

THE SEASONAL DECLINE IN TREE SWALLOW CLUTCH SIZE: PHYSIOLOGICAL CONSTRAINT OR STRATEGIC ADJUSTMENT?¹

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Abstract. The seasonal decline in clutch size has been explained as being due to either: (1) a constraining effect of female condition on both laying date and clutch size; or (2) a seasonal decline in the prospects of chick recruitment, leading to a strategic decrease in clutch size with laying date. In an effort to shed light on this area of disagreement, we analyzed the physiological condition (as measured by body mass, breast muscle thickness, and fat stores) and body size (as measured by wing and head lengths) of 184 female Tree Swallows (*Tachycineta bicolor*) nesting near Ithaca, New York in 1993, 1994, and 1995, and related their condition to their laying date and clutch size. Through multiple regressions, we found that female age and wing length were the only significant predictors of laying date and that female age and laying date were the only significant predictors of clutch size. Thus, when the effects of laying date were held constant, there was no detectable effect of condition on clutch size in this species. This result is inconsistent with the constraining-condition hypothesis, and it suggests that the seasonal decline of clutch size in Tree Swallows is most appropriately seen as a strategic adjustment by the female to varying prospects for her offspring. The lack of evolution in laying date in at least the Tree Swallow remains a paradox.

Key words: age effects; clutch size; directional selection; egg laying; experience effects; laying date; life history; New York; physiological condition; timing of breeding; *Tachycineta bicolor*; Tree Swallow.

INTRODUCTION

One of the most robust generalizations about avian life histories is that there is a negative correlation between clutch size and the timing of breeding within a season. Across the entire spectrum of birds, at least in temperate species (cf. Young 1994), individuals that lay later in the breeding season tend to lay fewer eggs per clutch than those that lay earlier (e.g., Klomp 1970, Winkler and Walters 1983, Murphy 1986, Daan et al. 1988, Stutchbury and Robertson 1988, Perrins and McCleery 1989, Hochachka 1990; for exceptions see Crick et al. 1993). There is considerable disagreement over the causes of this correlation. One hypothesis (Price et al. 1988; Kirkpatrick et al. 1990) assumes that the correlation between timing of breeding and clutch size is the effect of non-heritable variation in parental condition. We call this the "condition hypothesis" and contrast it with what we call the "environment hypothesis" (Perrins 1970, Daan et al. 1988, Young 1994), which assumes that seasonal declines in environmental quality lead to a decline in clutch size, either directly or through seasonal changes in offspring survival prospects.

The condition hypothesis has both theoretical and

empirical support. The theory of Price et al. (1988) was aimed at understanding how the correlation between timing of breeding and fitness could persist without any evidence for evolution of earlier breeding dates, especially in the face of evidence that breeding date has a heritable component (e.g., van Noordwijk et al. 1981, Findlay and Cooke 1982, O'Donald 1983). The only way out of this paradox for Price et al. (1988) was to assume that variation in condition is largely non-heritable and has such a strong effect on both breeding date and clutch size that "females that are in good nutritional condition are constrained to breed earlier than is optimal" (Price et al. 1988:799). These same authors (Kirkpatrick et al. 1990) have extended their analyses to a formalization of the earlier ideas of Darwin (1874:215-218) and Fisher (1958:153-155), whereby the advantage of gaining an earlier, higher fecundity mate can serve as the driving force for sexual selection in purely monogamous birds.

Some of the evidence on physiological condition and reproduction in birds is at least consistent with the condition hypothesis. Both timing of reproduction and clutch size are correlated with condition in waterfowl (Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979, Krapu 1981, Cooke et al. 1984) and gulls (Boersma and Ryder 1983). In passerines, condition sometimes seems to be important to clutch size (Jones and Ward 1976, Fogden and Fogden 1979), but in other studies, egg-laying appears to be based largely on direct

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input from foraging (e.g., Ojanen 1983). As evidence for a link between condition and timing of breeding, Price et al. (1988) cited studies in which food was supplemented in the pre-laying period (see reviews by Daan et al. 1988, Meijer et al. 1990). Of 26 such studies reviewed by Meijer et al. (1990), 15 showed a statistically significant advance in laying date when food was supplemented. Although many of these studies also document suggestive increases in clutch size, only two of these studies revealed a significant increase in clutch size. Paradoxically, neither of the significant clutch size increases was associated with an advance in breeding date. In short, the food supplementation experiments provide weak evidence, at best, of a causal link among condition, laying date, and clutch size.

Under the environment hypothesis, two types of environmental effects on clutch size and timing of breeding are possible. If the available food supply during or prior to laying deteriorates as the season goes on, this seasonal decline in the environment could directly affect the number and timing of eggs laid by limiting resources for laying females. The environment could also indirectly affect clutch size and timing of breeding through the evolution of a seasonal decline in clutch size in response to a cost of egg-laying (in terms of female survival) coupled with seasonally declining nestling food supplies or declining survival prospects of offspring fledged later in the season (e.g., Tinbergen and Daan 1990, Nilsson 1991, Young 1994). The environment hypothesis does not necessarily preclude a proximate role for female condition in affecting the timing and size of clutches. But regardless of any intermediary role played by female condition differences, the smaller clutch sizes of later laying birds are seen under the environment hypothesis as being an adaptive response to laying date, not the outcome of some joint physiological constraint on both laying date and clutch size (Daan et al. 1988:398). An early graphical model (Daan et al. 1988) predicted optimal clutch size by assuming that fledging and/or post-fledging success of offspring decline seasonally, an assumption for which there is reasonable empirical support (Daan et al. 1988: Fig. 5).

The recent paper by Rowe et al. (1994) incorporates parts of both the condition and environment hypotheses. Rowe et al. assume, as in the environment hypothesis, that there is a selective benefit to fledging young earlier in the season, and, as in the condition hypothesis, they assume that condition dictates the association between clutch size and timing. However, they model the seasonal decline in clutch size as a strategic response to environmental and physiological selective factors, rather than the result of a physiological constraint. Rowe et al.'s model notwithstanding, the simple contrast between the environment and condition hypotheses served as the rationale for the collection of the data presented here.

In sum, the condition hypothesis considers the link

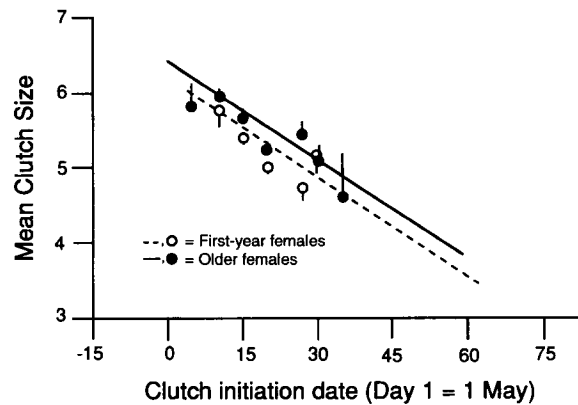


FIG. 1. The seasonal decline in mean clutch size in Tree Swallows at Ithaca, New York. Females in their first breeding season (○) are plotted separately from older females (●). The corresponding standard errors of the means are indicated by vertical lines extending below (1st-yr females) or above (older females) the plotting symbol. Only 5-d periods in which at least five clutches were recorded are plotted, but the least-squares regression lines superimposed over the points extend over the entire range of clutch initiation dates for first-year females (---) and older females (—). The equation for the regression line for 1st-yr females is clutch size = $6.170 - 0.046 \cdot \text{Date}$ ($P < 0.001$). For older females it is clutch size $6.354 - 0.042 \cdot \text{Date}$ ($P < 0.001$). Data plotted are from the years 1987–1991 at Ithaca.

between laying date and clutch size as a non-adaptive epiphenomenon of a physiological effect of condition on both. By contrast, the environment hypothesis considers the link between clutch size and laying date as a result of an adaptive response to a seasonally declining food supply for the laying female or to deteriorating prospects for the offspring. In this scenario, condition could play an important intermediary role, but the seasonal decline in clutch size is seen ultimately as an adaptive response to seasonal changes in the environment.

The two competing explanations for the seasonal decline in clutch size predict different results from statistical analyses of data from laying birds. If condition is the principal determinant of timing of breeding and clutch size, one would expect to see no effect of timing of breeding on clutch size once the effect of condition is factored out statistically. By contrast, if seasonal changes in the environment are most important, one would expect an effect of laying date on some of these components of fitness to remain, even when condition is factored out statistically.

We present here the results of statistical tests for the relative strength of the effect of laying date and a variety of condition measures on clutch size in Tree Swallows (*Tachycineta bicolor*), a species that exhibits a strong seasonal decline in clutch size, both in Canada (Stutchbury and Robertson 1988) and at our New York study site (Fig. 1).

METHODS

Study site and general methods

This study is based on Tree Swallows nesting during 1993, 1994, and 1995 at six separate sites, all within 10 km of Cornell University (42°28' N, 76°29' E) in Ithaca, New York. Two of these sites, known as Unit 1 and Unit 2, together accounted for 71–72% of the clutches initiated in each year. These sites were dominated by small ponds and lakes, whereas the remaining sites were open fields. All nests were in standard blue-bird boxes with a floor area of ≈ 160 cm², and all boxes were fitted with predator-deterrent devices (either a metal cone or a nest-box hole extender).

Beginning the third week of April each year, nest boxes were checked every other day to monitor the amount of nest material in each box and to detect clutch initiations. In 1993, laying females were trapped on the day after they laid their fourth egg (i.e., usually on the day of their fifth egg). In 1994 and 1995, to minimize disturbance to laying birds, nesting females were trapped on their second consecutive day without laying (i.e., two days after clutch completion). In 23% of the cases a female was not caught on the desired day, and trapping was then postponed until the next morning. (In another 3% of cases, the female was caught before the desired day.) Females were replaced in their boxes after 10–60 min of processing. In addition to these scheduled captures in nest boxes, we captured birds in mist nets at Unit 1 during April and early May as part of other studies on dispersal, and this allowed us to gather measurements of some females prior to laying.

Body size and condition

Two measurements of structural body size, head–bill length and wing length, were taken on captured females. Head–bill measurements, the maximal distance between the back of the head and the bill tip, were taken with dial calipers to the nearest 0.1 mm. Length of the straightened, flattened left wing (from the carpal joint to the tip of the longest primary feather) was measured to the nearest millimetre using a metal ruler with a perpendicular wing stop against which the carpal–radial joint was rested during measurements.

Condition variables measured were body mass, breast muscle thickness, and fat deposits. Mass was measured with a 50 g Pesola scale to the nearest 0.1 g. Because the mass of females can change dramatically with time of day, especially around the laying period, we conducted all of our analyses on body mass corrected with linear regression to a standard capture time of 0906, which was the mean capture time for all females reported here. (For analyses of mist-netted birds that form the basis for Fig. 3 and Table A8 we did not correct mass, as there was no significant regression of mass on time of day for those birds.) Birds captured at Unit 1 also had the combined thickness of their pectoralis-major and supracoracoideus muscles (hence-

forth “breast muscles”) measured with an ultrasound thickness instrument (Model USL 48, Krautkramer-Branson, Lewiston, Pennsylvania) using a 10-MHz contact transducer (cf. Newton 1993). (Because of the limited portability of the instrument, this measurement could be taken only at our field laboratory at Unit 1.) The breast muscles are by far the largest muscles in a passerine’s body, together comprising at least 15% of the total wet mass of the bird (e.g., Ojanen 1983, Burton 1985), and they are the muscles that have been identified in the past as an important store of protein for passerine reproduction (Kendall et al. 1973, Jones and Ward 1976). Breast muscle measurements were taken on both the left and right side of the breast, and the mean of the two measurements was used in the following analyses.

In 1993, two subcutaneous fat deposits were scored subjectively, the claviculo-coracoid (henceforth “furcular”) and composite abdominal. To increase the accuracy and scope of our assessment of fat stores, we devised a new protocol for external fat scoring in 1994 based on descriptions of subcutaneous fat bodies from King and Farner (1965). In 1994 and 1995, birds were scored on each of seven subcutaneous fat deposits: the furcular, composite abdominal, transverse abdominal, lateral abdominal, femoral, sartorial, and lateral thoracic.

Sample sizes and statistics

Tree Swallows normally raise at most one brood per season (cf. Hussell 1983a), and we excluded from our analyses females captured on known replacement clutches. We processed 120, 150, and 205 females from their first clutches in 1993, 1994, and 1995, respectively. This total of 475 captures represents 345 individuals since some females were present on our sites in >1 year.

Clutch initiation dates were standardized across years by subtracting from each initiation date the mean initiation date of all first clutches in the respective year. Female Tree Swallows wear a distinctive plumage in their first year (Hussell 1983b), and the age class factor appearing in the analyses is a binary flag that was set to zero for females making their first breeding attempt and set to one for older females.

The MGLH procedure of SYSTAT (1992) was used for the multiple regressions that are the foundation for the path analyses presented here. Path analyses provide a graphical means of visualizing the interconnections among sets of potential causal factors (Kingsolver and Schemske 1991), and we use them in this paper to clarify the connections between timing of breeding, clutch size and various aspects of condition.

RESULTS

For the most representative analysis of the effects of laying date and condition on clutch size, we chose the data set that best balanced the number of condition

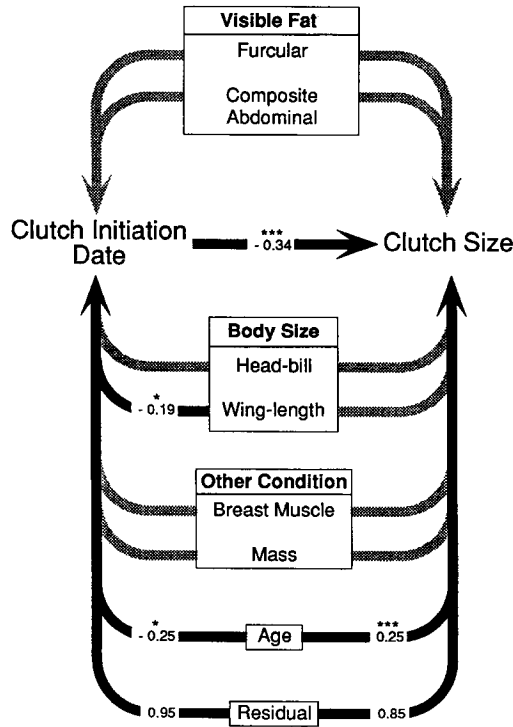


FIG. 2. Path analysis summarizing the effects of various individual attributes on laying date and clutch size in Tree Swallows nesting near Ithaca in 1993, 1994, and 1995. Sample includes all the $n = 184$ first clutches of unmanipulated females captured near the end of laying or shortly thereafter for which breast muscle measurements were taken. Paths representing significant effects are black, with * $P < 0.05$ and *** $P < 0.001$. Numbers in significant paths from variables are standardized partial regression coefficients representing relative strengths of effects, but those in paths from the residual component are $(1 - R^2)^{0.5}$ using the adjusted squared multiple R from the multiple regression underlying the path analysis. For nonsignificant effects see Appendix Table A3.

variables measured and the number of birds sampled: females from the 184 first-nest attempts at Unit 1 for which we had measurements of breast muscle thickness. The resulting path analysis (Fig. 2) reveals significant effects of wing length and age class on laying date and of age class and clutch initiation date on clutch size. Because we were concerned about failing to reject the null hypothesis of no condition effects when it was indeed false, we also analyzed the effects of condition, body size, and laying date on clutch size with a variety of other subsets of our condition variables. Effectively, this meant using different subsets of data for each combination of condition variables since we took measurements of breast muscle thickness only at Unit I and detailed measures of subcutaneous fat only in 1994 and 1995. Taking these analyses (Tables A1–A7) together with the path diagram (Fig. 2), there are four strong effects that emerge in all the analyses (Table 1): the effects of female age and wing length on laying date, and the effects of laying date and female age on clutch size. There are indications that two measures of condition (breast muscle thickness and lateral abdominal fat) may have significant effects on clutch size, but neither of these effects is robust to variation in the sample of birds used in the analyses. There is also an inconsistent effect of composite abdominal fat on laying date (Table A5), but it is opposite in sign from that expected for a condition effect. Overall, the effect of breeding date on clutch size emerges as the strongest and most consistent link in the reproductive decisions of Tree Swallows made early in the season.

Recall that the condition measures we have analyzed so far were taken from females after they had laid all (1994 and 1995) or most (1993) of their eggs. It could be the case that we see no significant effect of condition because, by the time the females' clutches are completed, they have used any "excess" condition to produce their clutch and have all depleted themselves to a common state. One test of this possibility is to consider only the 1993 data, in which females were captured after laying five eggs. If there were any pre-laying

TABLE 1. Summary of results presented in Appendix Tables A1–A7. For details on birds and measurements included in each analysis, see the relevant table. Tabulated here are all predictors that had significant effects in any of the analyses: seven other measures of condition never had significant effects in any of the analyses.*

Table	Effects on laying date			Effects on clutch size				
	Age	Wing length	Abdominal fat	Laying date	Age	Year	Breast muscle	Lateral abdominal fat
A1	**	**	NS	**	**	NT	NT	NT
A2	**	*	NS	**	**	NS	*	NT
A3	**	*	NS	**	**	NT	NS	NT
A4	**	*	NS	**	**	NT	NT	NT
A5	**	**	(**)	**	*	*	NT	NS
A6	*	**	NS	**	*	NS	*	*
A7	*	**	NS	**	**	NS	NT	*

* $P < 0.05$; ** $P < 0.01$; NS = not significant ($P > 0.05$); NT = not tested. () encloses effects that were opposite in sign to that expected for the condition.

TABLE 2. Multiple regression results for the effects of various predictors on laying date and clutch size for females captured in 1993 on the morning after their fourth egg was laid. Predictors that have significant effects on either laying date or clutch size are in bold type, as are the associated standardized coefficients and *P* values. All *P* values are two-tailed.

Variable	Laying date model		Clutch size model	
	Std. coef.	<i>P</i>	Std. coef.	<i>P</i>
Constant	0.000	0.679	0.000	0.202
Head-bill	0.086	0.595	0.230	0.083
Wing length	-0.101	0.493	0.073	0.543
Abdom. fat	0.262	0.117	0.114	0.407
Furcular fat	0.197	0.227	0.135	0.313
Mass	-0.401	0.042	-0.082	0.614
Age	-0.125	0.450	0.362	0.010
Breast muscle	-0.042	0.779	0.145	0.230
Laying date			-0.440	0.001
Overall model <i>P</i> value	0.226		<0.001	
Multiple <i>R</i>	0.428		0.693	
Adj. squared multiple <i>R</i>	0.053		0.383	
<i>N</i>	52		52	

condition differences among them, those differences would not be obscured by the fact that the females had laid different numbers of eggs. This analysis (Table 2) indicates again that there was no effect of condition; the only significant predictors are female mass on laying date and female age and laying date on clutch size. Thus, there is again no suggestion of a condition effect on clutch size once variation in laying date is controlled statistically. (Taking possible variation in egg size into account, we also did this analysis and all the analyses in the Appendix on total clutch volume and again found no effect of condition.)

To explore the possibility of undetected pre-laying condition differences further, we constructed another data set that contained measurements of females captured prior to the initiation of their first clutch. The majority of such captures were from mist-netting performed each year in April and early May prior to most clutch initiations. This data set consists of measurements from 94 captures of 84 females between 1 and 32 d (mean \pm 1 SD = 10.4 \pm 8.3 d) prior to clutch initiation. (Eight of the females were captured prior to clutch initiation in two of the years and one was captured prior to clutch initiation in all three years.) The path analysis of this data set (Fig. 3) reveals an important qualitative difference from the previous analyses: age class still has the only significant effect on laying date, and laying date has lost its significant effect on clutch size. On the face of it, this analysis seems to contradict Fig. 2 regarding the effect of laying date on clutch size, but we place little faith in the apparent loss of this effect in Fig. 3 because the subset of birds available for this analysis went from a 46-d range of clutch initiation dates in the analyses for Fig. 2 to a range of only 23 d in the analysis for Fig. 3. The im-

portant point to be made here, however, is that there is still no effect of any condition variable on either clutch initiation date or clutch size.

DISCUSSION

The analyses we report here suggest that physiological condition played a minor role in the determination of clutch size and its seasonal decline in Tree Swallows. Although some condition measures occasionally affected clutch size and/or breeding date in some analyses from some subsets of the data, the effect on clutch size was seldom as strong and never as consistent as the effect of laying date. The other important predictors in the analyses were female age, which had an effect on laying date and clutch size, and wing length, which had an effect on laying date. Thus, the picture that emerged from our study of the factors influencing early season reproductive decisions in female Tree Swallows was that females that were younger and/or had shorter wings tended to breed later and that females that were younger and/or laid later had smaller clutches, regardless of their overall mass or stores of fat and protein.

Possible problems in interpretation

This picture appears to refute the condition-dependent model proposed by Price et al. (1988) to explain the lack of evolution of breeding date in birds. To test their model, and the model of sexual selection that includes it, Kirkpatrick et al. (1990:189) suggested

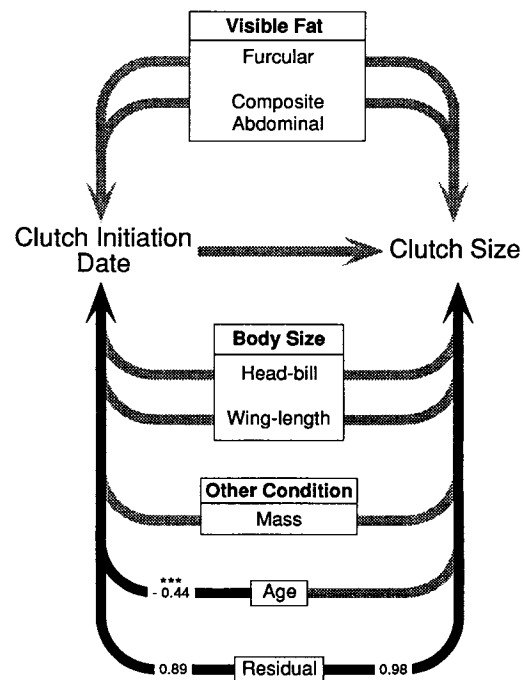


FIG. 3. Path analysis using data from the $n = 94$ female captures between 1 and 32 d prior to their clutch initiations. Conventions of symbols, etc. are the same as in Fig. 2. For nonsignificant effects see Appendix Table A8.

“checking for a zero partial regression of female fitness on breeding date when nutritional condition is held constant.” This is precisely what we have done in the analyses in this paper, and it is clear that condition did very little or nothing to reduce the partial regression of female fitness (measured by clutch size) on breeding date. If one accepts this result, then the model of Price et al. (1988) and the condition-dependent parts of Rowe et al.’s (1994) model are seriously questioned, and we next consider possible problems with interpreting our results in this way.

The first possible problem is that we have not measured condition appropriately, i.e., that we would have reduced the partial regression of fecundity on breeding date to zero if we had measured condition “completely.” There is, of course, no way to eliminate this potential criticism entirely, but we feel strongly that we have considered every likely source of variation in condition among breeding Tree Swallows. The three principal candidates for limiting resources during reproduction are calcium, protein, and fat reserves. Recent evidence (Graveland et al. 1994, Holford and Roby 1993) suggests that variation in calcium availability can limit reproductive output in some passerines, but all the evidence of which we are aware (e.g., Ojanen 1983) suggests that variation in calcium availability affects reproduction directly and not principally through variable somatic stores of the mineral, even in passerines that lay very large numbers of eggs (Ankney and Scott 1980). Using high-acuity X-radiographic methods (R. Pahl, D. W. Winkler, J. Graveland, and B. Batterman, *unpublished manuscript*) in a longitudinal study of females before and after laying, we have been unable to detect any evidence of somatic stores of calcium mobilized for egg production in Tree Swallows.

By contrast, fat and protein stores change in complex ways preceding and during reproduction in passerines (Ward 1969, Fogden 1972, Jones and Ward 1976, Ankney and Scott 1980, Ojanen 1983, Mertens 1987, Jones 1991), swifts (Hails and Turner 1985), waterfowl (Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979, Krapu 1981, Hohman 1986, Parker and Holm 1990), grouse (Thomas 1988), rails (Alisauskas and Ankney 1985), and shorebirds (Houston et al. 1983, Davidson and Evans 1988). The generalization emerging from these studies is that protein is most often the body component that is limiting as a raw material for actual gamete production. Fat enters into reproductive biology both as a resource for direct incorporation into egg yolk and as the energy source to support metabolic activity. Although it can be limiting in the former sense, fat is usually necessary, and potentially limiting, in supplying the energy either for gamete synthesis or for foraging to find protein and/or calcium that may be lacking in somatic stores. In measuring breast muscle thickness and a variety of subcutaneous fat deposits, we have measured condition on live birds more comprehensively than any other study of reproduction in

wild birds. It is still possible that we have missed meaningful variation in body components, but we do not feel this is the case for two reasons. First, our condition measures detected reductions in body mass, breast muscle thickness, and fat deposits associated with experimental removal of about one-third of females’ wing and tail feathers prior to laying (Winkler and Allen, *in press*). More importantly, the eggs of Tree Swallows each weigh $\approx 10\%$ of female mass, and we weighed the females to an accuracy of $\approx 1\%$ of their mass. Thus, even if we were to miss variation in individual body components, it is hard to imagine that we would miss variation in total body mass that would be of sufficient magnitude to affect differences in clutch size. In sum, we are confident that, if variation in either fat, protein, or overall body mass were sufficiently large to cause considerable variation in breeding date and/or clutch size, we would have detected that variation.

It might still be argued that condition is important to determining laying date and clutch size, but that we did not sample our birds on a sufficiently fine temporal scale to detect differences among females in the few days leading up to laying. This is a possibility, but we do not think it is very likely, nor, if true, would it be very satisfying as a condition-based explanation. Even if there were meaningful differences between females right before laying, it is difficult to see why we would not have detected differences among them when they were measured after having laid the same number of eggs in 1993 (Table 2). Also, female Tree Swallows weighed repeatedly during the pre-laying period exhibited considerable variation in their mass on both daily and day-to-day scales of comparison (Winkler, *unpublished observation*). This suggests that swallows are changing their nutritional condition (at least insofar as condition is reflected in body mass) considerably and rapidly during the pre-laying period according to their variable “income” from foraging. This variability makes any convincing designation of birds as being in good or bad condition difficult.

What does “condition” mean?

Let us for a moment assume that short-term condition differences between females in the few days leading up to laying are responsible for the variation we see in laying date and clutch size. If such differences are so short-term as to have been missed by our trapping 10 d (on average) in advance of the first egg (Fig. 3) and 5–8 d after the first egg (Fig. 2), we would argue that such differences, even if they exist, would not be sufficiently long-term to qualify as meaningful differences in “condition.” Unfortunately, the term “condition” is coming to have so many meanings to different authors that it is beginning to lose its usefulness. Condition can mean anything from “the nongenetic component of clutch size” (Schluter and Gustafsson 1993) to precise measurements of individual body components (e.g., Slagsvold 1982). Clearly, at some point

several hours to a day or so before laying an egg, a female Tree Swallow will have to be in better "condition" than a female not ready to lay. But to define the term relative to a time period so short would rob condition of any meaningful use in the context of laying date and clutch size variation. To be useful in the present context, condition must, in principle, be measurable on all birds at the beginning of the breeding season and allow prediction of both clutch size and laying date from that measure. Laying dates for the birds in this study had a range of 46 d, and detectable variation in condition that lasted less than this length of time would be unable to predict variation in laying date for all the birds in the population.

If not condition, then experience?

If variation in condition is not responsible for natural variation in laying date and clutch size, what other factors might explain the seasonal decline in clutch size? The ideas and models of Daan and Drent and their co-workers (e.g., Daan et al. 1988, Meijer et al. 1990, Tinbergen and Daan 1990) and parts of the model of Rowe et al. (1994) provide alternatives to the condition hypothesis. Tree Swallows in spring could be seen as responding to a number of different sources of information in determining their laying date. These could include recent success in foraging (which might include an individual-specific component relating to foraging skill) and variation in weather and the availability of a mate and nest site. In any event, once a determination of laying date is made, the female appears to be adjusting her clutch size in response to that laying date. This suggests strongly that females are adjusting their clutch sizes, not in adherence to the dictates of their condition, but rather as a strategic adjustment to the seasonally changing prospects of offspring to be reared from the eggs they are laying. Assuming a cost of reproduction for the laying female, a bird that finds herself laying later will benefit by expending less effort on less-valuable offspring, saving energy and resources for self-maintenance to increase the chances of her surviving to breed again. In the case of Tree Swallows, the source of decline in prospects for the females' offspring appears not to lie in environmental conditions for chick-rearing, as food availability during the chick-rearing period is steady or very slightly increasing (McCarty 1995). Rather, the principal source of declining prospects appears to be in post-fledging recruitment probabilities: chicks fledged later at the Ithaca study site have lower probabilities of surviving to the next breeding season (D. W. Winkler, *unpublished manuscript*).

Although we feel there is little evidence for differences in the physiological condition of females playing a role during the pre-laying period, there are likely other purely phenotypic differences among females that affect when they begin laying eggs and how many they will eventually lay. The most likely possibility in Tree

Swallows would appear to be differences in experience, perhaps associated with differences in wing length (e.g., Table 1). Condition variables must measure somatic resources that can be reallocated for reproduction, and thus differences in experience and/or wing length cannot be considered as condition variables. Older females are likely better at gathering resources for reproduction (as well as feather growth), and they are probably better at obtaining early mates and nest cavities and at building nests, incubating eggs, and feeding chicks. Differences in experience could explain many if not all of the observed age effects on reproduction reported here (Figs. 1–3). The availability of aerial insects at the Ithaca site increases throughout the laying period (Winkler, *unpublished data*), and less experienced females may be waiting to lay until the increase in food availability compensates, in part, for their lesser foraging efficiency. Although there are many stochastic factors (e.g., weather, mortality of mates) that affect the timing of breeding, variation in experience appears likely to be the most important deterministic cause of the variation that we observe in laying date.

Why no evolution in breeding date?

The existence of such experience or quality differences could have some of the effects on laying date and clutch size that the model of Price et al. (1988) requires. But could such differences in quality explain the lack of evolution in breeding date in these birds? In terms of the model of Price et al., a lack of directional selection on breeding date could only result if birds of greater quality were "constrained to breed earlier than is optimal" (Price et al. 1988:799). While it seems possible that such a constraint might exist for birds that have large amounts of resources stored for reproduction, it is more difficult to imagine that a bird that is superior only by virtue of its experience or quality should be so constrained. One possible explanation for the lack of evolution in breeding date is that there are selective forces that balance the apparent directional selection for earlier breeding. Nilsson (1994) recently showed through supplemental feeding experiments that female Blue Tits (*Parus caeruleus*) that lay "too early" pay a selective price in reduced fledging success and female survival. As mentioned above, Tree Swallow chicks fledged earlier in the season have higher chances of post-fledging survival, suggesting that selection would favor, rather than disfavor, earlier breeding. Analyses of return probabilities of breeding females indicate no penalty for breeding early in unmanipulated birds (Winkler, *unpublished observation*), but experiments to parallel Nilsson's study will be difficult in the Tree Swallow, since it is difficult to supplement their food supply.

It is also possible that there is no evolution in laying date because there is no additive genetic variance for the trait (cf. Lande and Arnold 1983). This interpre-

tation requires that additive variance in individual quality has been exhausted, and given the ways in which such variance could be maintained (e.g., fluctuating selection, mutation), it seems unlikely to be the principal explanation for the lack of directional evolution in laying dates.

Tree Swallows as income breeders

Drent and Daan (1980) introduced a dichotomy for avian life histories consisting of "income breeders" (which base their reproduction on resources ingested near the time of breeding) and "capital breeders" (which breed using resources stored in advance of the breeding season). It is likely that there is a continuum of life histories among birds, with arctic-nesting geese (e.g., Ankney and MacInnes 1978) at the "capital" extreme. It is not clear what species might lie at the extreme "income" end of the spectrum, but the hypothesis that emerges from this study is that Tree Swallows are likely near that end. We suspect that many, if not most, passerines are sufficiently small, and their clutches sufficiently large, that it is unfeasible for them to store sufficient resources for the formation of their clutch and still remain sufficiently agile to forage and avoid predators. There is considerable empirical work that would be needed to prove an income-breeder characterization in any species, including a demonstration of the fine-scaled time course of resource intake and redistribution within the laying female's body immediately before laying. In any event, our evidence suggests that the model of Price et al. (1988) and perhaps the condition-dependent parts of Rowe et al. (1994) do not apply to the Tree Swallow, nor possibly to many other passerines. Further work with these models in species that seem more likely to be capital breeders (e.g., waterfowl and gulls) seems worthwhile.

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APPENDIX

Results of multiple regressions to investigate the effects of predictor variables on laying date and clutch size of Tree Swallows at Ithaca, New York. Each set of regressions uses a subset of data drawn from the basic data set of all first

clutches of unmanipulated females. Predictors that have significant effects on either laying date or clutch size are in bold type, as are the associated standardized coefficients (Std. coef.) and *P* values. All *P* values are two-tailed.

TABLE A1. All females. This is the most inclusive data set with the least detailed measures of condition.

Variable	Laying date model		Clutch size model	
	Std. coef.	<i>P</i>	Std. coef.	<i>P</i>
Constant	.000	.799	.000	.287
Head-bill	.059	.216	.044	.328
Wing length	-.174	.001	.084	.083
Abdominal fat	.087	.069	.040	.371
Furcular fat	-.042	.436	-.055	.273
Mass	-.032	.565	.102	.053
Age	-.280	<.001	.161	.001
Year	.022	.645	.048	.293
Laying date			-.345	<.001
Overall model <i>P</i> value	<.001		<.001	
Multiple <i>R</i>	.394		.499	
Adj. squared multiple <i>R</i>	.142		.235	
<i>N</i>	444		444	

TABLE A3. All females with breast muscle measurements and with the nonsignificant year effect in Table A2 removed. This table is the basis for Fig. 2 in the text.

Variable	Laying date model		Clutch size model	
	Std. coef.	<i>P</i>	Std. coef.	<i>P</i>
Constant	.000	.313	.000	.930
Head-bill	.044	.541	.017	.788
Wing length	-.194	.011	.092	.185
Abdominal fat	.053	.491	.053	.447
Furcular fat	-.027	.752	-.038	.626
Mass	.051	.551	.036	.637
Age	-.252	.001	.254	<.001
Breast muscle	-.027	.724	.128	.065
Laying date			-.340	<.001
Overall model <i>P</i> value	.001		<.001	
Multiple <i>R</i>	.359		.554	
Adj. squared multiple <i>R</i>	.094		.275	
<i>N</i>	184		184	

TABLE A2. All females with breast muscle measurements. This consists of females from Unit 1, and note that there is no significant effect of year on either laying date or clutch size.

Variable	Laying date model		Clutch size model	
	Std. coef.	<i>P</i>	Std. coef.	<i>P</i>
Constant	.000	.828	.000	.400
Head-bill	.041	.582	.030	.655
Wing length	-.191	.015	.081	.248
Abdominal fat	.053	.498	.055	.428
Furcular fat	-.030	.729	-.026	.735
Mass	.054	.536	.027	.732
Age	-.251	.002	.249	.001
Breast muscle	-.041	.681	.178	.047
Year	.022	.827	-.079	.376
Laying date			-.339	<.001
Overall model <i>P</i> value	.002		<.001	
Multiple <i>R</i>	.359		.557	
Adj. squared multiple <i>R</i>	.089		.274	
<i>N</i>	184		184	

TABLE A4. Same set of females as in Table A3, but not using breast muscle measurements as a predictor. This allows an evaluation of the subsetting of the dataset per se without the effects of breast muscle on other *P* values in the models. Note the similarity of these results to those in Table A1.

Variable	Laying date model		Clutch size model	
	Std. coef.	<i>P</i>	Std. coef.	<i>P</i>
Constant	.000	.333	.000	.699
Head-bill	.043	.551	.023	.722
Wing length	-.190	.012	.074	.285
Abdominal fat	.058	.441	.029	.674
Furcular fat	-.034	.686	-.006	.936
Mass	.046	.585	.060	.430
Age	-.255	.001	.266	<.001
Laying date			-.343	<.001
Overall model <i>P</i> value	<.001		<.001	
Multiple <i>R</i>	.358		.541	
Adj. squared multiple <i>R</i>	.099		.265	
<i>N</i>	184		184	

TABLE A5. All females in 1994 and 1995, using more detailed fat measures taken in those years. This data set includes females breeding at all sites. Note that, though abdominal fat is significant in the laying date model, the sign of its effect is opposite to what would be expected. For full names of fat stores see *Methods: Body size and condition*.

Variable	Laying date model		Clutch size model	
	Std. coef.	P	Std. coef.	P
Constant	.000	.395	.000	.054
Head-bill	.094	.082	.023	.667
Wing length	-.252	<.001	.089	.134
Abdominal fat	.201	.006	.138	.058
Furcular fat	-.050	.452	-.069	.295
Mass	-.006	.931	.066	.338
Age	-.253	<.001	.130	.025
Femoral fat	.008	.904	-.077	.263
Lat. ab. fat	.135	.111	.079	.346
Lat. thor. fat	-.133	.193	.024	.814
Sartorial fat	-.044	.654	-.089	.363
Trans. ab. fat	.054	.346	-.046	.416
Year	.094	.224	.158	.040
Laying date			-.356	<.001
Overall model P value	<.001		<.001	
Multiple R	.453		.476	
Adj. squared multiple R	.175		.195	
N	334		334	

TABLE A6. All females in 1994 and 1995, using expanded fat measures and breast muscle measurements. This reduces the dataset to females breeding at Unit 1. For full names of fat stores see *Methods: Body size and condition*. There is a significant effect of both breast muscle thickness and lateral abdominal fat on clutch size, but the effect of laying date on clutch size remains more highly significant.

Variable	Laying date model		Clutch size model	
	Std. coef.	P	Std. coef.	P
Constant	.000	.211	.000	.922
Head-bill	.079	.354	.003	.970
Wing length	-.256	.008	.073	.432
Abdominal fat	.066	.575	.012	.912
Furcular fat	-.155	.177	-.062	.568
Mass	.137	.248	-.019	.867
Age	-.238	.016	.240	.012
Femoral fat	-.017	.890	-.167	.149
Lat. ab. fat	.251	.096	.350	.016
Lat. thor. fat	-.210	.229	.033	.842
Sartorial fat	.079	.652	-.090	.587
Trans. ab. fat	.011	.918	-.068	.479
Breast muscle	-.063	.588	.242	.030
Year	.196	.156	.020	.880
Laying date			-.337	<.001
Overall model P value	.002		<.001	
Multiple R	.479		.567	
Adj. squared multiple R	.144		.241	
N	132		132	

TABLE A7. All females in 1994 and 1995 from Unit 1, using expanded fat measures but not using breast muscle measurements as a predictor. This serves as the control on the subsetting necessitated to include breast muscle measurements in Table A6 as compared to Table A5. For full names of fat stores see *Methods: Body size and condition*. Note that the significant effect of lateral abdominal fat on clutch size present in Table A6 remains, but that this effect was absent in the larger analysis of females from all sites (Table A5).

Variable	Laying date model		Clutch size model	
	Std. coef.	P	Std. coef.	P
Constant	.000	.256	.000	.341
Head-bill	.084	.324	-.013	.871
Wing length	-.255	.008	.067	.475
Abdominal fat	.071	.548	-.004	.974
Furcular fat	-.156	.173	-.059	.591
Mass	.128	.274	.017	.878
Age	-.249	.010	.279	.004
Femoral fat	-.017	.889	-.167	.155
Lat. ab. fat	.265	.074	.300	.038
Lat. thor. fat	-.217	.212	.057	.732
Sartorial fat	.074	.671	-.071	.673
Trans. ab. fat	.000	.998	-.029	.765
Year	.165	.188	.140	.246
Laying date			-.346	<.001
Overall model P value	.001		<.001	
Multiple R	.477		.542	
Adj. squared multiple R	.149		.216	
N	132		132	

TABLE A8. All females with measurements taken prior to clutch initiation in 1993, 1994, and 1995. This analysis forms the basis for Fig. 3.

Variable	Laying date model		Clutch size model	
	Std. coef.	P	Std. coef.	P
Constant	.000	.258	.000	.517
Wing length	-.165	.140	.193	.120
Head-bill	.141	.161	.037	.741
Abdominal fat	-.077	.470	-.004	.972
Furcular fat	.157	.160	-.167	.178
Mass	-.014	.899	.124	.300
Age	-.444	<.001	.174	.179
Year	-.152	.143	.057	.620
Laying date			.086	.473
Overall model P value	<.001		.188	
Multiple R	.515		.346	
Adj. squared multiple R	.206		.037	
N	94		94	