | 5.02 ± 0.62 | 4.80 ± 0.73 | 0.161 | 0.032 |
| Relative brood size | −0.711 ± 0.944 | −0.415 ± 1.03 | 0.129 | 0.703 |
| Number of fledglings | 3.62 ± 0.96 | 3.53 ± 1.13 | 0.733 | 0.046 |
| Relative number of fledglings | −1.40 ± 1.09 | −1.29 ± 1.18 | 0.629 | 0.585 |

$> 0.089$). Interestingly, first brood initiation date (within the period when some females had second broods) did not affect initiation of second broods. This result was also unaffected by repeating the analysis with initiation date corrected for yearly differences (logistic regression, $P = 0.822$).

REPRODUCTIVE SUCCESS IN SECOND BROODS

Table 4 shows measures of second brood reproductive success partitioned by first brood manipulation in 1988 for those females that initiated second clutches. I evaluated the effect of brood size manipulations two ways: by manipulated brood size (Table 4A); and by manipulated brood size relative to clutch size (Table 4B). First brood size did not affect interclutch interval, second clutch size, or the number of fledglings from second broods. As a covariate, date of hatching of the first brood did not affect interclutch interval. In the analysis by brood size, date of second clutch initiation was a significant covariate for second clutch size, but not for number of fledglings. Second clutch size declined over time.

Comparing enlarged broods (relative brood size $>0$) and normal broods (relative brood size $\leq 0$) revealed a significant decline in second clutch size for females rearing enlarged first broods (Table 4B), but second brood fledging success did not differ between the groups. Again, the covariate effect revealed a decrease in second clutch size over time. Number of fledglings from second broods was distributed bimodally as a result of the high proportion of failures, so I also analyzed fledging success with a non-parametric Kruskall-Wallis test. For neither the comparison of brood size nor the comparison of relative brood size was this result qualitatively different from the ANCOVA results.

A prediction of the parental efficiency hypothesis is that costs of synchronous hatching in first broods should reduce reproductive success in second broods. So few females had second broods that a meaningful analysis of all levels of brood size and hatching pattern could not be performed. Sample sizes were sufficient, however, to analyze the effects of first brood hatching pattern for females rearing first broods larger than the clutches they laid ('Enlarged broods' in Table 4B). Asynchronous hatching should be most advantageous to females forced to rear enlarged broods, since brood reduction soon after hatching quickly reduces brood size for these females (Stouffer and Power 1991). Interclutch interval, second clutch size, and number of fledglings in second broods were not affected by first brood hatching pattern (Table 4C). As in the other analyses of Table 4, a non-parametric test of number of fledglings was also non-significant.

I also examined the relationship between first and second brood reproductive effort for females with second broods in 1984–1987. As in the previous comparisons, I considered four measures of first brood investment: two absolute measures (clutch size and brood size), and two relative measures (relative brood size and relative number of fledglings). These four variables were highly correlated (Pearson product-moment correlation; all $P < 0.015$). None correlated significantly with date of second brood initiation (all $P > 0.129$), so I examined the effect of each first brood variable on second brood reproductive success using a separate multiple regression with the date of second brood initiation as a second predictor for all second brood variables except interclutch interval (Table 5). Date of hatching in the first brood did not correlate with any other first brood variables (all $P > 0.242$), so I used this as the second predictor for inter-

TABLE 4. Means ± SD for measures of second brood reproductive success as a function of first brood manipulations. The covariate for interclutch interval is date of hatching of the first brood. The covariate for clutch size and number of fledglings is second clutch initiation date. Analyses are by ANCOVA if the covariate effect is significant. If the covariate is not significant, $P$ values are from ANOVA. For no ANCOVA were slopes heterogeneous (all $P > 0.395$).

A. Comparison of manipulated first brood sizes.

| Second brood variable | Brood size | | | $P$ means | $P$ covariate |
| | 5 | 6 | 7 | | |
|---|---|---|---|---|---|
| Number of females | 10 | 7 | 9 | | |
| Interclutch interval | 30.1 ± 2.6 | 30.6 ± 3.2 | 30.1 ± 3.2 | 0.366 | 0.781 |
| Clutch size | 4.40 ± 0.70 | 4.00 ± 1.00 | 3.75 ± 0.46 | 0.156 | 0.010 |
| Number of fledglings | 0.71 ± 1.25 | 1.00 ± 1.41 | 1.57 ± 1.27 | 0.475 | 0.752 |

B. Comparison of enlarged and normal broods.

| Second brood variable | Treatment | | $P$ means | $P$ covariate |
| | Enlarged | Normal | | |
|---|---|---|---|---|
| Number of females | 17 | 9 | | |
| Interclutch interval | 30.6 ± 3.22 | 29.6 ± 2.06 | 0.410 | 0.637 |
| Clutch size | 3.81 ± 0.75 | 4.55 ± 0.53 | 0.040 | 0.022 |
| Number of fledglings | 1.33 ± 1.30 | 0.714 ± 1.25 | 0.374 | 0.122 |

C. Comparison of synchronous and asynchronous enlarged broods.

| Second brood variable | Treatment | | $P$ means | $P$ covariate |
| | Synchronous | Asynchronous | | |
|---|---|---|---|---|
| Number of females | 9 | 8 | | |
| Interclutch interval | 30.2 ± 2.91 | 31.0 ± 3.70 | 0.207 | 0.530 |
| Clutch size | 3.89 ± 0.78 | 3.70 ± 0.76 | 0.465 | 0.083 |
| Number of fledglings | 1.17 ± 1.33 | 1.50 ± 1.38 | 0.122 | 0.374 |

clutch interval. None of the first brood variables were significant predictors of interclutch interval, second brood clutch size, or number of fledglings produced by second broods. The effect of second brood initiation date was significant for clutch size, indicating that females that initiated second clutches later laid smaller second clutches. As in 1988, second brood fledging success was distributed bimodally. Including only successful second broods did not affect these results.

To examine seasonal effects on late broods in more detail, I considered all broods initiated during the second brood period, regardless of the experience of the female parent (Table 6). Clutch size declined in all years, although significance levels varied with sample size. Combining years revealed a highly significant decline of 0.065 eggs/day, or about 1.3 eggs during the second brood initiation period (24 May–15 June). Second brood fledging success did not decline significantly over time in late broods in any year or in all years combined. Only in 1985 was clutch size significantly correlated with number of fledglings from

second broods. The lack of correlation in other years reflected the unpredictability of late broods, partially due to frequent failure. Excluding failed broods, clutch size and number of fledglings correlated weakly for the entire sample. I examined seasonal effects on failure using logistic regression. Unpredictable productivity of second broods was also reflected in this analysis: for no year nor for all years combined did timing of second brood initiation affect the likelihood of failure (all $P > 0.286$).

## DISCUSSION

### SECOND CLUTCH INITIATION

The best predictor of whether a female would initiate a second brood was the initiation date of the first brood. In all years the only females that had second broods were those that initiated first broods during the first few days of laying for the population. Among non-manipulated broods in 1984–1987 there were no differences in either relative or absolute measures of first brood pa-

TABLE 5.   First brood investment and second brood productivity in 1984–1987. Analyses, except for interclutch interval, are by multiple regression of the general form: second brood variable = (coefficient a) × first brood variable + (coefficient b) × date of second brood initiation + constant. For interclutch interval the second predictor is date of hatching in the first brood. Given are coefficients (slopes) and significance (* = $P < 0.05$, ** = $P < 0.01$, *** = $P < 0.001$). In parentheses are the coefficients and significance of the second predictor. $n$ = 45 females.

| Second brood variable | First brood variable | | | |
| --- | --- | --- | --- | --- |
| | Clutch size | Relative brood size | Number of fledglings | Relative number of fledglings |
| Interclutch interval | 0.127 (0.006) | 0.152 (−0.004) | −0.695 (−0.020) | 0.166 (−0.004) |
| Clutch size | 0.146 (−0.067**) | −0.002 (−0.069**) | −0.003 (−0.070**) | −0.055 (−0.071**) |
| Number of fledglings | 0.008 (−0.076) | 0.186 (−0.082) | −0.077 (−0.079) | −0.067 (−0.078) |
| Number of fledglings (0 excluded) | 0.039 (−0.057) | −0.340 (−0.072) | 0.186 (−0.051) | 0.089 (−0.058) |

rental investment between those females that later initiated second broods and those that did not (Table 3). In 1988, females that initiated second broods laid smaller first clutches than did females without second broods, but, as a result of brood size manipulations, reared larger broods relative to their original clutches (Table 2). Since the energetic cost of egg production is far less than the cost of rearing a nestling (e.g., Ricklefs 1974), females with enlarged first broods invested more in first broods. Therefore this result cannot be construed as demonstrating that reduced clutch size meant a decrease in parental investment in first broods by females that later initiated second broods.

These results provide no evidence for a trade-off between first brood investment and likelihood of initiating a second clutch. Similar results were reported by Den Boer-Hazewinkel (1987), who found that breeding Great Tits given supplemental food were no more likely to initiate second broods than were control parents. However, other studies showed fewer second broods by Great Tit females rearing artificially enlarged first broods (Smith et al. 1987, Tinbergen 1987, Lindén 1988). Annual differences affecting first brood productivity (e.g., Stouffer and Power 1991) may affect experimental results from a single year. Perhaps first broods enlarged more than those in this study would depress the frequency of second broods in starlings, although higher nestling mortality and lower fledgling mass in enlarged first broods indicated that these manipulations reduced parents' ability to meet the needs of their nestlings (Stouffer and Power 1991).

## SECOND BROOD PRODUCTIVITY

The only significant effect of first brood effort on second brood productivity was reduced second clutch size by females that reared first broods larger than their first clutches (Table 4). This relationship could also be due to a positive correlation between first and second clutch size; random treatment assignments, which were made before completion of first clutches, made it more likely that females laying smaller first clutches reared enlarged first broods. Reduced second clutch size did not lead to a difference in second brood fledglings between the two groups.

I could detect no other trade-offs between first brood effort and second brood effort in manipulated or natural broods (Tables 4 and 5). In natural broods, females rearing larger broods or fledging more nestlings, either in absolute terms or relative to clutch size, did not suffer increased interclutch intervals nor did they differ in second brood reproductive success. Similarly, first brood hatching pattern did not affect second brood productivity (Table 4). As in first clutches, second clutch size was significantly influenced by initiation date. Other studies have shown increased interclutch intervals for Great Tits rearing enlarged broods (Smith et al. 1987, Tinbergen 1987, Lindén 1988) and decreased interclutch intervals for House Wrens rearing artificially reduced broods (Finke et al. 1987). For starlings in this study, it appears that the breeding season is only long enough for two broods for those females that are able to start first clutches early and initiate second clutches within about 10 days of first

TABLE 6.   Regression results of late brood clutch size or number of fledglings on date of late brood initiation. Also given is the Pearson correlation coefficient for clutch size and number of fledglings. Only broods initiated after 24 May are included. Sample sizes for 'All broods' are smaller than for analysis of clutch size because females used for other experiments are excluded. Significance levels are indicated as in Table 5.

| Year | n | Clutch size | All broods | | | Failures excluded | | |
| | | | n | Number of fledglings | Correlation | n | Number of fledglings | Correlation |
|---|---|---|---|---|---|---|---|---|
| 1984 | 27 | −0.013 | 23 | −0.122 | 0.102 | 10 | −0.116 | 0.149 |
| 1985 | 37 | −0.039 | 30 | −0.022 | 0.429* | 14 | −0.031 | 0.705** |
| 1986 | 12 | −0.005 | 8 | 0.076 | 0.010 | 4 | −0.372 | 0.010 |
| 1987 | 41 | −0.084*** | 30 | −0.043 | 0.161 | 24 | −0.024 | 0.312 |
| 1988 | 59 | −0.080** | 40 | 0.007 | −0.114 | 21 | −0.014 | −0.033 |
| Combined | 176 | −0.065*** | 131 | −0.026 | 0.095 | 73 | −0.035 | 0.254* |

brood fledging. Increased interclutch interval, like late first clutch initiation, may quickly push females beyond the time when second clutches can be laid. Factors limiting the breeding season remain to be quantified.

THE PARENTAL EFFICIENCY HYPOTHESIS

The results of this study provide no support for the parental efficiency hypothesis. Neither synchronizing hatching nor increasing brood size affected subsequent reproductive success. The parental efficiency hypothesis may find support in species in which a stable dominance hierarchy among siblings, such as produced by asynchronous hatching, prevents energy waste as a result of fighting among siblings (e.g., Hahn 1981, Mock and Ploger 1987). However, under such circumstances it remains to be shown that future reproductive success of parents is affected. It may be that the advantage of asynchronous hatching in the present effort (by improving nestling numbers or condition) is far greater than subtle effects on future success of parents, making a more contrived adaptive scenario relatively unimportant (*sensu* Williams 1966a).

Since a hypothetical female that hatched her first clutch asynchronously would begin her second brood a day earlier than would a female hatching her eggs synchronously (assuming the post-fledgling care of surviving late-hatched nestlings to terminate at the same time as care of their older siblings), any advantage to early second brood initiation would be a potential benefit to asynchronous hatching in a first brood. Clutch size declined with date of second brood initiation, so this one day difference would mean a clutch size difference of 0.065 eggs (based on data from 1984–1988 combined; Table 6). How-

ever, the number of fledglings from second broods did not decline with date of initiation, nor did it correlate strongly with clutch size (Table 6). Thus second brood reproductive success appears unlikely as a selective force on asynchronous hatching in first broods, either due to seasonal effects on second brood productivity or as implied by the parental efficiency hypothesis.

WHY SO FEW SECOND BROODS?

These results show no measurable intraseasonal trade-offs in reproductive effort. If intraseasonal costs were negligible, it is curious that only 44% of females had second broods, even though they initiated first broods very early. Although second brood productivity was unpredictable in time, correlated poorly with clutch size, and had high variance due to failure of many broods (Table 6), some broods produced fledglings. Females without second broods did not lose their nest boxes to other females; in most cases the boxes remained unoccupied. Other studies of starlings in North America report more frequent second broods (Kessel 1953, Collins and deVos 1966, Royall 1966), although all reports show reduced productivity in second broods in comparison to first broods (see also Feare 1984:164, Lack 1948).

There are several possibilities why more starlings do not have second broods. First, post-fledging mortality may increase seasonally, as has been found in Great Tits (Perrins 1965, Kluyver et al. 1977), reducing the relative fitness contributions of second brood fledglings. Feare (1984: 170) reported no recruitment of second brood starling fledglings into the breeding population, although so few first brood fledglings returned that the difference was insignificant. But, if second brood costs are negligible to parents (as first

brood costs appear to be, at least as reflected by subsequent second brood success in this study), there would be no selective pressure not to have second broods even if the benefit is very small. This hypothesis is most consistent with the highly variable productivity of second broods in starlings, and possibly with Great Tits (see discussion in Smith et al. 1989), but needs to be tested with interseasonal return data.

Second, the cost to parents, in the form of reduced interseasonal survival, may be higher relative to the gain in second broods. This seems unlikely for starlings, since the effort I measured in first broods did not affect second broods, although the combined expense of first and second broods may reduce survival. Clobert et al. (1987), in a study of unmanipulated starling broods, found that females that had reared the largest broods had lower winter survival after an especially severe winter than did females that had reared smaller broods, although they make no mention of second broods. Bryant (1979) reported reduced interseasonal survival in House Martins (*Delichon urbica*) rearing two broods. In such cases rearing a second brood may reduce the time available for maintenance activity such as molting or fat deposition.

Third, initiating a second brood may require reduced post-fledging investment in first brood fledglings. Since starlings receive little post-fledging parental care (Feare 1984:168) and nestlings from the same brood separate and disperse from their nest area soon after fledging (Caccamise and Morrison pers. comm.) this factor is probably unimportant, although it may contribute to the paucity of second broods in species with more protracted parental care (e.g., House Wrens, Finke et al. 1987, Wrentits, *Chamaea fasciata*, Geupel and DeSante 1990).

Finally, ectoparasite infestation (primarily by northern fowl mites, *Ornithonysus sylviarum*), which increases seasonally (Clark and Mason 1988), may reduce survival of parents or nestlings or may make some nest boxes unusable. Starlings select nesting material that reduces mite infestation (Clark and Mason 1985, 1988), and mites do not affect survival or growth of nestlings (Clark and Mason 1988). However, mite parasitism lowers hemoglobin levels of nestlings, possibly reducing their post-fledging survival (Clark and Mason 1988). The effect of ectoparasites on parents has not been investigated.

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