

# Individual quality and age affect responses to an energetic constraint in a cavity-nesting bird

Daniel R. Ardia<sup>a</sup> and Ethan D. Clotfelter<sup>b</sup>

<sup>a</sup>Program in Organismic and Evolutionary Biology, University of Massachusetts, Amherst, MA 01003, USA and <sup>b</sup>Department of Biology, Amherst College, Amherst, MA 01002, USA

Individual variation in life-history trade-offs can be caused by differences in quality and age. We tested for individual variation in parental investment in incubating tree swallows (*Tachycineta bicolor*) subjected to a feather-clipping manipulation. Individual quality influenced how females were affected by feather clipping; lower quality clipped females showed a greater reduction in incubation and a greater loss of body condition than higher quality clipped females compared with controls. Most importantly, responses during incubation influenced nestling traits; lower quality clipped females, particularly those losing the most body mass, raised nestlings in the poorest condition. There was no difference in incubation patterns of control females, but older clipped females suffered self-maintenance costs and raised offspring in better condition. In contrast, younger clipped females passed costs on to offspring through lower egg temperatures and reduced nestling condition while maintaining their own condition. Overall, we found a strong individual quality effect: at the population level, there was a trade-off between investing in incubation and maintaining parental condition, but among individuals, there was a positive correlation between change in parental condition and offspring quality. Individual differences in parental strategy can be important causes of life-history variation, especially through subtle, but important, aspects of reproduction such as maintaining egg temperature during incubation. *Key words*: age differences, energetic constraint, incubation, individual quality, life-history trade-offs, tree swallow. [*Behav Ecol* 18:259–266 (2007)]

That individuals differ in their ability to survive and reproduce is a central tenet of natural selection theory (Darwin 1859; Williams 1966). Individual-level differences can lead to variation in life histories as individuals optimize their investment in the face of variation in costs and benefits (Pettifor et al. 1988; Risch et al. 1995; Both et al. 1998). Divergence in parental investment can arise due to differences in condition and ability or due to differences in overall strategy, such as may occur among age classes (Pugesek 1981; Pugesek and Diem 1983; Clutton-Brock 1984). We investigated individual variation in parental investment as a function of individual quality and age. We chose avian incubation as a study system as the direct transfer of metabolic heat to eggs has important implications for both embryonic development and parental investment (Webb 1987; Conway and Martin 2000; Ilmonen et al. 2002; Reid, Monaghan et al. 2002), and experimental studies have found that incubation is costly (Williams 1996; Turner 1997; Thomson et al. 1998; Reid et al. 2000; Tinbergen and Williams 2002; Cresswell et al. 2003). Previous work has demonstrated individual differences in incubation behavior (Gorman and Nager 2003; Hanssen et al. 2003). Consequently, we sought to explicitly examine factors that cause individual variation in incubation constancy, a measure of parental investment in the tree swallow (*Tachycineta bicolor*), a cavity-nesting bird with female-only incubation.

To disentangle the positive correlations among traits that arise from linkages with individual quality (Partridge and Harvey 1988; Winkler and Wilkinson 1988), we experimentally modified flight efficiency during incubation via wing feather clipping to introduce a physiological cost, which affects body

condition and reproduction in tree swallows (Winkler and Allen 1995; Nooker et al. 2005; Whittingham et al. 2005). We examined whether individuals varied along a gradient of quality, as well as among age groups, in order to determine whether different patterns of parental investment reflected individual optimization (Pettifor et al. 1988) or simply variation in condition (Moran 1992; Roff 1996). Clutch initiation date is a measure of individual quality, as it is the best predictor of annual reproductive success in tree swallows (Stutchbury and Robertson 1988; Winkler and Allen 1996). Individuals arrive at breeding sites at similar times (Stutchbury and Robertson 1987) but differ in their timing of breeding based in large part on their ability to gather resources necessary for breeding (Winkler and Allen 1995; Winkler and Allen 1996; Nooker et al. 2005).

Another important cause of variation in reproductive success in iteroparous species is age, where optimal levels of investment vary based in part on future reproductive value in a variety of taxa (Cam et al. 2002; Broussard et al. 2003; Richard et al. 2005). Generally, younger females invest less than older females (Reid 1988; Cam and Monnat 2000; Reid et al. 2003; Mauck et al. 2004); these differences may reflect different resource-gathering ability or differences in parental investment among age groups. Female tree swallows can be reliably placed into one of 2 age categories on the basis of plumage: birds in their second year (SY) and those after their second year of age (ASY) (Robertson et al. 1992). Younger (SY) female tree swallows tend to have lower reproductive success (Stutchbury and Robertson 1988; Winkler and Allen 1996; Robertson and Rendell 2001). Thus, we sought to evaluate whether younger females differed in investment in incubation due to energetic constraints or because their higher future reproductive potential makes them less willing to do so.

We first tested whether females with clipped feathers would reduce investment by allocating resources away from incubation by measuring 1) incubation constancy (total time spent incubating) and 2) egg temperature during incubation. Our

Address correspondence to D. Ardia, who is now at Department of Biology, Franklin and Marshall College, PO Box 3003, Lancaster, PA 17604-3003. E-mail: daniel.ardia@fandm.edu.

Received 31 August 2006; revised 12 October 2006; accepted 18 October 2006.

hypothesis was that individual quality, assessed via clutch initiation date, would affect responses to our manipulation. Specifically, we predicted that later laying, lower quality, females would pay a greater cost following feather clipping and would show a more extensive reduction in incubation investment than would earlier laying clipped females. We also predicted that younger females (SY) would be affected more strongly by feather clipping than older females (ASY). We also compared the effect of clipping and incubation behavior on incubation period and hatching asynchrony, 2 factors that affect offspring quality (Thomson et al. 1998; Wiebe and Martin 2000; Nilsson and Persson 2004).

Because incubation behavior has delayed effects during the nestling stage and thus influences nestling quality (Engstrand and Bryant 2002; Ilmonen et al. 2002; Eikenaar et al. 2003), we also examined the correlates of female incubation strategies on offspring. We used nestling body condition, an indicator of resource stores (Ardia 2005b) and offspring return rates (Hochachka and Smith 1991; Lindén et al. 1992; Hórák et al. 1999), as our measure of offspring quality. We predicted that females that reduced incubation investment would produce nestlings in lower condition. Second, we tested whether younger clipped females, because of their higher residual reproductive value, would be less likely to bear greater incubation costs and more likely to pass costs along to offspring than clipped older females, consistent with life-history theory.

## METHODS

### General field methods and feather-clipping experiment

We conducted our experiment from May to July 2005 in a series of open fields (81 ha) in Amherst, MA (42°22'N, 72°31'W), on which we placed 153 nest-boxes in April 2004. We checked nests daily during egg laying to determine date of clutch initiation and clutch size. We visited nests daily, beginning 3 days prior to the estimated hatching date, to determine actual hatching dates, hatching success, and the number of eggs that hatched on each day. After all eggs had hatched, we measured the body mass (to the nearest 0.1 g) of each nestling using a digital scale. We returned to nests on day 13 to measure nestling body mass and head-bill length (to the nearest 0.1 mm with digital calipers).

Four to five days after clutch completion, we captured, weighed, measured, and aged by plumage (SY vs. ASY) each breeding female. We measured body mass with a digital scale to the nearest 0.1 g, head-bill length with digital calipers to the nearest 0.1 mm, and straightened flattened ninth primary wing feather length to the nearest 0.5 mm with a wing rule. We allocated females to 2 treatment groups, balanced for timing of breeding and clutch size: 1) control and 2) feather clipped; balance between treatments was maintained during the nestling period. For females assigned to the feather-clipped treatment, we then removed 4 of 9 primary wing feathers (primaries 2, 4, 6, and 8) on both wings by clipping them at the base with scissors. We recaptured all females 11–12 days after clutch completion to measure change in body mass.

Insect availability was recorded using a 2-m aerial insect sampler powered by a Robbins and Myers 1650 rpm ( $12.95 \text{ ms}^{-2}$ ) 1/12 HP motor (Dayton, OH) (McCarty and Winkler 1999) to collect daily samples of aerial insect abundance during the breeding season; sampling began prior to egg laying and continued until the end of the nestling period. The sampler was located in the same open field in which nests were located; habitat was homogenous throughout, and females were observed traveling across the entire study area to forage. After removing seeds and other debris, we dried insect samples in a drying oven for 24 h and weighed the resulting samples to

the nearest 0.0001 g on an analytical balance. For each female, insect availability and average temperature were averaged over the length of the incubation period and the first 13 days of the nestling period (coinciding with our measurements of nestlings up to day 13). Insect biomass showed no trend over the breeding season ( $P = 0.4$ ,  $R^2 = 0.02$ ) due to a 3-day cold spell in the middle of the breeding season. When those days are removed, insect availability shows a linear increase over the breeding season ( $P = 0.03$ ,  $R^2 = 0.18$ ,  $y = 0.004x + 0.05$ ).

### Incubation behavior and egg temperature

Once a breeding attempt was discovered, we placed a data logger (Thermocron iButton, Dallas Semiconductor, Dallas, TX; accuracy  $\pm 0.5^\circ\text{C}$ ) in each nest cup adjacent to the eggs, so as to not interfere with heat transfer among eggs. This data logger was set to record temperature at 4-min intervals in order to monitor incubation behavior of females. The data loggers themselves do not affect female behavior as there were no qualitative differences in behavior between control nests with data loggers and without (Ardia DR, Clotfelter ED, unpublished data). We determined onset of incubation from temperature profiles using previously established criteria (Ardia et al. 2006). Prior to placement in the field, we compared each data logger against 2 independent instruments: a HOBO U12 Thermocouple thermometer (Onset Corporation, Bourne, MA) and a Roetemp TM99-A Thermometer (Roetemp, San Diego, CA). Data loggers that did not record temperatures within  $0.5^\circ\text{C}$  of both additional thermometers were not used in the study. To record ambient temperature, we placed a single data logger in the shade under a centrally located nest-box.

We characterized incubation behavior as incubation constancy (percent time spent incubating eggs). We analyzed incubation rhythms of females for a 48-h period on incubation days 2–4, prior to allocating them to feather-clipping treatment, and for a 48-h period on incubation days 9–11, post-feather clipping. We used the program Rhythm (1.0) to determine offbouts after a visual rechecking of the output, with a minimum off-bout duration of 5 min and a minimum off-bout change in temperature of  $4^\circ\text{C}$  (Cooper and Mills 2005). Incubation constancy was calculated by subtracting the time consumed by offbouts from the total period under observation.

We measured egg temperature by placing an artificial egg in nests for a 24-h period between incubation days 7 and 8. We filled a 13-mm-long plastic egg (Berenice's Crafts, <http://www.berenicecrafts.com>) with wire-pulling lubricant (Clear-Glide, Ideal Industries, Sycamore, IL). This fluid closely mimics the thermal properties of an egg (Voss MA, personal communication). In the center of each plastic egg, we placed the probe of a HOBO U12 type-T thermocouple thermometer (Onset Corporation). We calculated 2 measures of incubation egg temperature: 1) average maximum temperature during onbouts and 2) average minimum temperature during on-bouts.

### Statistics

Before beginning analyses, we tested our variables for assumptions of normality using Shapiro-Wilk's  $W$  (all variables  $W \geq 0.97$ ,  $P \geq 0.20$ ). We estimated female body condition and nestling body condition as the residual body mass from a regression of body mass versus head-bill length (Ardia 2005b). For each nest, we averaged the residual body mass for the entire brood on day 13. We calculated hatching asynchrony as the ratio of the largest nestling body mass to the smallest nestling body mass on nestling day 1.

Table 1

General linear model analysis of factors predicting incubation constancy, change in body condition, egg temperature during incubation, incubation period, and hatching asynchrony in tree swallows subjected to a feather-clipping experiment during incubation

Predictors	Dependent variable in model				
	Incubation constancy	Change in residual body mass	Egg temperature	Incubation period	Hatching asynchrony
Feather-clipping treatment	-5.2; $P < 0.001$	1.33; $P < 0.001$	-4.31; $P = 0.02$	0.94; $P = 0.20$	-0.29; $P = 0.46$
Clutch initiation date	-0.64; $P = 0.08$	-0.14; $P = 0.37$	0.24; $P = 0.75$	-0.34; $P = 0.31$	0.04; $P = 0.33$
Age	-0.36; $P = 0.83$	0.41; $P = 0.03$	5.73; $P = 0.22$	-1.45; $P = 0.04$	2.93; $P = 0.002$
Clutch size	0.11; $P = 0.18$	-0.38; $P = 0.6$	-0.02; $P = 0.99$	-0.67; $P = 0.17$	0.43; $P = 0.41$
Average ambient temperature during incubation	1.12; $P = 0.15$	-0.45; $P = 0.12$	0.53; $P = 0.70$	0.22; $P = 0.42$	-0.02; $P = 0.83$
Insect availability during incubation	-1.6; $P = 0.16$	4.39; $P < 0.01$	0.33; $P = 0.88$	0.66; $P = 0.78$	0.89; $P = 0.56$
Change in female residual body mass			1.64; $P = 0.23$	-0.22; $P = 0.31$	0.03; $P = 0.70$
Incubation constancy			0.21; $P = 0.56$	-0.8; $P = 0.04$	0.02; $P = 0.33$
Number of nestlings on day 4					0.67; $P < 0.0001$
Significant Interactions					
Clutch initiation date × Clipped treatment	1.82; $P = 0.001$				
Age × feather-clipping treatment		5.77; $P = 0.003$	-4.14; $P = 0.01$	2.03; $P = 0.01$	5.1; $P < 0.001$
Insect availability × feather-clipping treatment		-3.61; $P = 0.002$			
Number of females	48	48	48	37	24

Each dependent variable was analyzed separately and included the covariates listed below. Variables in each model are shown with the standardized parameter estimates and  $P$  values. Average ambient temperature and insect availability are the averages during the incubation period for each individual female. See text for further details.

We tested change in incubation behavior and body mass in 2 ways: 1) change in incubation behavior (or residual body mass) between the early (preclipping) and late (postclipping) incubation period using repeated measures ANOVA (SAS 1988), with time in incubation period (preclipping vs. postclipping) as the repeated measure for each female and 2) percent change in incubation behavior (or residual body mass) between early (preclipping) and late (postclipping) incubation period using a general linear model in order to generate parameter estimates (PROC GLM) (SAS 1988). We also used general linear models to examine factors affecting incubation period, egg temperature, change in female residual body mass, and the degree of hatching asynchrony. For model compositions, see Table 1. For all models, we included the following covariates: clutch initiation date, clutch size, average ambient temperature, insect availability during incubation, and female age (SY vs. ASY). All 2-way interaction terms were included initially in each model and then removed sequentially by highest  $P$  value for those interactions with  $P > 0.20$ ; removal of interactions did not change the significance of main effects. When means are reported, they are least square means with standard errors (SE), which are calculated to include the effects of covariates. Differences were considered statistically significant at  $P < 0.05$ .

## RESULTS

### Effect of feather clipping

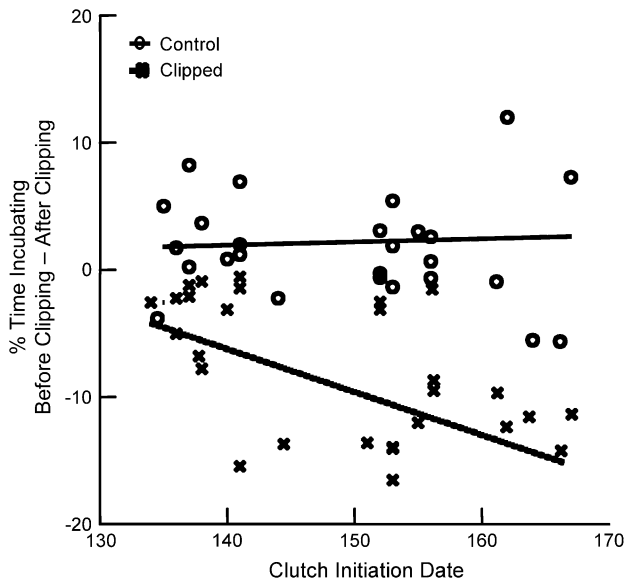
Feather clipped females reduced the amount of time they spent incubating, whereas unclipped control females showed no change in incubation behavior over the same time period (mean incubation constancy (%): unclipped females,  $N = 24$ , preclipping  $71.66 \pm 1.28$ , postclipping  $72.89 \pm 1.29$ ; clipped females,  $N = 24$ , preclipping  $72.75 \pm 1.30$ , postclipping  $66.49 \pm 1.30$ ; repeated measures ANOVA effect of clipping  $F_{1,43} = 28.09$ ,  $P < 0.0001$ ). We found a significant effect of clipping

on time spent incubating (repeated measures effect of time  $F_{1,46} = 5.05$ ,  $P = 0.01$ ; time × clipping interaction  $F_{1,46} = 67.46$ ,  $P < 0.0001$ ).

Feather clipping diminished the body condition of females; in unclipped females, residual body mass increased slightly over the incubation period ( $0.13 \pm 0.41$  to  $0.81 \pm 0.53$ ), whereas clipped females decreased residual body mass over the incubation period ( $0.15 \pm 0.42$  to  $-1.23 \pm 0.56$ ; repeated measures ANOVA: effect of clipping  $F_{1,40} = 4.52$ ,  $P = 0.03$ ; effect of time  $F_{1,40} = 4.05$ ,  $P = 0.04$ ; time × clipping interaction  $F_{1,40} = 14.18$ ,  $P < 0.001$ ).

As predicted, there was an interaction between clipping treatment and clutch initiation date; later laying clipped females showed a greater decrease in time spent incubating behavior than did earlier laying clipped females, whereas control females showed no change in incubation behavior over the same period (Table 1, Figure 1). There was no effect of any other covariate on change in time spent incubating following clipping, including age (Table 1). Our experimental manipulation affected the energy balance of incubating females. In examining changes in residual body mass, we found an interaction between age and clipping; younger clipped females were less likely to lose body mass over the incubation period than were older clipped females (age  $F_{1,40} = 4.42$ ,  $P = 0.04$ , age × clipping interaction  $F_{1,40} = 9.73$ ,  $P = 0.003$ ), whereas control females showed no difference. There was an interaction in the effect of insect availability on changes in residual body mass; increasing insect availability led to a smaller change in residual body mass but only in clipped females (Table 1). There was no statistical effect of other covariates on changes in residual body mass (Table 1).

Neither feather clipping nor age affected maximum average egg temperature (temperature °C ± SE; unclipped  $34.1^\circ \pm 0.64$ , clipped  $34.5^\circ \pm 0.68$ ;  $F_{1,29} = 0.19$ ,  $P = 0.65$ , no effect of other variables  $F_{1,29} \leq 1.61$ ,  $P \geq 0.21$ ). However, younger clipped females maintained eggs at a lower average minimum temperature during incubation bouts than older clipped



**Figure 1**

The interaction between clutch initiation date and feather-clipping status influences percent change in time spent incubating by female tree swallows. Clutch initiation date is listed as day in year from 1 January. Change in time spent incubating calculated by subtracting time spent incubating postclipping from time spent incubating preclipping. Preclipping period was days 2–4 of the incubation period, prior to removing 4 of 9 primary wing feathers; postclipping refers to days 9–11 of the incubation period.

females (ASY clipped females  $30.7^\circ \pm 0.74$ ; SY clipped females  $27.9^\circ \pm 0.70$ ; Table 1).

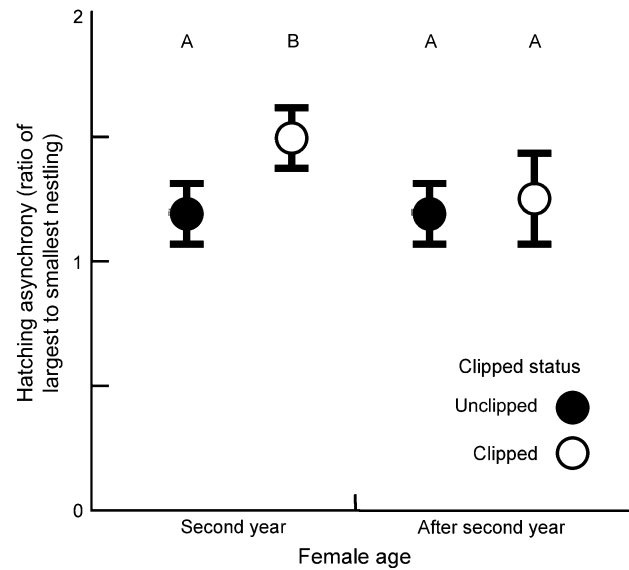
### Incubation period and hatching asynchrony

On average, tree swallows began incubating prior to clutch completion ( $0.53 \pm 0.1$  days prior to clutch completion). The duration of the incubation period was affected by the time females spent incubating. Females that spent more time incubating at the end of the incubation period tended to have shorter incubation periods ( $\beta = 0.01$ ,  $F_{1,23} = 4.66$ ,  $P = 0.04$ ). Younger females responded to feather clipping by extending incubation period (incubation period in days  $\pm$  SE; ASY females: unclipped  $15.8 \pm 0.42$ ,  $n = 13$ , clipped  $15.8 \pm 0.46$ ,  $n = 12$ ; SY females: unclipped  $15.9 \pm 0.50$ ,  $n = 11$ , clipped  $17.3 \pm 0.67$ ,  $n = 10$ ; Table 1). There was no effect of other covariates (Table 1).

Differences in incubation period led to differences in hatching asynchrony. SY females reacted differently to the clipping experiment than did ASY females, with a significant interaction between age and clipping status (Table 1). Younger clipped females were more asynchronous than were older clipped females (Figure 2, Table 1). Females with longer incubation periods had lower levels of hatching asynchrony, as did females with more nestlings on day 4 (Table 1). No other covariates had a significant effect (Table 1).

### Nestling condition

Feather clipping reduced nestling body condition. There was no relationship between time spent incubating and nestling condition in control females ( $F_{1,18} = 0.86$ ,  $P = 0.36$ ); however, among clipped females there was an interaction between clutch initiation date and change in incubation constancy in affecting nestling condition (clutch initiation date  $\times$  change



**Figure 2**

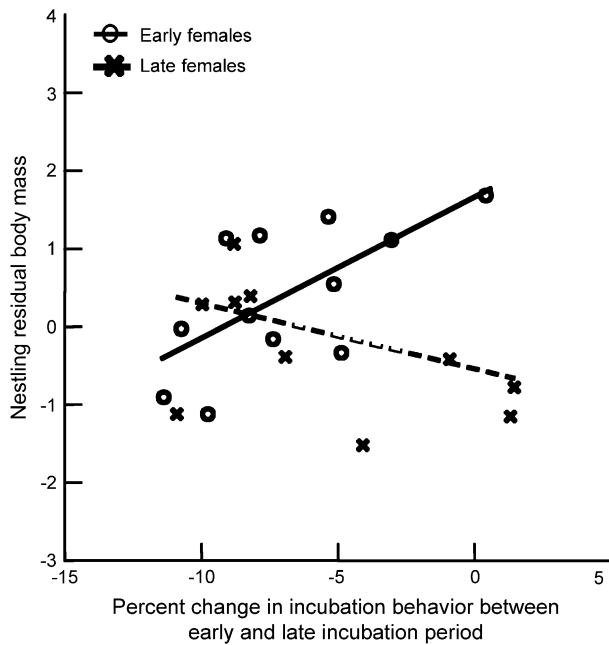
The influence of female age class and feather clipping on degree of hatching asynchrony. Values are least square means  $\pm$  SE, calculated correcting for covariates (see text for more detail); values less than a ratio of 1 are due to least square mean corrections. Letters refer to significant differences among means. ASY females,  $N = 13$ ; SY females  $N = 11$ .

in incubation constancy  $F_{1,18} = 15.1$ ,  $P = 0.001$ ). Among early-breeding clipped females, individuals who reduced incubation behavior the least raised nestlings in highest condition ( $\beta = 0.07$ ,  $F_{1,18} = 8.1$ ,  $P = 0.01$ ; Figure 3). However, among later breeding females, the opposite was true; individuals who reduced incubation behavior the least raised nestlings in the lowest condition ( $\beta = -0.05$ ,  $F_{1,18} = 14.8$ ,  $P = 0.001$ ; Figure 3). Age did not directly affect nestling condition, but rather there was an interaction between female age and feather clipping; SY clipped females raised nestlings in lower condition than did ASY clipped females (Figure 4;  $F_{1,18} = 8.1$ ,  $P = 0.01$ ). Minimum egg temperature during on-bouts was related to nestling condition ( $F_{1,18} = 7.9$ ,  $P = 0.01$ ); lower egg temperatures led to lower nestling condition. Clutch initiation date had no direct effect on nestling condition ( $F_{1,18} = 0.8$ ,  $P = 0.38$ ), but there was an interaction between timing of breeding and female residual body mass change. Among later laying females, those that lost greater residual body mass raised nestlings in lower condition, but those early-laying females who lost less body mass did not (clutch initiation date  $\times$  change in residual body mass  $F_{1,18} = 8.9$ ,  $P = 0.008$ ). Insect availability, incubation behavior, and ambient temperature had no predictive effect of nestling condition ( $F_{1,18} \leq 1.9$ ,  $P \geq 0.18$ ).

## DISCUSSION

### Individual quality

Clipped female tree swallows lost body mass, suggesting that feather clipping reduced foraging efficiency. Our finding that control females gained body mass indicates that tree swallows generally gain body mass over the incubation period, similar to results from other species (Kullberg et al. 2002). Quality of female tree swallows, measured by clutch initiation date, influenced the response of breeding individuals to an experimental manipulation aimed to affect incubation investment. Later laying, lower quality, females were less able to deal with the energetic costs imposed by feather clipping; they showed a greater reduction in time spent incubating following feather

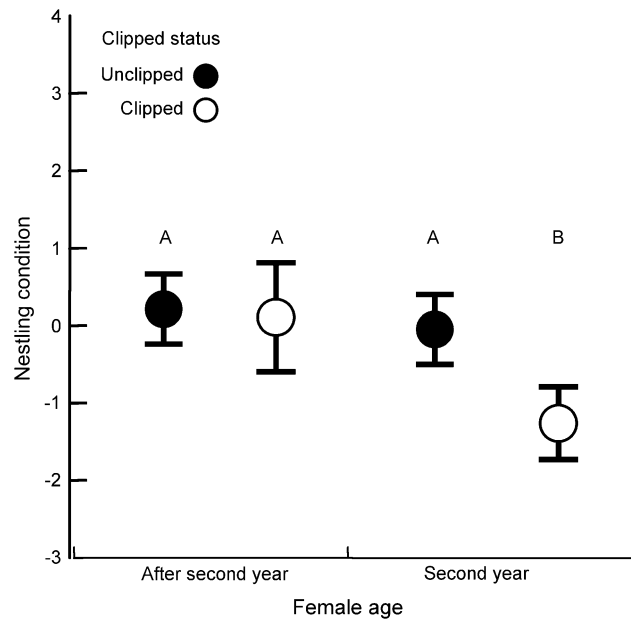


**Figure 3**

The relationship between change in incubation behavior and nestling residual body mass (body condition) as a function of timing of breeding in feather clipped female tree swallows. Change in incubation represents change from days 2–4 of incubation period to days 9–11. Nestling condition is the residual of a regression of head-bill length versus body mass. Early indicates females breeding before median clutch initiation date at site (28 May) and late indicates females breeding after median clutch initiation date.

clipping relative to earlier laying, presumably higher quality, females. Lower responses by later breeding birds were not directly due to food availability; insect abundance did not decline seasonally—it actually increased once statistical outliers were removed—and has been shown to increase seasonally at other sites (Ardia 2005a, 2005c). Earlier breeding females were better able to maintain body mass; individual variation in female quality may be due in large part to differences in foraging efficiency. Early-breeding female tree swallows tend to have higher average flight acceleration speeds (Bowlin and Winkler 2004); differences in foraging performance is apparently the proximate factor that allows some birds to begin breeding early even though most birds arrive at the site at similar times.

Food resources are generally lower for early-breeding tree swallows than for later breeding swallows; however, early-breeding birds are better able to forage and to invest in incubation following our feather manipulation than are later laying birds. Positive correlations among life-history traits indicate that a subset of individuals fare better at the challenges associated with reproduction (Cam et al. 2002). Our result suggests that the positive correlation reported here between 2 life-history stages, timing of breeding and incubation, may arise from a single proximate cause: variation in flight performance. Interestingly, timing of breeding is only marginally heritable in tree swallows (Winkler DW, personal communication), so the factors that drive variation in individual quality in tree swallows likely entail a major component of nonheritable phenotypic variation. This suggests a limited ability of timing of breeding to respond to natural selection and thus explains the considerable variation observed in tree swallow breeding phenology (Winkler and Allen 1996).



**Figure 4**

The influence of age and feather clipping on nestling condition. Nestling condition is the residual of a regression of head-bill length versus body mass. Values are least square means  $\pm$  SE, calculated correcting for covariates (see text for more detail). Letters refer to significant differences among means. ASY females,  $N = 13$ ; SY females,  $N = 11$ .

Parental responses to an experimental manipulation can only be fully evaluated when examining their consequences for offspring must also be examined. In this regard, our study is one of few to report that female incubation investment influences the quality of offspring (Monaghan and Nager 1997; Reid et al. 2000). Our results suggest that trade-offs associated with earlier stages of reproduction in birds can be related to consequences in later stages and these trade-offs differ among individuals. Those feather-clipped, earlier breeding females that incubated more (i.e., showed a lower reduction in time spent incubating) raised offspring with higher body condition. One factor that mediates investment and led to differences among individuals is body condition. Our feather clipping manipulation led to reduced body mass, but individuals differed in a way that reveals the complexity of individual quality. Earlier breeding clipped females were able to raise nestlings in similar condition as control females, but later breeding females, particularly those who lost residual body mass, raised nestlings in lower condition. Both incubation constancy and change in residual body mass predicted nestling quality. On the population level, there was a trade-off between investing in incubation and maintaining residual body mass. However, when patterns are examined on an individual level, there was a positive correlation: some females were better able to deal with the challenges of reproduction, as illustrated by the fact that females who lost less body mass did not incubate less, and raised offspring in better condition.

We cannot determine whether variation in timing of breeding relates to divergent strategies or simply condition-related investment. Early-laying clipped females are able to allocate resources toward both incubation and raising high-quality offspring. Later laying clipped females appear to make a trade-off between incubation behavior and nestling condition. It is not clear whether this represents different optimal strategies. In some species, individuals lay optimal clutch sizes for their quality; deviation from the optimal clutch size leads to lower

recruitment (Pettifor et al. 1988). In tree swallows, there is no indication that low-condition females would behave similarly if their condition was increased. In this study, seasonal changes likely reflect a filtering effect of females coping with low food conditions in the breeding season. The factors, especially flight performance, that cause this pattern to carry over during incubation, leading some females to be better at both foraging and investing in incubation than others. It is important to note that these differences are not due to changes in the behavior of male tree swallows. We found no variation in the number of foraging visits made by males to either clipped or unclipped nests (Ardia DR and Clotfelter ED, unpublished data).

### Age-related variation

We also found support for our prediction that younger females would respond differently to feather clipping. Younger (SY) clipped females showed a similar reduction in incubation behavior relative to older (ASY) clipped females. However, SY clipped females reduced the minimum egg temperature of clutches during incubation bouts, indicating that these females invested less energy during incubation bouts than ASY females. SY females may have similar strategies but a reduced ability to invest in incubation or they may differ in strategy. If clipped females in both age groups had similar strategies but differing abilities to implement the strategy, we would have expected SY females to lose both body mass (as ASY females did) and lower egg temperature, suggesting their inability to maintain optimal investment. However, SY clipped females did not reduce body mass but rather appeared to implement a different strategy of preferentially allocating resources toward retaining body mass at the cost of maintaining egg temperature.

As predicted, the consequences of the contrasting levels of parental investment of younger versus older females are consistent with life-history theory (Wiebe and Martin 2000; Nager et al. 2001; Gorman and Nager 2003). Tree swallows show a standard pattern of senescence with improvement in breeding up to 4 years of age and then a decline, suggesting that older females have lower future reproductive value (Robertson and Rendell 2001). Older females, therefore, would be expected to suffer costs themselves, reflected in lower body mass, while allocating resources toward maintaining offspring quality. In contrast, younger females have higher residual reproductive value due to their higher probability of survival, and thus, they would be less likely to bear significant costs themselves (Stearns 1992). Younger clipped females may allow their offspring to suffer in order to retain their own body condition. The lowered egg temperature in the nests of younger females lead to extended incubation periods, which may increase predation risk (Ghalambor and Martin 2000; Martin et al. 2000; Hepp et al. 2005). In addition, younger clipped females had nestlings with greater hatching asynchrony that can lead to greater sibling competition (Magrath 1989; Stoleson and Beissinger 1997). Most importantly, younger clipped females raised nestlings in lower body condition than older clipped females, which was due in part to the direct role of egg temperature. These differences were not due to age-related difference in incubation behavior in control birds, as our results were similar to results reported in other studies (Wheelwright and Beagley 2005). The differing responses of age groups indicate that younger females pass costs on to offspring rather than bear those costs directly. Although differences between age groups could be due to the inexperience of younger females, our data suggest otherwise. There was no difference in many important variables between control ASY and SY females (e.g., egg temperature, incubation period, and incubation con-

stancy); in addition, SY clipped females increased body mass relative to ASY clipped females, which strongly indicates a change in strategy, not constraint.

### Costs of incubation

Our experimental manipulation of feather clipping clearly affected incubation investment in tree swallows. Clipped birds reduced time spent incubating, whereas control birds showed no change in incubation behavior over the same time period. This result suggests that incubation is costly, as clipped birds allocated time and energy away from incubation toward self-maintenance. In addition, feather clipping caused females to lose body mass in contrast to control females that gained body mass over the same time period. Taken together, this suggests our manipulation was successful at changing the energy balance for incubating tree swallows.

Incubation had previously been viewed as a period of limited energy expenditure relative to other components of avian reproduction (King 1973). However, our results corroborate other recent experimental studies demonstrating the cost of incubation in intermittent incubators (Bryan and Bryant 1999; Reid et al. 2000; Cresswell et al. 2004), as well as constant incubators (Hanssen et al. 2005). We found that when faced with a shift in energy balance, incubating females allocate resources (energy and time) away from incubation. If incubation was not costly, females would forage and incubate normally, thus maintaining both their own and their offspring's body condition, regardless of the feather-clipping manipulation. However, we report 2 patterns that suggest that incubation is indeed costly. First, individuals differed in their incubation investment in predictable ways that reflect either differences in either individual quality or life-history strategies. Second, aspects of individual responses, particularly egg temperature and time spent incubating, influenced offspring quality. As a whole, our results indicate that incubation is an important period of parental investment in birds, especially, in those species that incubate during periods of low temperatures or food availability. However, we found no effect of either clutch size or ambient temperature on the response of birds to our manipulations, contrary to the predictions of other studies (Reid, Ruxton et al. 2002; Hanssen et al. 2003). In contrast to our results, a recent clutch size manipulation experiment in house wrens revealed that females incubating enlarged clutches increased feeding (Dobbs et al. 2006), suggesting that species with similar ecology may vary in response to changes in incubation costs.

We observed 2 different strategies used by female tree swallows in responding to our manipulation: reducing time spent incubating or modifying egg temperature. Reducing time spent incubating minimizes the overall cost of maintaining egg temperature as less total time is spent on eggs; however, the cost of rewarming eggs may increase due to more time off eggs (Biebach 1986; Reid et al. 2000). In contrast, lowering egg temperature may be a strategy to minimize direct energetic costs of incubation without incurring greater rewarming costs, as long as eggs are maintained above a minimum threshold (Webb 1987). However, lower egg temperatures translated into longer incubation periods and lower nestling condition for younger clipped females.

We thank Jessamyn Conell-Price and Jonathan Pérez for valuable field assistance, Elizabeth Rice, Ben Taft, and Natasha Korobov for assistance in erecting nest-boxes, Jim Brassord, Bob Shea, and Ron Hebert for logistical support, and Margaret Voss and David Winkler for help in designing the study. Mark Hauber, Linda Whittingham, Peter Dunn, Becca Safran, Jonathan Pérez, Elise Chad, Elizabeth Kuperberg, and 2 anonymous reviewers provided helpful comments on an earlier

version of the manuscript. Funding for the research was provided by the Organismic and Evolutionary Biology Program at the University of Massachusetts and the Faculty Research Award Program as funded by The H. Axel Schupf '57 Fund for Intellectual Life at Amherst College. Our work was conducted with the approval of the Institutional Animal Care and Use Committees of the University of Massachusetts-Amherst and Amherst College.

## REFERENCES

- Ardia DR. 2005a. Individual quality mediates tradeoffs between reproductive effort and immune function in tree swallows. *J Anim Ecol.* 74:517–524.
- Ardia DR. 2005b. Super size me: an experimental test of factors affecting lipid content and the ability of residual body mass to predict lipid levels in nestling European starlings. *Funct Ecol.* 19:414–420.
- Ardia DR. 2005c. Tree swallows tradeoff immune function and reproductive effort differently across their range. *Ecology.* 86:2040–2046.
- Ardia DR, Cooper CB, Dhondt AA. 2006. Warm temperatures lead to early onset of incubation, shorter incubation periods and greater hatching asynchrony in tree swallows at the extremes of their range. *J Avian Biol.* 37:137–142.
- Biebach H. 1986. Energetics of rewarming a clutch in starlings (*Sturnus vulgaris*). *Physiol Zool.* 59:69–75.
- Both C, Tinbergen JM, van Noordwijk AJ. 1998. Offspring fitness and individual optimization of clutch size. *Proc R Soc Lond B Biol Sci.* 265:2303–2307.
- Bowlin MS, Winkler DW. 2004. Natural variation in flight performance is related to timing of breeding in tree swallows (*Tachycineta bicolor*) in New York. *Auk.* 121:345–353.
- Broussard DR, Risch TS, Dobson FS, Murie JO. 2003. Senescence and age-related reproduction of female Columbian ground squirrels. *J Anim Ecol.* 72:212–219.
- Bryan SM, Bryant DM. 1999. Heating nest-boxes reveals an energetic constraint on incubation behaviour in great tits, *Parus major*. *Proc R Soc Lond B Biol Sci.* 266:157–162.
- Cam E, Link WA, Cooch EG, Monnat JY, Danchin E. 2002. Individual covariation in life-history traits: seeing the trees despite the forest. *Am Nat.* 159:96–105.
- Cam E, Monnat JY. 2000. Apparent inferiority of first-time breeders in the kittiwake: the role of heterogeneity among age classes. *J Anim Ecol.* 69:380–394.
- Clutton-Brock TH. 1984. Reproductive effort and terminal investment in iteroparous animals. *Am Nat.* 123:212–229.
- Conway CJ, Martin TE. 2000. Evolution of passerine incubation behavior: influence of food, temperatures, and nest predation. *Evolution.* 54:670–685.
- Cooper CB, Mills H. 2005. New software for quantifying incubation behavior from time-series recordings. *J Field Ornithol.* 76:352–356.
- Cresswell W, Holt S, Reid JM, Whitfield DP, Mellanby RJ. 2003. Do energetic demands constrain incubation scheduling in a biparental species? *Behav Ecol.* 14:97–102.
- Cresswell W, Holt S, Reid JM, Whitfield DP, Mellanby RJ, Norton D, Waldron S. 2004. The energetic costs of egg heating constrain incubation attendance but do not determine daily energy expenditure in the pectoral sandpiper. *Behav Ecol.* 15:498–507.
- Darwin C. 1859. *The origin of species*. London: John Murray.
- Dobbs RC, Styrsky JD, Thompson CF. 2006. Clutch size and the costs of incubation in the house wren. *Behav Ecol.* 17:849–856.
- Eikenaar C, Berg ML, Komdeur J. 2003. Experimental evidence for the influence of food availability on incubation attendance and hatching asynchrony in the Australian reed warbler *Acrocephalus australis*. *J Avian Biol.* 34:419–427.
- Engstrand SM, Bryant DM. 2002. A trade-off between clutch size and incubation efficiency in the barn swallow *Hirundo rustica*. *Funct Ecol.* 16:782–791.
- Ghalambor CK, Martin TE. 2000. Parental investment strategies in two species of nuthatch vary with stage-specific predation risk and reproductive effort. *Anim Behav.* 60:263–267.
- Gorman HE, Nager RG. 2003. State-dependent incubation behaviour in the zebra finch. *Anim Behav.* 65:745–754.
- Hanssen SA, Erikstad KE, Johnsen V, Bustnes JO. 2003. Differential investment and costs during avian incubation determined by individual quality: an experimental study of the common eider (*Somateria mollissima*). *Proc R Soc Lond B Biol Sci.* 270:531–537.
- Hanssen SA, Hasselquist D, Folstad I, Erikstad KE. 2005. Cost of reproduction in a long-lived bird: incubation effort reduces immune function and future reproduction. *Proc R Soc Lond B Biol Sci.* 272:1039–1046.
- Hepp GR, Folk TH, Manlove CA. 2005. Nest temperature, incubation period, and investment decisions of incubating wood ducks *Aix sponsa*. *J Avian Biol.* 36:523–530.
- Hochachka W, Smith JNM. 1991. Determinants and consequences of nestling condition in song sparrows. *J Anim Ecol.* 60:995–1008.
- Hörak P, Lea T, Ots I, Møller AP. 1999. Immune function and survival of great tit nestlings in relation to growth conditions. *Oecologia.* 121:316–322.
- Ilmonen P, Taarna T, Hasselquist D. 2002. Are incubation costs in female pied flycatchers expressed in humoral immune responsiveness or breeding success? *Oecologia.* 130:199–204.
- King JR. 1973. Energetics of avian reproduction. In: Farner DS, ed. *Breeding biology of birds*. Washington (DC): National Academy of Science.
- Kullberg C, Metcalfe NB, Houston DC. 2002. Impaired flight ability during incubation in the pied flycatcher. *J Avian Biol.* 33:179–183.
- Lindén M, Gustafsson L, Pärt T. 1992. Selection on fledging mass in the collared flycatcher and the great tit. *Ecology.* 73:336–343.
- Magrath RD. 1989. Hatching asynchrony and reproductive success in the blackbird. *Nature.* 339:536–538.
- Martin TE, Scott J, Menge C. 2000. Nest predation increases with parental activity: separating nest site and parental activity effects. *Proc R Soc Lond B Biol Sci.* 267:2287–2293.
- Mauck RA, Huntington CE, Grubb TC. 2004. Age-specific reproductive success: evidence for the selection hypothesis. *Evolution.* 58:880–885.
- McCarty JP, Winkler DW. 1999. Relative importance of environmental variables in determining the growth rates of nestling Tree swallows *Tachycineta bicolor*. *Ibis.* 141:286–296.
- Monaghan P, Nager RG. 1997. Why don't birds lay more eggs? *Trends Ecol Evol.* 12:270–274.
- Moran NA. 1992. The evolutionary maintenance of alternative phenotypes. *Am Nat.* 139:971–989.
- Nager RG, Monaghan P, Houston DC. 2001. The costs of egg production: increased egg production reduces future fitness in gulls. *J Avian Biol.* 32:159–166.
- Nilsson J-A, Persson I. 2004. Postnatal effects of incubation length in mallard and pheasant chicks. *Oikos.* 105:588–594.
- Nooker JK, Dunn PO, Whittingham LA. 2005. Effects of food abundance, weather, and female condition on reproduction in tree swallows (*Tachycineta bicolor*). *Auk.* 122:1225–1238.
- Partridge L, Harvey PH. 1988. The ecological context of life-history evolution. *Science.* 241:1449–1455.
- Pettifor RA, Perrins CM, Mcleery RH. 1988. Individual optimization of clutch size in great tits. *Nature.* 336:160–162.
- Pugesek BH. 1981. Increased reproductive effort with age in the California gull (*Larus californicus*). *Science.* 212:822–823.
- Pugesek BH, Diem KL. 1983. A multivariate study of the relationship of parental age to reproductive success in California gulls. *Ecology.* 64:829–839.
- Reid JM, Bignal EM, Bignal S, McCracken DI, Monaghan P. 2003. Age-specific reproductive performance in red-billed choughs *Pyrrhocorax pyrrhocorax*: patterns and processes in a natural population. *J Anim Ecol.* 72:765–776.
- Reid JM, Monaghan P, Nager RG. 2002. Incubation and the costs of reproduction. In: Deeming DC, ed. *Avian incubation: behaviour, environment and evolution*. Oxford: Oxford University Press.
- Reid JM, Monaghan P, Ruxton GD. 2000. Resource allocation between reproductive phases: the importance of thermal conditions in determining the cost of incubation. *Proc R Soc Lond B Biol Sci.* 267:37–41.
- Reid JM, Ruxton GD, Monaghan P, Hilton GM. 2002. Energetic consequences of clutch temperature and clutch size for a uniparental intermittent incubator: the starling. *Auk.* 119:54–61.
- Reid WV. 1988. Age-specific patterns of reproduction in the glaucous-winged gull—increased effort with age. *Ecology.* 69:1454–1465.
- Richard M, Lecomte J, de Fraipont M, Clobert J. 2005. Age-specific mating strategies and reproductive senescence. *Mol Ecol.* 14:3147–3155.

- Risch TS, Dobson FS, Murie JO. 1995. Is Mean litter size the most productive—a test in columbian ground-squirrels. *Ecology*. 76:1643–1654.
- Robertson RJ, Rendell WB. 2001. A long-term study of reproductive performance in tree swallows: the influence of age and senescence on output. *J Anim Ecol*. 70:1014–1031.
- Robertson RJ, Stutchbury BJ, Cohen RR. 1992. Tree swallow. In: Poole A, Stettenheim P, Gill F, eds. *Birds of North America*. Philadelphia (PA): Academy of Natural Sciences. p. 27.
- Roff DA. 1996. The evolution of threshold traits in animals. *Quart Rev Biol*. 71:3–35.
- SAS. 1988. *SAS/STAT user's guide*. Cary (NC): SAS Institute.
- Stearns SC. 1992. *The evolution of life histories*. Oxford: Oxford University Press.
- Stoleson SH, Beissinger SR. 1997. Hatching asynchrony, brood reduction, and food limitation in a neotropical parrot. *Ecol Monogr*. 67:131–154.
- Stutchbury BJ, Robertson RJ. 1987. Do nest building and 1st egg dates reflect settlement-patterns of females. *Condor*. 89:587–593.
- Stutchbury BJ, Robertson RJ. 1988. Within-season and age-related patterns of reproductive-performance in female tree swallows (*Tachycineta bicolor*). *Can J Zool*. 66:827–834.
- Thomson DL, Monaghan P, Furness RW. 1998. The demands of incubation and avian clutch size. *Biol Rev*. 73:293–304.
- Tinbergen JM, Williams JB. 2002. Energetics of incubation. In: Deeming DC, ed. *Avian incubation: behavior, environment and evolution*. Oxford: Oxford University Press.
- Turner JS. 1997. On the thermal capacity of a bird's egg warmed by a brood patch. *Physiol Zool*. 70:470–480.
- Webb DR. 1987. Thermal tolerance of avian embryos: a review. *Condor*. 89:874–898.
- Wheelwright NT, Beagley JC. 2005. Proficient incubation by inexperienced Savannah Sparrows *Passerculus sandwichensis*. *Ibis*. 147:67–76.
- Whittingham LA, Dunn PO, Nooker JK. 2005. Maternal influences on brood sex ratios: an experimental study in tree swallows. *Proc R Soc Lond B Biol Sci*. 272:1775–1780.
- Wiebe KL, Martin K. 2000. The use of incubation behavior to adjust avian reproductive costs after egg laying. *Behav Ecol Sociobiol*. 48:463–470.
- Williams GC. 1966. *Adaptation and natural selection*. Princeton (NJ): Princeton University Press.
- Williams JB. 1996. Energetics of avian incubation. In: Carey C, ed. *Avian energetics and nutritional ecology*. London: Chapman and Hall.
- Winkler DW, Allen PE. 1995. Effects of handicapping on female condition and reproduction in tree swallows (*Tachycineta bicolor*). *Auk*. 112:737–747.
- Winkler DW, Allen PE. 1996. The seasonal decline in tree swallow clutch size: physiological constraint or strategic adjustment. *Ecology*. 77:922–932.
- Winkler DW, Wilkinson GS. 1988. Parental effort in birds and mammals: theory and measurement. In: Partridge L, Harvey PH, eds. *Oxford surveys in evolutionary biology*. Oxford: Oxford University Press.