FEATHER REGROWTH IN FEMALE EUROPEAN STARLINGS REARING BROODS OF DIFFERENT SIZES

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ABSTRACT.—To assess the idea that daily growth increments of experimentally induced replacement feathers can be used to measure net nutritional status of free-ranging birds (ptilochronology), we compared tail feather regrowth in female European Starlings (*Sturnus vulgaris*) that reared manipulated broods of 2, 4, or 6 nestlings. Broods of 6 nestlings taxed females based on feeding observations, patterns of brood reduction, and fledgling mass. Females that reared broods of 6 had significantly narrower daily growth bars on their replacement rectrices than did females that reared broods of small ($n = 2$ nestlings) or normal ($n = 4$) size. Mass of replacement feathers also decreased as brood size increased. Replacement feather length was an unreliable index of stress because added days of growth tended to compensate for slow daily growth. In females that laid and incubated replacement clutches but did not rear broods, replacement feather growth bars were intermediate in width to those of females that reared normal and enlarged broods. Ptilochronology was corroborated by the relationship between female reproductive effort and growth bars in induced rectrices. Nevertheless, field studies using this technique entail several risks, including low bird recapture rates, absences of and delays in feather regrowth, indistinct feather barring, and unexplained variance in bar width. *Received 3 October 1990, accepted 25 April 1991.*

ORNITHOLOGISTS often wish to make inferences about the comparative nutritional status of birds that differ in dominance rank, breeding commitment, habitat, or any of a variety of other factors. Recently, Grubb (1989) proposed that the study of feather growth rates (termed ptilochronology) would allow experimental tests of differences in the nutritional ecology of birds based on the assumption that individuals under nutritional stress would show diminished feather growth (cf. King and Murphy 1985). Ptilochronology has been used successfully in winter food supplementation experiments on Downy Woodpeckers (*Picoides pubescens*; Grubb 1989) and Gray Jays (*Perisoreus canadensis*; Waite 1990). Two features of feather growth are pivotal to the successful application of Grubb's method: (1) the presence on feathers of transverse bars that delineate daily increments of growth, and (2) the capacity to induce a bird to grow a replacement feather during a desired period by plucking an existing feather. Each growth bar consists of a pair of faint bands, one dark (daytime growth) and one light (nighttime growth). Barring is most prominent in flight feathers of the tail (rectrices) (Wood 1950). To apply ptilochronology to free-ranging birds, each individual must be captured twice, first when the feather is plucked and again sometime after the growth of the induced feather (but before its normal molt), an interval of at least 4 weeks.

To evaluate further the efficacy of the ptilochronology technique, we examined feather regrowth in female European Starlings (*Sturnus vulgaris*) that reared broods of different sizes. We chose this experimental system because brood size is a readily manipulable variable likely to yield a strong treatment effect, and because we could capture large numbers of female starlings at an established trail of nest boxes during both early and late breeding periods.

Reproduction is a major, evolutionarily important period of potential nutritional stress for altricial nestlings. Increased brood size may lead to a reduced share of food, lowered fledgling mass, or death (e.g. Askenmo 1977, Crossner 1977). Thus, for a given parental effort, there should be a particular brood size that yields the most surviving offspring (Lack 1954, 1966). Although less well known, it appears that the energy requirements of the parents are high and increase with brood size (see Skutch 1976), and that parents with large broods may subsequently suffer reduced probability of survival and

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reproductive success (Bryant 1979, Nur 1984). In European Starlings, energy consumption by incubating females increases with clutch size (Biebach 1984), the rates at which parents feed their nestlings increase with brood size (Westerterp et al. 1982), females lose mass during the nestling period (Westerterp et al. 1982, Ricklefs and Hussell 1984, Feare 1984), brood-rearing females have daily metabolic rates 4–4.5 times their basal rates (Ricklefs and Williams 1984), and females that previously raised large broods may be less likely to survive in harsh winters (Clobert et al. 1987). Experimental manipulations of brood size and observations of natural broods at our study site have shown that increasing brood size reduces nestling survival (Stouffer 1989, Stouffer and Power 1990) and growth rates of nestlings that survive (Crossner 1977, Stouffer 1989). Brood size does not affect the proportion of females that attempt second broods (Stouffer 1989), which allowed us to manipulate first broods without making females unavailable for recapture on their second broods.

METHODS

Our study was conducted on the Livingston College campus of Rutgers University, Piscataway, New Jersey, during April–June 1989 using an established trail of 121 nest boxes placed on utility poles. The breeding biology of European Starlings that use these boxes has been studied intensively since 1983 (Power et al. 1989).

Beginning in late April, we inspected nest boxes periodically to determine individual nesting chronologies. Between 3–18 May, we plucked the outer left rectrix from each of 90 females captured on the nest between 0330 and 0520 on brood day 6 (day 1 is the day of hatching). Capture hour was chosen to target night-brooding females (*see* Feare 1984), and capture brood day was chosen to minimize nest abandonment. Minimum age of females was determined from banding records and hackle feathers. Fifty-three of the brooding females had been banded in previous years; 37 unbanded females were banded with a numbered USFWS aluminum band. Hackle feathers were taken to distinguish between first-year and after-hatching-year individuals (Kessel 1951, Davis 1960). We gave each female an orange color band for female identification, weighed the bird to the nearest 0.1 g, and measured the wing chord to the nearest millimeter.

Natural brood size of starlings in the study population varies between 2 and 6, with broods of 3–5 accounting for 86% of all broods (Stouffer 1989). To create small, normal, and large broods within the natural brood size range, we moved nestlings between nests of matched development to produce broods of 2, 4, and 6 nestlings each. In our population, parents appear incapable of increasing their food-delivery rates sufficiently to rear broods of >6 nestlings without a precipitous drop in fledgling mass (Crossner 1977). Nestlings were moved between 1000 and 1300 on the same day (day 6) that their mothers had been caught. In assembling broods, we placed birds of similar mass together to lower the risk of mortality for relatively small nestlings (Stouffer 1989). A total of 40 nests failed within two days after manipulations, apparently because of cold rain storms during the manipulation periods. Thus, our sample sizes for broods of 2, 4, and 6 were reduced to 15, 15, and 18, respectively, and a fourth treatment group of females that renested was created inadvertently. In addition, two broods of three were created; to avoid confusion, these were omitted from all analyses of treatment effects. While females with successful nests reared their experimental broods, females from failed nests laid and incubated replacement clutches. Usually incubation began with the penultimate egg and lasted for 12 days (Stouffer and Power 1990).

To determine the relationship between brood size and the frequency of parental feeding visits, we observed each active nest for one 10-min period between brood day 12 and day 17. Although feeding rates plateau for nestlings after day 7 (Westerterp et al. 1982), we observed nests in an alternating order by brood size to counterbalance any temporal biases. We obtained the total weight for each brood on day 17; at this stage nestlings are near their maximum prefledging mass (Stouffer 1989). We examined each nest between days 20 and 24 to determine fledging success.

After the young fledged, we monitored all nests periodically for replacement or second clutches. Induced (replacement) L6 rectrices were plucked from females recaptured during incubation of their replacement or second-brood clutches. Also at recapture, females were weighed and the orange color bands were removed. The mean between-capture interval for feather regrowth was 36 days (range: 33–48 days) for females with successful first broods and 28 days (range: 18–55 days) for females that renested. During the annual molt that begins after the breeding period, individual primary feathers grow to full length in 20–30 days (Feare 1984).

We examined original and induced tail feathers for overall length, mass, average growth-bar width, and defects including fault bars (Wood 1950, King and Murphy 1984, Grubb 1989). Comparisons of induced and original feathers were based on the 10 growth bars surrounding the "proximal two-thirds" point on each feather according to the technique of Grubb (1989). When only 4 full growth bars were present between the two-thirds point and distal tip on either the original or induced rectrix, we compared sets of only 8 growth bars. Only induced feathers in which vane growth had been completed were used in com-

TABLE 1. Initial characteristics of European Starlings that were subsequently recaptured after rearing broods of different sizes. Values are $\bar{x} \pm$ SD; sample sizes are in parentheses.

Measurement	Treatment brood size 2	4	6	F^a
Minimum age (yr)	3.2 ± 1.3 (11)	2.6 ± 1.0 (10)	3.8 ± 2.0 (12)	1.80
Body mass (g)	80 ± 4 (9)	81 ± 4 (9)	80 ± 3 (11)	0.19
Wing chord (mm)	124 ± 1 (11)	126 ± 3 (10)	126 ± 3 (12)	1.43
First clutch size	4.7 ± 0.5 (11)	4.8 ± 0.4 (10)	5.1 ± 0.3 (12)	2.61
Initial capture date[b]	10 ± 2 (11)	10 ± 3 (10)	11 ± 2 (12)	0.08
Original L6 rectrix				
Length (mm)	70.0 ± 1.7 (11)	70.4 ± 1.3 (10)	69.4 ± 1.5 (12)	1.19
Mass (mg)	26.1 ± 1.6 (11)	26.7 ± 1.3 (10)	26.7 ± 1.4 (12)	0.56
Growth bar width (mm)	3.8 ± 0.2 (11)	3.9 ± 0.2 (10)	3.8 ± 0.2 (12)	0.79

[a] F value for the comparison of means by analysis of variance (all $P > 0.05$).
[b] Day 1 = 1 May.

parisons of bar widths. To test for a temporal trend in daily growth increments, we compared the width of the 4 most distal (early) growth bars to that of the 4 distal bars plus the 4 most proximal (late) bars. A percentage of early growth of <50% would suggest that a female's nutritional status improved during the regrowth period. Percentages were used to emphasize within-feather trends in growth rates by controlling for differences in absolute growth bar width.

To examine whether characteristics of replacement feathers were related to brood size, we used analysis of covariance (ANCOVA) with the length, mass, and growth bar width of the induced feathers as dependent variables and the corresponding values for these traits in original feathers as covariates. This approach controls statistically for any intrinsic individual differences in feather growth patterns.

RESULTS

Independence of treatment groups.—We recaptured 63 of 90 (70%) females overall, and 33 of 50 (66%) females that reared treatment broods of 2, 4, or 6. Recaptures occurred independently of brood size ($G = 0.22$, $P > 0.75$); thus, the recaptured sample was unlikely to have been biased by intrinsic differences in female nutritional status. Among recaptured females that had reared broods, no significant differences existed among brood sizes in female age, body mass, wing chord, first clutch size, initial capture date, or the length, mass, or growth bar width of the original rectrix (Table 1). Overall, clutch size for first broods (including eggs of any conspecific parasites) was 2-6 eggs; 65 of 90 (72%) nests had 5-egg clutches.

Size of the original rectrix (likely grown the previous summer) often correlated with measures of female size and productivity (Table 2). Because experienced birds might be expected to be best able to meet the nutritional demands of molting, we examined the relationship between the size of original rectrices and female age. Of the 90 females captured, 11 were first-year adults, 45 had a minimum age of 2 yr, and 34 had minimum ages of 3-6 yr. Contrary to expectations, no reliable differences existed among these three age classes in rectrix length, mass, or growth bar width or in wing chord or bird mass (ANOVA, all $Ps > 0.05$).

Breeding effort and brood size.—Starling feeding rates and success in rearing nestlings were influenced strongly by brood size. The frequency of feeding visits to 12-17-day-old nestlings increased significantly with brood size, although not proportionally to the number of nestlings (Table 3). This pattern has been reported by

TABLE 2. Correlations of dimensions of the original L6 rectrix with female size and number of eggs in the first clutch of European Starlings. Values are Pearson correlation coefficients; sample sizes are in parentheses; NS = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.005$; *** = $P < 0.001$.

Rectrix dimension	Wing chord	Body mass	Clutch size
Length	0.327** (90)	0.076NS (83)	0.129NS (90)
Mass	0.366*** (82)	0.248* (82)	0.309** (89)
Growth bar width	0.099NS (90)	0.235* (83)	0.149NS (90)

TABLE 3. Breeding effort in European Starlings that reared broods of different sizes. Values are $\bar{x}$ ± SD; sample sizes are in parentheses.

Measurement	Treatment brood size			Test statistic[a]
	2	4	6	
Female mass (% init.)[b]	104 ± 4 (9)	105 ± 4 (8)	106 ± 4 (10)	0.97NS
Feeding visits (visits/h)	15 ± 8 (14)	23 ± 10 (12)	28 ± 18 (17)	3.33*
Nests with reduced broods	0 (14)	1 (14)	5 (18)	[7.15]*
Fledgling mass (g)	77 ± 5 (14)	74 ± 11 (14)	69 ± 8 (18)	3.61*
Females recaptured	11 (14)	10 (15)	12 (18)	[0.69]NS
Eggs in second clutch	3.5 ± 0.8 (11)	4.1 ± 1.4 (10)	4.2 ± 0.9 (12)	1.16NS

[a] Test statistic from an F-test or, in brackets, a G-test (NS = $P > 0.05$; * = $P < 0.05$).

[b] Percentage of mass at recapture versus that at initial capture.

Westerterp et al. (1982), who also found that the quantity of food delivered per visit increased with brood size. On average in our study, females made 62% of feeding visits, irrespective of brood size (proportion of feeding by the female was subjected to angular transformation before ANOVA; $F_{2, 38} = 1.33$, $P > 0.25$). Thus, costs of rearing a brood for females were not obscured by changes in relative male effort. Also the incidence of brood reduction (the death of one or more nestlings) increased with brood size, and the mean mass of individual fledglings declined (Table 3).

Three additional indices of breeding effort failed to show a brood size effect (Table 3). First, percentage change in female mass between initial capture (brooding 6-day-old nestlings of the first brood) and recapture (incubating eggs of the second clutch) did not vary among treatments. That females showed a slight gain in mass (an average of 5%) between captures is not surprising because females are known to lose mass when feeding nestlings (Ricklefs and Hussell 1984). Second, females were equally likely to produce second clutches regardless of the size of their first brood; overall, 70% of females that reared treatment broods were recaptured while incubating a second clutch. Third, the number of eggs in the second clutch did not differ significantly with first-brood size.

Feather regrowth.—Ptilochronology measures differed among the treatment groups. Induced (replacement) tail feathers from females that reared broods of six had narrower growth bars than rectrices from females that reared broods of small to average size (2–4 nestlings; Table 4). Mass of induced rectrices also declined significantly with increasing brood size, but no significant difference existed in length of the induced rectrix (Table 4). The daily length increment of replacement feathers in females that reared broods of 6 averaged (±SD) only 69 ± 8% of the daily growth of feathers formed during the annual molt; growth bars on induced feathers from females with broods of 2 and 4 averaged 78 ± 6% and 77 ± 6% of the width of bars on original feathers, respectively.

Treatment differences in feather length may have been obscured by compensatory growth. Induced feathers commonly had 2–5 more growth bars than original feathers, and the number of additional bars tended to increase with treatment brood size, which suggests that lesser growth rates may be sustained over a

TABLE 4. Characteristics of the induced L6 rectrix in European Starlings that reared broods of different sizes. Values are $\bar{x}$ ± SD; sample sizes are in parentheses.

Measurement	Treatment brood size			Test statistic[a]
	2	4	6	
Length (mm)	66.0 ± 1.7 (10)	64.9 ± 2.2 (8)	63.7 ± 2.5 (6)	1.88NS
Mass (mg)	23.1 ± 2.2 (10)	22.7 ± 1.7 (8)	21.8 ± 1.3 (6)	5.81**
Growth bar width (mm)	3.0 ± 0.3 (10)	3.0 ± 0.3 (8)	2.6 ± 0.4 (6)	3.96*
Number of growth bars (induced-original)	2.7 ± 2.6 (10)	3.5 ± 1.3 (8)	4.5 ± 1.0 (6)	1.61NS
Rectrix incomplete, absent	1 (11)	2 (10)	6 (12)	[5.32]NS

[a] Test statistic from an F-test or, in brackets, a G-test (NS = $P > 0.05$; * = $P < 0.05$; ** = $P < 0.025$). Mean feather length, mass, and growth-bar widths were compared among broods by ANCOVA with values for original feathers used as covariates.

greater number of days (Table 4). Original feathers had 11–16 (mean = 13.2) visible growth bars. In 2 cases, no replacement feather was found at recapture, in 7 other cases feathers had not regrown sufficiently to expose >4 growth bars, and, in an additional case, the induced rectrix of a female that renested was still a pin feather. Incidences of failed or delayed feather regrowth may indicate severely depressed nutritional status (Waite 1990); however, deficiencies in feather regrowth were too rare in our study to establish a statistically significant association with brood size (Table 4). Birds with deficiencies in feather regrowth did not differ significantly from other birds in change in body mass between capture and recapture ($t = 0.45$, df = 25, $P > 0.5$).

We found no relation between the mean width of growth bars on induced feathers and location within the study area or timing of the breeding cycle. Breeding was highly synchronous; 61% of recaptured females were from first nests that had begun hatching on 5–6 May.

Females that laid and incubated replacement clutches following failure of their experimental broods grew replacement rectrices with mean daily growth bars of 2.9 ± 0.3 mm ($n = 26$), a width that averaged 73 ± 9% of that observed for original rectrices. Thus, feather regrowth in females with replacement nests was intermediate between that observed for females that reared 4 and 6 nestlings. The widths of induced growth bars in females that renested could not be distinguished statistically from those for females in any of the groups that reared broods (comparisons by ANCOVA with growth-bar width of original feathers as the covariate; all $P > 0.20$). A remnant of a sheath was present on the proximal portion of the rachis of the induced rectrix of all but 4 females with replacement nests, which indicates that the 28-day average interval between captures fell just short of the period needed to complete rectrix regrowth. Because feather regrowth was incomplete in most females with replacement nests, mass and length of induced rectrices could not be compared with other samples.

No reliable pattern existed among broods of different sizes in the percentage of growth occurring in early vs. early-plus-late growth bars of induced feathers (brood size 2, 47%; 4, 48%; 6, 50%). However, a significantly smaller percentage of growth occurred early in feathers of females with replacement nests (41%; $F = 5.99$, $P < 0.005$). Early bars were narrower (2.3 ± 0.5 mm) and late bars were wider (3.2 ± 0.5 mm) than midfeather bars from females that reared broods (2.6–3.0 mm). We suggest that the nutritional status of female starlings increased in order from renesting and egg laying, to brood rearing, to incubation.

The frequency of rectrices with and without fault bars did not differ among broods of different sizes ($G = 1.17$, $P > 0.5$). We observed an average of 1.3 fault bars per feather (range: 0–5). Fault bars were less common among renesters (1 of 26 birds) than among the more frequently visited brood-rearing females (13 of 28 birds) $G = 14.656$, $P < 0.001$), which supports the idea of King and Murphy (1984) that fault bars result from episodes of shock rather than from dietary stress.

DISCUSSION

Induced feathers grew equally well in female starlings with broods of reduced and normal sizes, but feathers grew significantly more slowly in females with enlarged broods. If feather growth is nutritionally controlled as suggested by Grubb (1989) and Waite (1990), the nutritional status of breeding females declined nonlinearly with increasing brood size. However, we made no independent direct measure of nutritional status, and treatment effects might alternatively have been due to differences in reproductive hormone or receptor levels. In the parasitism insurance hypothesis, Power et al. (1989) held that starlings leave space for conspecific parasitic eggs to prevent parasitism from producing overcrowded clutches. Our results bolster this hypothesis. Broods of 6 are overcrowded not only from the perspective of nestling survival and fledgling mass (Crossner 1977) but also in terms of nutritional stress on the female. Clutches of 6 most commonly resulted in broods of 4 in our population (Power et al. 1989). Thus, elevated stress in brood-rearing females would be likely only when natural clutch size exceeded 6 eggs. Although enlargement of early broods resulted in reduced feather growth and reduced brood stress, this stress did not carry over to late broods. Similarly, Stouffer (1989) found that second-brood reproduction in this population in previous years was more strongly associated with the date of first-brood initiation than with first-brood effort. Based on feather regrowth, laying and incubating a replacement clutch combined high nutritional stress during egg laying with low stress during incubation, which yielded a net cost at least as great as rearing a brood of normal size. Over 3-6 days, females that renested produced egg sets equal in total to about 25-50% of their body mass. In contrast, studies of oxygen consumption by incubating female starlings have indicated that rates of energy use during incubation may be little greater than during a comparable nonbreeding period, especially for moderate clutch sizes and ambient temperatures (Biebach 1984). That growth bar widths on individual feathers reflected a temporal switch from egg laying to incubation provides support for viewing ptilochronology as an index of nutritional stress.

Across all treatments, daily growth of induced tail feathers was only about 74% of that during postreproductive molt the previous year. Because reproduction is keyed to a period of high growth potential for nestlings, it is unlikely that reduced feather growth in breeders was due to a deficiency in a specific nutrient, short day length, or low effective temperature (see Grubb 1989). Instead, sharply limited feather growth during the nesting cycle suggests (1) that females experience greater nutritional demands during reproduction than during their normal molting period, or (2) that hormonal relationships during the breeding period are unfavorable for feather regrowth.

That broods with two nestlings appeared no less stressful to females than broods of four may reflect a balance between thermal advantages and nestling costs. Because small broods lose heat rapidly, they may require longer brooding (Dunn 1976), which leaves less time for feeding. Also, heat loss from a small brood reduces nestling growth efficiency, which counterbalances a potentially low food demand (Westerterp et al. 1982).

Ptilochronology pitfalls.—Although treatment effects have been demonstrated using ptilochronology in starlings and in previous studies on Downy Woodpeckers (Grubb 1989) and Gray Jays (Waite 1990), designers of ptilochronology field experiments face at least three risks. First, replacement feathers may fail to grow or may be delayed in their growth relative to feathers of simultaneously treated birds. Induced feathers were absent or incomplete in 10 of 63 starlings. It may be that some species of birds simply do not reliably regrow plucked feathers. However, even if faltering regeneration actually represents an especially low nutritional status (Waite 1990), such qualitative data cannot be combined with quantitative measures of growth. Furthermore, where treatment effects are of short duration, lags in the initiation of feather regrowth could lead to temporal mismatches between nutritional status during the presumed regrowth period and growth bars that could go unrecognized if induced feathers were collected after a long interval. Second, capturing individuals twice with an approximately 1-month interlude is a challenging protocol that may not be feasible for migratory, nomadic, or single-brooded species. We recaptured only 70% of starlings. The potential for treatment biases in recaptures should grow as recapture rates drop. And third, growth bars may be indistinct or concealed by pigmentation (Wood 1950, Grubb pers. comm.). In starlings, bars on induced rectrices were somewhat bolder than those on original feathers. Feather mass and length may be examined in place of growth-bar width if feathers are all fully grown. Any compensatory growth, as seen for feather length in starlings, will tend to obscure treatment differences.

Given the extent of variance in growth-bar width, it may prove impractical to use ptilochronology to test for small treatment effects in systems where recapture and regrowth success are poor, where growth bars are indistinct, or where nutrient status changes rapidly. Finally, further experiments are needed to calibrate feather regrowth deficiencies to direct measures of nutritional status.

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