

Effects of Food Abundance, Weather, and Female Condition on Reproduction in Tree Swallows (*Tachycineta bicolor*) (Efectos de la Abundancia de Alimento, del Clima y de la Condición de las Hembras sobre la Reproducción en *Tachycineta bicolor*)

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EFFECTS OF FOOD ABUNDANCE, WEATHER, AND FEMALE CONDITION ON REPRODUCTION IN TREE SWALLOWS (*TACHYGINETA BICOLOR*)

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ABSTRACT.—Food abundance, weather, and female body condition are believed to influence the timing of breeding and reproductive performance of birds. We simultaneously studied the effects of weather and food abundance on reproduction in Tree Swallows (*Tachycineta bicolor*) while experimentally reducing female condition and foraging efficiency by clipping some flight feathers prior to egg laying. Control females laid larger clutches earlier in the season, had longer incubation periods, and raised heavier nestlings than experimental females. Fledging success did not differ after controlling for laying date and brood size. Greater insect abundance was associated with laying earlier in the season, heavier eggs, and shorter incubation periods. Most likely, feather-clipping affected clutch size through reduced foraging efficiency, which delayed the date of laying, rather than through loss of body condition. This outcome is consistent with the idea that Tree Swallows are “income” breeders that base their timing of reproduction on short-term rates of food intake near the time of breeding. Contrary to studies of other species, Tree Swallows do not appear to time their laying so that hatching will coincide with seasonal peaks in food supply. Rather, they appear to breed when temperature and food abundance are sufficient to allow females of a given body condition to initiate egg laying. Received 4 February 2004, accepted 8 April 2005.

Key words: clutch size, female condition, food supply, laying date, reproductive success, *Tachycineta bicolor*, Tree Swallow, weather.

Efectos de la Abundancia de Alimento, del Clima y de la Condición de las Hembras sobre la Reproducción en *Tachycineta bicolor*

RESUMEN.—Se cree que la abundancia de alimento, el clima y la condición corporal de las hembras influyen sobre el momento de la reproducción y el desempeño reproductivo de las aves. Estudiamos simultáneamente el efecto del clima y de la abundancia de alimento sobre la reproducción de *Tachycineta bicolor*, al mismo tiempo que redujimos experimentalmente la condición y eficacia en el forrajeo de las hembras cortándoles algunas de las plumas para el vuelo antes del período de la puesta. Las hembras control pusieron nidadas mayores y más tempranas en la estación, tuvieron períodos de incubación más largos y criaron polluelos de mayor peso que las hembras experimentales. El éxito de emplumamiento no difirió luego de controlar por la fecha de la puesta y el tamaño de la nidada. Una mayor abundancia de insectos se asoció con una puesta más temprana en la estación, con huevos de mayor peso y con períodos de incubación más cortos. Lo más probable es que el corte de las plumas afectó el tamaño de la nidada a través de la reducción de la eficiencia del forrajeo, lo que atrasó la fecha de puesta, y no a través de un deterioro en la condición corporal.

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Este resultado concuerda con la idea de que *T. bicolor* cría en función de los “ingresos”, basándose en las tasas de adquisición de alimento a corto plazo antes del periodo reproductivo para determinar el momento de inicio de la reproducción. En contraste con estudios para otras especies, *T. bicolor* no parece sincronizar la puesta, de manera que la eclosión coincida con el periodo de mayor abundancia de alimento. Más bien, esta especie parece reproducirse cuando la temperatura y la abundancia de alimento son suficientes como para permitirles a las hembras que cuentan con una determinada condición corporal iniciar la puesta.

IN MANY ANIMALS, including birds, timing of breeding has a strong effect on reproductive success. Typically, reproductive success declines over the course of a breeding season. Such effects may be caused by variation in phenotypic quality of individuals (e.g. body condition) or changes in environmental quality (e.g. food and temperature). Numerous studies indicate that females in poor condition initiate egg laying later (Pietiäinen and Kolunen 1993, Weidinger 1996, Hipfner et al. 1999), lay smaller clutches (Houston et al. 1983, Goodburn 1991), and fledge fewer young (Reid and Boersma 1990, Wendeln and Becker 1999), which are also in poor condition (Schluter and Gustafsson 1993). Environmental factors, particularly food abundance and air temperature, may directly influence female condition, future ability to feed young, or survival of the parent (Perrins 1970, Daan et al. 1986, Winkler and Allen 1996). Other studies, particularly of small passerines, have suggested that timing of laying is influenced more by the rate of food intake near the time of egg formation than by body condition. These species have been referred to as “income breeders,” whereas birds that rely more on endogenous reserves (stored fat or nutrient reserves) for laying are referred to as “capital breeders” (Drent and Daan 1980). Temperature and precipitation often influence insect abundance (e.g. Bryant 1975, Eeva et al. 2000); as a consequence, we expect the reproductive performance of income breeders that feed primarily on insects to be linked closely to weather (Bryant 1978).

The specific effects of food abundance, weather, foraging efficiency, and female condition on reproduction are difficult to untangle. Ambient temperature is often related to date of egg laying, clutch size and fledging success (Järvinen and Väisänen 1984, Martin 1987, Perrins 1991, Dunn and Winkler 1999, Hussell 2003). Similarly, food supplementation experiments have shown that food abundance

influences female condition and many of these same reproductive parameters (reviewed in Boutin 1990). Even though temperature is often used as an indicator of food abundance, these two variables do not always correspond closely, nor do they necessarily affect reproduction in similar ways (Bryant 1975, Perrins 1991).

One way to disentangle these effects is to manipulate foraging efficiency while measuring the effects of both temperature and food abundance on female condition and reproductive output. Foraging ability is a potentially important interindividual difference (Bryant 1979) and may be one reason why older females are more successful than yearling females (Wheelwright and Schultz 1994), but it is difficult to quantify without experimentation. Previous field studies have manipulated foraging efficiency by adding weights (Wright and Cuthill 1990, Tveraa et al. 1997) or clipping feathers (Slagsvold and Lifjeld 1988, 1990; Whittingham et al. 1994; Winkler and Allen 1995). However, to our knowledge, no experimental studies of foraging efficiency have examined reproductive performance and female condition while simultaneously measuring temperature and food abundance.

For several reasons, the Tree Swallow (*Tachycineta bicolor*) is an ideal species for examining the effects of foraging efficiency, female condition, weather, and food abundance on reproduction. First, aerial insect abundance influences reproductive performance of Tree Swallows (Quinney et al. 1986, Hussell and Quinney 1987, McCarty and Winkler 1999, Murphy et al. 2000, Lifjeld et al. 2002), and reliable methods are available for estimating aerial insect abundance (Lifjeld et al. 2002). Second, experiments that clipped flight feathers of Tree Swallows have shown a significant reduction in female condition and decreased rates of nestling feeding (Winkler and Allen 1995). Finally, female Tree Swallows can be caught reliably at specific points in their reproductive cycle to

monitor changes in condition without compromising reproductive performance.

We studied the reproductive behavior of Tree Swallows in two years with dramatically different weather and food abundance. May 2001 in Wisconsin was unusually warm and wet (28th warmest and 12th wettest May in 107 years of records), whereas May 2002 was unusually cool, with average precipitation (25th coldest and 61st wettest May) (National Climatic Data Center; see Acknowledgments). This variation allowed us to examine how weather, food abundance, and female condition interact to affect reproductive success at all stages of reproduction, from egg laying to fledging. We reduced female condition and foraging ability experimentally by clipping flight feathers of females before egg laying. Tree Swallows are income breeders; they base their timing of reproduction on short-term rates of food intake near the time of breeding (Winkler and Allen 1996, Bowlin and Winkler 2004). We predicted that, with decreased foraging efficiency, clipped females should postpone egg laying until food is more abundant. Reduced foraging efficiency of clipped females should also result in relatively more time spent foraging for self-maintenance and, hence, smaller clutches, lighter eggs, more days spent incubating, and overall lower reproductive performance. However, we also expected that these effects might be moderated by (1) high levels of food availability; (2) warmer temperatures, which reduce thermoregulatory costs; and (3) the contribution of male partners to the feeding of young.

METHODS

Study area and species.—We studied Tree Swallows nesting in two grids (600 m apart) at the University of Wisconsin-Milwaukee Field Station near Saukville, Wisconsin, (43°23'N, 88°01'W). The study area (6 ha) contained 92 nest boxes with predator guards, of which 88 and 87 were occupied by Tree Swallow pairs in 2001 and 2002, respectively.

Breeding in Tree Swallows is highly synchronous (Robertson et al. 1992). Females build grass cup nests in nest boxes during late April and early May and lay one egg per day during the middle of May. Incubation starts with the penultimate egg and lasts 12–15 days. After hatching, young remain in the nest 18–22 days.

Field techniques.—We checked nest boxes every other day during the nest-building period from late April through the second week of May. Females were caught in the nest box when nests had ≥ 3 cm of nest material. Females were classified as second-year (SY) or after-second-year (ASY) on the basis of plumage coloration (Hussell 1983). We used only first nesting attempts of ASY females, because first nests of SY females and renesting attempts are made later in the season and have smaller clutches (Robertson and Rendell 2001). Females were randomly assigned to the control or experimental group, with the exception that 10 females from 2001 that returned in 2002 were assigned to the alternative group. Experimental birds had three primaries on each wing (numbers three, five, and seven, counting from the innermost feather outward) and four central tail feathers clipped at the base of each feather, similar to our previous experiment on males (Whittingham et al. 1994). All females were marked with a federal band on the right leg and a red plastic band on the left leg. To monitor the effects of feather-clipping on body condition, females were recaptured and weighed on the second day of incubation and again when nestlings were 4 days old.

Female Tree Swallows began egg laying when nests were 4–8 cm high (5.4 ± 0.1 [mean \pm SE], $n = 73$). Nest boxes were checked daily from when the height of a nest reached 4 cm until clutch completion, and again from day 13 of incubation until the nestlings were 12 days old. These observations enabled us to determine laying date, clutch size, hatch date, duration of incubation (hatch date minus clutch completion date), and number of young fledged. In 2001, eggs were weighed to the nearest 0.01 g on the day they were laid and numbered with a non-toxic ink marker. To monitor nestling growth, we measured mass (to nearest 0.01 g) and tarsus length (to nearest 0.1 mm with digital calipers) when nestlings were 4 and 12 days old to determine nestling condition (mass corrected for tarsus length; see below). Fledging success was estimated as number of young in the nest at 12 days of age minus any dead young found in the nest after fledging (usually 18–20 days).

Estimates of body condition.—Body condition of adults and nestlings was estimated as the residuals of body mass regressed on tarsus length (a measure of structural size). For adults,

this regression was performed using only control females. The condition of experimental females was then estimated by the residual of each experimental female from the regression line for control females. This measure of body condition is the most reliable method for estimating condition, because it separates condition from body size, is easily interpreted, and produces residuals with a normal distribution (Jakob et al. 1996). To justify the use of tarsus length as a measure of size, we used a principal component analysis (PCA) of several size measurements (lengths of wing, ninth primary, tail, keel, and tarsus; and distance between back of head and tip of bill). Condition estimates from the regression of mass on tarsus were highly correlated with condition estimates obtained using the first principal component (PC1; primarily feather lengths: wing, ninth primary, and tail length) or PC2 (primarily structural size: keel, tarsus, and distance from head to bill) as estimates of size (both regressions: $r^2 > 0.92$, $P < 0.0001$).

Weather and insect biomass.—Temperature and precipitation data were obtained from an automated weather station located between the two grids of nest boxes. A 1-m-tall suction trap next to the weather station was used to measure abundance of aerial insects (fig. 4.2 in Southwood and Henderson 2000). It operated from 0600 to 1900 hours from the first week of May through the first week of July. Daytime food abundance was expressed as total dry biomass of insects collected per day (Lifjeld et al. 2002).

To examine the effect of food abundance and weather on reproduction, we averaged the daily insect biomass and weather data for each period of reproduction. The period of rapid yolk synthesis is believed to be about four days in small passerines (King 1973), so we averaged the insect biomass and weather variables over the five days before each female laid her first egg to estimate environmental conditions immediately before laying. For the incubation period, we averaged the insect biomass and weather data for the first 10 days after clutch completion (incubation is typically 11–15 days long) and 3 and 10 days after hatching (to coincide with our measurements of nestlings on days 4 and 12, respectively).

Statistical analyses.—We used JMP, version 4.0.4 (SAS Institute, Cary, North Carolina) for all analyses. Multiple regression models with all predictors were tested with stepwise regression

using a mixed procedure (forward and backward) to choose a final model that was simple yet had high predictive power. We set P to enter or leave the model at 0.15 to avoid type II errors (not including variables in the final model, even though they may be important). For the analysis of laying date, we compared several regression models, and in this case we chose the model that minimized Akaike's Information Criterion (AIC) and computed the support for this model using Akaike weights (w_i) (Burnham and Anderson 1998). Individual variables that were nonsignificant in the final model were included if they were part of a significant interaction term (the combine rule; SAS Institute, Cary, North Carolina). The initial set of predictors in the regression models (Tables 1 and 2) included all six two-way interactions between temperature, precipitation, insect biomass, and experimental treatment. These interactions allowed us to test for differing effects of environmental conditions on clipped and control females and to explore the effect of annual differences in weather on reproduction. We did not include interactions with year, because, on its own, year does not provide any biological insight. Our analyses controlled for previous levels of reproductive performance; for example, laying date was included in the analysis of clutch size, and brood size (number hatched) was included in the analysis of number of fledglings. Similarly, environmental variables were used that most closely coincided with a reproductive period (prelaying, incubation, or nestling). Control and clipped birds were coded as "1" and "0," respectively, for analyses. Coefficients of determination for the multiple regression models (r^2) were adjusted for number of parameters. For eggs and nestlings, variables in the analyses were based on the mean for each brood. Sample sizes vary among analyses, because it was not always possible to measure every variable for each female or brood. Means are presented with SE. All tests were two-tailed unless otherwise noted.

RESULTS

Experimental treatment.—We captured 116 ASY female Tree Swallows before egg laying, of which 60 had feathers clipped and 56 were controls. Residual body condition at initial capture did not differ between clipped ($-0.09 \pm$

TABLE 1. Multiple regression analysis of factors influencing laying date in Tree Swallows ($n = 93$ females). Predictors included in models 1–4 are indicated by their regression coefficients and P values. The initial set of variables in the stepwise model included all the individual predictors and all two-way interactions between temperature, insect biomass, precipitation, and treatment. Predictors included in the final model are indicated by their regression coefficients and P values. Temperature, precipitation, and insect biomass were averaged for the five days before each female began laying.

| Predictors | Model 1 | | Model 2 | | Model 3 | | Model 4 | | Model 5 ^a | |
|---------------------------|---------|--------|---------|--------|---------|--------|---------|--------|----------------------|--------|
| | β | P | β | P | β | P | β | P | β | P |
| Year | 9.30 | <0.001 | 8.90 | <0.001 | 10.4 | <0.001 | 10.1 | <0.001 | 10.2 | <0.001 |
| Treatment | -3.72 | <0.001 | -2.68 | <0.001 | -3.3 | <0.001 | -2.8 | <0.001 | -2.6 | <0.001 |
| Female condition | | | | | | | | | | |
| at initial capture | -1.02 | 0.003 | -0.80 | 0.015 | -1.010 | 0.003 | -0.90 | 0.006 | -0.68 | 0.034 |
| Temperature | | | 0.82 | 0.002 | | | 0.43 | 0.001 | 0.65 | 0.011 |
| Precipitation | | | -0.14 | 0.525 | | | | | -0.65 | 0.027 |
| Insect biomass | | | -0.12 | 0.078 | 0.068 | 0.049 | | | -0.11 | 0.091 |
| Significant interactions: | | | | | | | | | | |
| Biomass * temperature | | | | | | | | | -0.03 | 0.010 |
| r^2 adjusted | 0.660 | | 0.700 | | 0.670 | | 0.690 | | 0.720 | |
| AIC | 273.100 | | 264.100 | | 271.000 | | 263.800 | | 258.800 | |
| w_i | 0.001 | | 0.061 | | 0.002 | | 0.071 | | 0.865 | |

^aStepwise model.

TABLE 2. Stepwise regression analysis of factors influencing clutch size, incubation length, and number of eggs hatched in Tree Swallows. Predictors in the initial stepwise model included those listed on the left and all the two-way interactions between temperature, insect biomass, precipitation, and treatment. Variables included in the final multiple-regression model are indicated by their regression coefficients and *P* values. Temperature, precipitation, and insect biomass are based on data from 1 to 5 days before laying for the analysis of clutch size, and on data from the first 10 days after clutch completion for the analysis of incubation length and number of eggs hatched. See text for further details.

| Predictors | Dependent variables | | | | | |
|--------------------------------|---------------------|----------|-------------------|----------|---------------------------|----------|
| | Clutch size | | Incubation length | | Eggs hatched (<i>n</i>) | |
| | β' | <i>P</i> | β' | <i>P</i> | β' | <i>P</i> |
| Year | | | | | | |
| Treatment | 0.15 | 0.098 | -0.40 | 0.023 | | |
| Laying date | -0.04 | <0.001 | | | | |
| Clutch size | | | -0.30 | 0.150 | 0.63 | 0.020 |
| Female condition | | | | | | |
| at initial capture | | | | | | |
| at incubation | | | -0.17 | 0.069 | 0.29 | 0.053 |
| Temperature | -0.04 | 0.032 | -0.70 | <0.001 | | |
| Precipitation | | | | | | |
| Insect biomass | | | 0.05 | 0.052 | | |
| Significant interactions: | | | | | | |
| Biomass * temperature | | | | | | |
| Treatment * temperature | 0.06 | 0.004 | 0.09 | 0.072 | | |
| <i>r</i> ² adjusted | | 0.41 | | 0.56 | | 0.11 |
| Females or broods (<i>n</i>) | | 93 | | 67 | | 88 |

0.15) and control females (0.14 ± 0.19 ; *t*-test = 0.93, *P* = 0.36). Twenty-two of 116 females did not lay eggs; however, this was not related to treatment (logistic regression $\chi^2 = 2.66$, *df* = 1, *P* = 0.10) or to condition at initial capture ($\chi^2 = 0.01$, *df* = 1, *P* = 0.91). Clipped females lost 5.5% of their body mass (-1.1 ± 0.2 g, *n* = 40), whereas control females gained 1.5% of their body mass (0.3 ± 0.2 g, *n* = 47) between initial capture before laying and second day of incubation (*t* = 4.5, *P* < 0.0001). This 7.0% difference in body mass between clipped and control females is similar to results of a previous handicapping experiment in Tree Swallows (clipped females weighed 7.5% less than controls; Winkler and Allen 1995). Consequently, clipped females were in poorer condition than controls by at least the second day of incubation (clipped: -1.26 ± 0.19 , *n* = 40; control: 0.12 ± 0.22 , *n* = 48; *t*-test = 4.6, *P* < 0.0001).

Weather and insect biomass.—Daily estimates of insect biomass were correlated positively with daily mean temperature in 2001 ($r^2 = 0.36$, *P* < 0.001, *n* = 53 days) and 2002 ($r^2 = 0.47$, *P* < 0.0001,

n = 57 days), but not with daily precipitation (2001: $r^2 = 0.03$, *P* = 0.23; 2002: $r^2 = 0.04$, *P* = 0.16). During the five days prior to laying, 84% of the variation in mean insect biomass (mg day^{-1}) was explained by prelaying temperature ($b = 3.1 \pm 0.17$, *P* < 0.001) and year ($b = -10.0 \pm 1.42$, *P* < 0.001; higher in 2001) in a multiple regression (*F* = 245, *df* = 2 and 91, *P* < 0.001).

Seasonal patterns of insect biomass and temperature differed markedly between May 2001 and May 2002 (Fig. 1). In 2001, mean daily temperatures and insect biomass declined throughout May but were higher than in 2002, when temperatures and biomass were consistently low but steadily increasing (during egg laying and incubation; Fig. 1). As a consequence, females laying early in 2002 experienced lower temperatures and insect biomass than females laying at the same time in 2001. Because of their earlier hatch dates in 2001 (Fig. 1), most females experienced colder temperatures ($13.2 \pm 0.6^\circ\text{C}$) during the first 10 days after hatch than in 2002 ($17.2 \pm 0.2^\circ\text{C}$; *t* = 7.5, *df* = 68, *P* < 0.001). Insect biomass during the first three days after

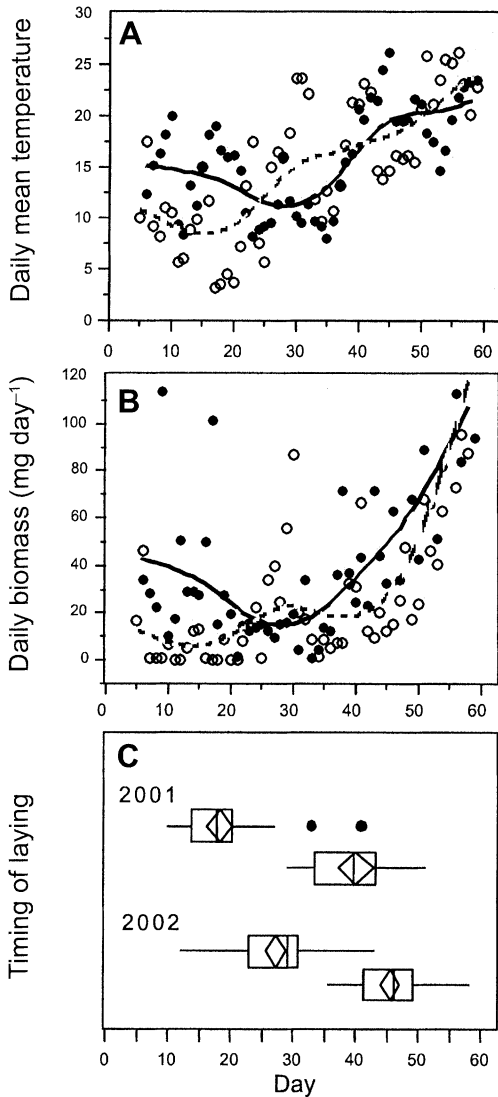


FIG. 1. (A) Mean daily temperature (°C); (B) insect biomass (mg day⁻¹) during 2001 (solid dots and line) and 2002 (open dots and dashed line); and (C) timing of laying and hatch of Tree Swallows at the University of Wisconsin-Milwaukee Field Station, Saukville, Wisconsin. Day 1 is 1 May. Lines in (A) and (B) are splines fit using $\lambda = 1,000$ in JMP, version 4.0.4; (C) has box plots of laying date (left side) and hatch dates (right side) in 2001 and 2002. Each box plot displays the mean (center of diamond), median (vertical line inside box), 25th and 75th percentiles (ends of the box), and 10th and 90th percentiles (ends of lines outside each box). Dots outside the lines indicate data beyond these percentiles.

hatch was not related to temperature (bivariate regression: $r^2 = 0.03$, $n = 70$, $P = 0.17$), precipitation ($r^2 < 0.01$, $n = 70$, $P = 0.92$), or insect biomass ($r^2 < 0.01$, $n = 70$, $P = 0.80$) over the five-day period before laying.

Laying date.—Mean laying date was earlier in 2001 (18.4 ± 1.0 May, $n = 38$) than in 2002 (27.3 ± 0.8 May, $n = 56$), and clipped females laid eggs later (27.2 ± 1.0 May, $n = 45$) than control females (20.4 ± 0.9 May, $n = 49$). Females in poorer condition also laid later in a multiple regression that included year and experimental treatment (Model 1 in Table 1; Fig. 2). The contribution of environmental variables was examined in three subsequent models that included all environmental variables (temperature, precipitation, and insect biomass; Model 2 in Table 1), insect biomass only (Model 3 in Table 1), and temperature only (Model 4 in Table 1). Temperature was related positively to laying date whenever it was included (Models 2 and 4 in Table 1), but insect biomass had variable effects because of an interaction with temperature (Models 2 and 3 in Table 1). The best model, as indicated by both stepwise regression and AIC values, included year, treatment, female condition, all environmental variables, and the interaction between temperature and insect biomass (Model 5 in Table 1). This model indicated that females started laying earlier when temperatures were colder and insect biomass and precipitation greater. The positive relationship between laying date and temperature was unexpected; however, this effect was attributable simply to an increase in temperatures during the laying period in 2002 (12 May–12 June; $b = 0.44$, $r^2 = 0.40$, $P < 0.001$, $n = 32$), so it is not likely a causal relationship (Figs. 1 and 2). Note that temperatures did not increase during the laying period in 2001 (10–27 May; $b = -0.27$, $r^2 = 0.14$, $P = 0.13$, $n = 18$), so females laying later in May do not always encounter warmer temperatures (Figs. 1 and 2). The significant interaction between insect biomass and temperature in Model 5 (Table 1) occurred because when both temperature and insect biomass were low, as in early May 2002, birds laid relatively later than when temperatures were warmer (i.e. insect biomass had a smaller effect on laying date in warmer weather).

Clutch size and egg mass.—After controlling for laying date, clutch size was influenced by treatment and temperature (Table 2). As expected, there was a seasonal decline in clutch size, and the slopes of these relationships were

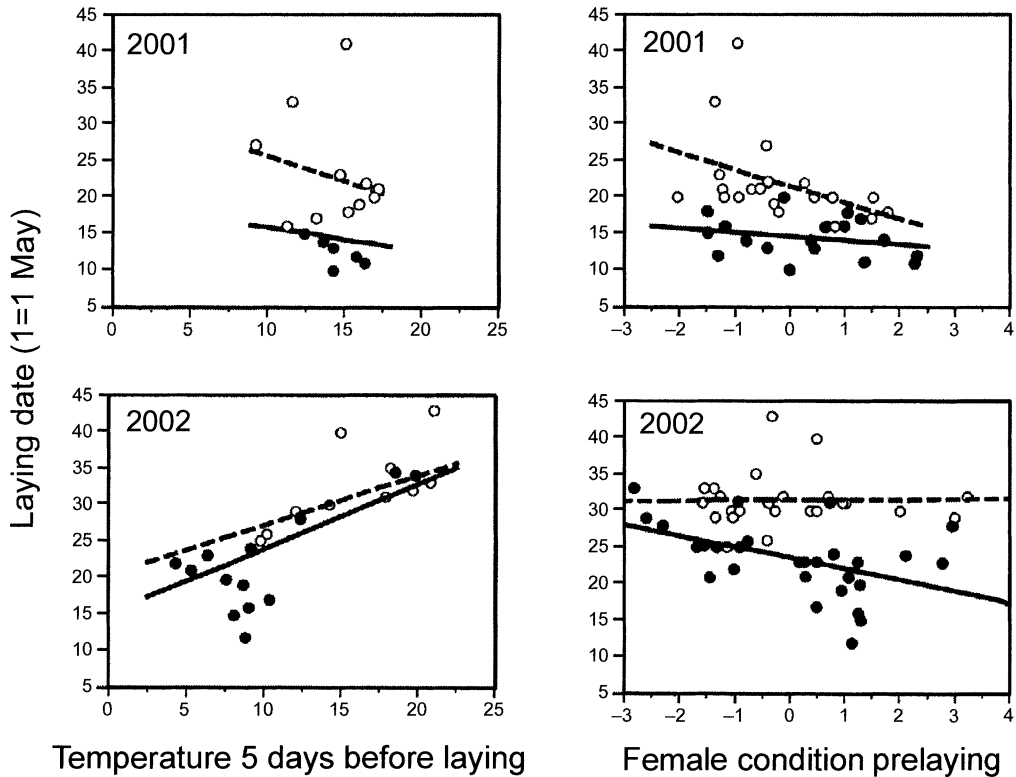


FIG. 2. Laying dates of Tree Swallows in relation to temperature averaged for the five days before each female began laying in 2001 and 2002. Lines are from regression analyses of control (solid lines, filled circles) and clipped (dashed lines, open circles) females.

similar between clipped and control females in an analysis of covariance (Fig. 3; interaction: $F = 0.76$, $df = 1$ and 90 , $P = 0.39$). However, clipped females (4.5 ± 0.1 , $n = 44$) laid smaller clutches than controls (5.3 ± 0.1 , $n = 49$) that started laying concurrently (treatment $F = 8.3$, $df = 1$ and 90 , $P = 0.005$; Table 2). Contrary to expectation, clutch size decreased with increasing temperature (bivariate regression: $r^2 = 0.12$, $P < 0.001$, $n = 93$), but this was also influenced by an interaction between temperature and treatment ($P = 0.004$; Table 2). Closer inspection of the data revealed that clutch sizes of clipped females declined with temperature (bivariate regression: $r^2 = 0.15$, $P = 0.008$, $n = 44$), primarily because some clipped females nested late in 2001, after 1 June, when females typically have smaller clutches and temperatures are also warmer. There was no relationship between clutch size and temperature among control females ($r^2 = 0.06$, $P = 0.60$, $n = 49$). Egg mass was not influenced by feather-clipping, but eggs were heavier when

there was greater insect biomass ($b = 0.06$, $P = 0.002$) and precipitation ($b = 0.05$, $P = 0.029$) one to five days before laying (overall r^2 adjusted = 0.26 , $P = 0.004$, $n = 33$ nests).

Length of incubation.—Length of incubation was influenced primarily by feather-clipping and temperature during the first 10 days of incubation (Table 2). Incubation was longer for clipped females and shorter in warmer weather. However, there tended to be an interaction between temperature and treatment ($P = 0.072$), because clipped females had a relatively longer incubation than control females when weather was colder (Table 2). Incubation also tended to be shorter when females were in better condition, clutch size was smaller, and insect biomass was lower, but these effects were marginal in significance and explained only 8% of the variation in length of incubation.

Hatching success.—After controlling for the effect of clutch size, the number of eggs that hatched tended to be greater ($P = 0.053$) among

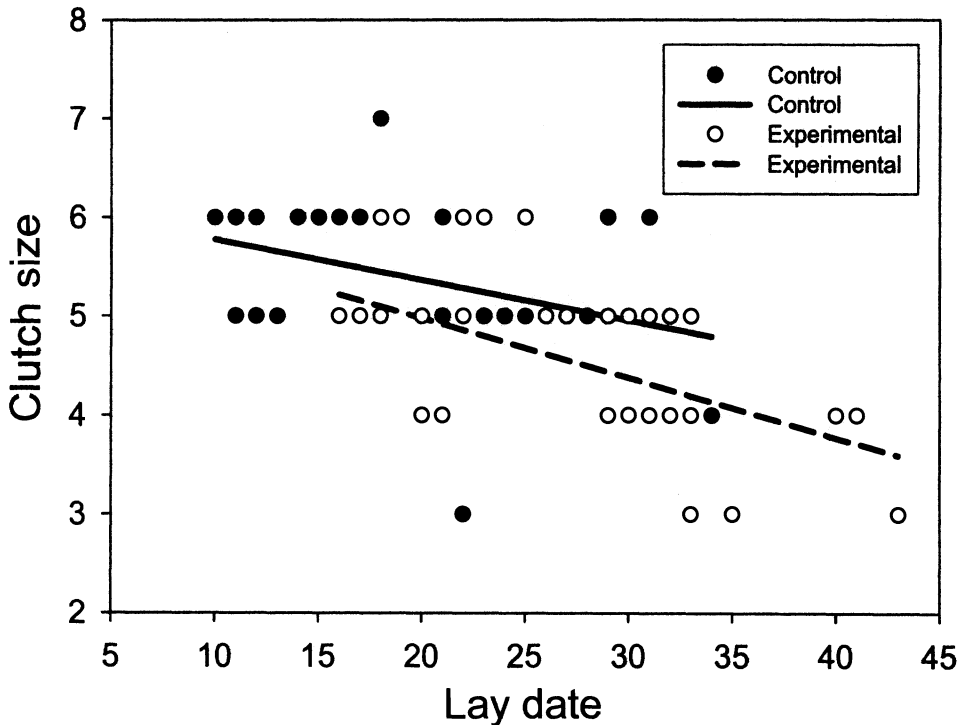


FIG. 3. Seasonal decline in clutch size of control (closed circles and solid line) and clipped (open circles and dashed line) females. Regression lines are from an analysis of covariance ($r^2 = 0.38$, $P < 0.001$, $n = 93$). There was no significant interaction between laying date and treatment ($F = 0.76$, $df = 1$ and 90 , $P = 0.39$). However, clipped females laid smaller clutches than controls that started laying concurrently (treatment: $F = 8.3$, $df = 1$ and 90 , $P = 0.005$). Inclusion of year as a factor had no qualitative effect on the results.

females that were in better body condition on day 2 of incubation (Table 2). Hatching success was not affected significantly by feather-clipping or environmental variables (during the first 10 days of incubation).

Nestling condition.—Four-day-old nestlings were in better body condition when it was warmer during the previous three days and their mother was in better condition on day 4 (Table 3). Nestlings were also in better condition when raised at nests of control rather than of clipped females, and the effect was somewhat more pronounced when temperatures were cooler (temperature and treatment interaction; Table 3). The effect of feather-clipping on nestling condition persisted to 12 days of age (Table 3). At this age, there was also a negative effect of brood size on condition and a tendency for warmer temperatures (1 to 10 days after hatch) to reduce nestling condition in nests of clipped

females (temperature and treatment interaction, $P = 0.053$; Table 3). There was no such relationship at nests of control females (bivariate regression: $r^2 < 0.02$, $P = 0.57$, $n = 39$).

Nesting success.—Among nests that hatched at least one egg, there were more young fledged per nest in 2002 than in 2001 ($F = 17.9$, $df = 1$ and 65 , $P = 0.002$) after controlling for number of eggs that hatched ($F = 89.0$, $df = 1$ and 65 , $P < 0.001$) and date of hatching ($F = 5.1$, $df = 1$ and 65 , $P = 0.09$), but this was attributable primarily to there being more nest failures in 2001 (seven nests: five clipped, two control) than in 2002 (one clipped nest). After nest failures were removed from analysis, the year effect disappeared ($F = 0.05$, $df = 1$ and 58 , $P = 0.84$). Overall, 79% (23 of 29) of experimental and 95% (38 of 40) of control nests fledged young (Fisher's exact test, $P = 0.062$; only nests that hatched at least one egg).

TABLE 3. Stepwise regression analysis of factors influencing nestling condition at 4 and 12 days of age and fledging success (i.e. number of fledglings at successful nests). Predictors in the initial stepwise model included those listed on the left and all the two-way interactions between temperature, insect biomass, precipitation, and treatment. Variables included in the final multiple-regression model are indicated by their regression coefficients and *P* values. Temperature, precipitation and insect biomass were based on data from after hatch; see text for further details.

| Predictors | Nestling condition | | | | | |
|--------------------------------|--------------------|----------|--------|----------|------------------|----------|
| | Day 4 | | Day 12 | | Fledging success | |
| | β | <i>P</i> | β | <i>P</i> | β | <i>P</i> |
| Year | | | | | | |
| Treatment | 0.21 | 0.006 | 0.61 | 0.021 | | |
| Laying date | | | | | | |
| Eggs hatched (<i>n</i>) | | | −0.46 | 0.024 | 0.94 | <0.001 |
| Female condition on | | | | | | |
| day 4 of nestling period | 0.18 | 0.004 | | | 0.15 | 0.070 |
| Temperature | 0.09 | <0.001 | −0.16 | 0.08 | 0.05 | 0.044 |
| Insect biomass | | | | | | |
| Precipitation | | | | | | |
| Significant interactions: | | | | | | |
| Temperature * treatment | −0.04 | 0.067 | 0.18 | 0.053 | | |
| <i>r</i> ² adjusted | | 0.23 | | 0.17 | | 0.74 |
| Broods (<i>n</i>) | | 66 | | 66 | | 60 |

Fledging success.—Among nests that successfully fledged at least one young, the number of fledglings was greater, after controlling for the number of young that hatched, when the female was in better body condition (on day 4 of the nestling period) and temperatures were greater during days 1 to 3 after hatch (Table 3). In this analysis, the initial stepwise-regression model included weather and insect biomass variables with estimates for both 1–3 and 1–10 days after hatch to determine whether environmental conditions early or late in the nestling period had different effects. Indeed, in this case, temperatures 1–3 days after hatch were more important to fledging success than those averaged over the first 10 days, which suggests that younger nestlings are more sensitive to colder temperatures.

DISCUSSION

Dramatic differences in environmental conditions between the two years of our study provided an opportunity to investigate the influence of weather, food abundance, and experimental handicapping on the reproductive performance of female Tree Swallows. These variables affected numerous aspects of

reproduction, from timing of laying to fledging success. Females that had their flight feathers clipped experimentally started laying eggs later in the season, produced smaller clutches, had longer incubation periods, and raised young that were in poorer condition at 4 and 12 days of age. Note that in these analyses, there was a treatment effect while controlling for female condition (or after finding no effect), which suggests that the experimental effect occurred as a consequence of its effects on foraging efficiency rather than female condition. When insects were more abundant, females started laying earlier in the season and produced larger clutches and heavier eggs. Temperature had some unexpected effects on laying date and clutch size, but these trends probably reflect the general increase in temperature during the 2002 breeding season and, thus, are unlikely to be causal relationships. In 2001, temperatures did not increase during the laying period. In general, temperatures tend to increase during May at our study area (data from 1997–2003; *r*² = 0.03, *P* = 0.01, *n* = 217); however, temperatures during May declined or showed no change in three of seven years, so it does not appear that females can always expect conditions to improve during

laying. Later in the breeding season, it appeared that females had shorter incubation periods, nestlings in better body condition at four days of age, and greater fledging success when temperatures were warmer. Overall, our results suggest that there were independent effects of weather, food abundance, foraging efficiency, and female body condition on various aspects of reproduction. Furthermore, variation in environmental conditions between years made predicting the optimum time for breeding unreliable (see also Hussell and Quinney 1987), so it is unlikely that females time their breeding so that nestlings are fed during the seasonal peak of food abundance, as was suggested by Lack (1954).

Food abundance is often believed to constrain the timing of breeding in birds (Perrins 1970, Martin 1987). Food supplementation experiments have generally shown that supplemented birds lay their eggs earlier but usually do not increase their clutch size (Martin 1987, Daan et al. 1986). Using multiple regression, we found independent effects of food and feather-clipping (treatment) on laying date. We also found a positive association between egg mass and insect biomass, but not female condition, which supports the idea that egg production is limited by daily energy intake and not stored fat reserves (Murphy et al. 2000). Furthermore, we did not find any good environmental predictors of food abundance after hatch, which suggests that females are not using such factors as cues to time their breeding (Hussell and Quinney 1987). Thus, it is more likely that food, temperature, foraging efficiency, and body condition act as constraints on timing of laying. These results are similar to those of a previous feather-clipping experiment on female Tree Swallows (Winkler and Allen 1995), in which clipped females laid later than controls. As suggested by Winkler and Allen (1995), it was likely that the feather-clipping had an immediate effect on foraging efficiency, which led to a delay in laying and, eventually, a decrease in condition.

Our feather-clipping treatment had effects on reproductive performance that were independent of female body condition (Tables 1–3). Thus, the effect of feather-clipping on reproduction was most likely through reduced foraging efficiency, which delayed the date of laying, rather than through loss of body condition (fat levels). This outcome is consistent with the idea that Tree Swallows are income breeders, which

base their timing of reproduction on short-term rates of food intake near the time of breeding, rather than capital breeders, which rely more on stored fat reserves (i.e. condition; Drent and Daan 1980).

Winkler and Allen (1995) also found that clipped females laid later and had smaller clutches. They argued that laying date *per se* was the main determinant of clutch size. Although laying date may be influenced by body mass (Winkler and Allen 1996) or food abundance (present study), once the female began to lay on a particular date she appeared to adjust her clutch size in response to that date (Winkler and Allen 1996; see also Winkler et al. 2002). Consistent with this hypothesis, we found no effect of food abundance on clutch size after controlling for laying date. Note that Hussell and Quinney (1987) found a positive relationship between clutch size and food abundance, but they did not examine the relationship after controlling for laying date. The adjustment of clutch size to laying date appeared to be a strategic decision in response to declining prospects for the survival of fledglings as the season progressed (Winkler and Allen 1996), rather than deteriorating environmental conditions, given that food abundance increased or remained steady during most of the nestling period (Fig. 1). Cliff Swallows (*Petrochelidon pyrrhonota*) also appeared to make a strategic decision about clutch size based on laying date; however, Brown and Brown (1999) argued that a seasonal decline of reproductive success in that species was caused by increasing ectoparasitism on the nestlings. No such effects of ectoparasites on reproduction have been found in Tree Swallows (Rogers et al. 1991).

Experiments in which the flight feathers of adults were clipped have shown variable effects on reproductive success after clutch completion. The number of fledglings and their body mass were reduced in broods of clipped females in three tit species (*Parus* spp.) and Pied Flycatchers (*Ficedula hypoleuca*) (Slagsvold and Lifjeld 1988, 1990). In Tree Swallows, clipping of flight feathers of adult females or males did not appear to influence nestling condition or fledgling success in previous studies (Whittingham et al. 1994, Winkler and Allen 1995), but we found significant negative effects on nestling condition (both days 4 and 12) of clipping the flight feathers of adult females. We may have

found an effect because we had unusually severe weather in one year that resulted in significant interactions between treatment and temperature (both cold and warm temperatures produced interactions). In previous studies, feather-clipping reduced the rate at which handicapped parents fed their young (Whittingham et al. 1994; Winkler and Allen 1995; Slagsvold and Lifjeld 1988, 1990). In Tree Swallows, males with clipped feathers reduced their rate of food delivery to nestlings by 41%, as compared with control males. However, females mated to these males increased their delivery rates by 21%; as a consequence, the overall rate of food delivery to nestlings was not significantly lower than at control nests (Whittingham et al. 1994). Thus, compensation for reduced food delivery by the mate, even though it is not entirely complete (see Whittingham et al. 1994), was likely the reason for the weak or nonexistent effects of treatment and condition on fledging success.

Previous work based primarily on European tits (*Parus* spp.) has led to the widespread belief that birds time their laying so that hatching coincides with seasonal peaks in food supply (Lack 1950, Perrins 1970, Daan et al. 1986). However, these results may not generalize to other species living in less predictable environments. Our results showed that birds cannot always predict the best time for hatching. In 2001, the temperature was unusually warm during the beginning of May, and many Tree Swallows laid eggs in mid-May. However, the temperature dropped during late May to early June, when many eggs hatched. As a consequence, these early-hatching chicks were in poorer condition when four days old than those that hatched later. At least in our population of Tree Swallows, this indicated that environmental conditions at laying cannot be used reliably to predict conditions at hatch, and these conditions can have dramatic effects on annual variation in reproductive success. Relatively few studies have examined the predictability of food abundance during the nestling period; but overall, it appears that food supplies (over the short term) are either unpredictable on the basis of conditions prior to laying (Eeva et al. 2000, present study) or not related to reproductive performance (reviewed by Nol 1989). Hussell and Quinney (1987) examined eight years of data from Tree Swallows breeding in Ontario and also concluded that females could not predict food abundance during the

nestling period on the basis of conditions during laying. Of course, on a broader scale, food supplies are often predictable, in the sense that they generally increase over the course of the entire season. Laying date could be influenced by both the current rate of food intake for egg production and the likelihood of adequate food during the nestling period. This "future nestling energy" hypothesis seems to explain breeding in crossbills (*Loxia* spp.), which will cease nesting if food supplies decline after egg laying (Benkman 1990). Thus, it is probable that food abundance acts as both a constraint and a cue for breeding.

Conclusions.—We examined the effect of female condition, weather and insect biomass on reproduction in Tree Swallows while manipulating female foraging ability (by clipping flight feathers). Our results suggest that reproduction in Tree Swallows was influenced strongly and independently by ambient environmental conditions, the foraging ability of females, and their body condition. This supports the idea that Tree Swallows are income breeders. We also found that environmental conditions were variable and that there were no strong predictors of conditions during the nestling period at the time when females were deciding to lay their eggs. Thus, it is likely that environmental conditions act as constraints on the timing of reproduction, rather than as cues for the optimum timing of hatch.

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