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EFFECTS OF HANDICAPPING ON FEMALE CONDITION AND REPRODUCTION IN TREE SWALLOWS (*TACHYCINETA BICOLOR*)

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ABSTRACT.—We reduced the foraging efficiency of female Tree Swallows (*Tachycineta bicolor*) during the prelaying period by removing one-third of their flight feathers by clipping them at their bases. Clipped females laid later and smaller clutches, and their clutch sizes were reduced more than what would be expected from the normal seasonal clutch-size decline. Feather clipping reduced subsequent female condition as measured by mass, breast-muscle thickness, and fat deposits, but these effects did not become significant until after the females laid their eggs. Females that were clipped fed their young at lower frequencies and were less likely to return the following breeding season. There were no effects of female condition near clutch completion on laying date, and there was a strong effect of laying date on clutch size, with only the most ambiguous of four condition measures (body mass) having a significant, albeit weaker, effect. Coupling these results with those of another study on unmanipulated swallows, it appears likely that female Tree Swallows base their early-season reproductive decisions largely on their income from foraging rather than the size of somatic stores of resources. *Received 13 February 1995, accepted 25 April 1995.*

IN MOST SPECIES OF BIRDS, females that lay later in the breeding season lay smaller clutches (Klomp 1970, Winkler and Walters 1983, Murphy 1986, Daan et al. 1988, Hochachka 1990; for exceptions see Crick et al. 1993, Young 1994). There is considerable disagreement over the causes of this pattern, with some researchers hypothesizing a constraining effect of somatic stores of resources (e.g. Price et al. 1988, Kirkpatrick et al. 1990), others attributing the pattern to strategic adjustments to environmentally related seasonal declines in nestling and juvenile survival (e.g. Perrins 1970, Daan et al. 1988, Young 1994), and some (Rowe et al. 1994) proposing a mixture of these two hypotheses. The evidence pertaining to these hypotheses is varied. Both clutch size and timing of reproduction are correlated with somatic stores of resources in waterfowl (Korschgen 1977, Ankney and MacInnes 1978, Raveling 1979, Krapu 1981, Cooke et al. 1984) and gulls (Boersma and Ryder 1983). In passerines, body 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 input from foraging (e.g. Ojanen 1983, Winkler and Allen in press).

Studies in which food has been supplemented in the prelaying period (see reviews by Daan et al. 1988, Meijer et al. 1990) often have been cited (e.g. Price et al. 1988, Rowe et al. 1994) to help evaluate the links among condition, environment, laying date, and clutch size. Our study is the converse of these food supplementations: rather than supplement food, we decreased a bird's foraging profitability by clipping feathers off at their bases in the wing and tail (cf. Lifjeld and Slagsvold 1988, Slagsvold and Lifjeld 1988, Slagsvold and Lifjeld 1990, Whittingham et al. 1994). Because our study organisms, Tree Swallows (*Tachycineta bicolor*), are obligate aerial insectivores, supplementing food is difficult, if not impossible. Experimental reductions in foraging ability have the added advantage that manipulated birds, if anything, will lay smaller and later clutches. Thus, experimental birds will be free of any hidden, upper constraints on clutch size that might prevent increases in clutch size in food-supplementation experiments.

We predicted that manipulations reducing the foraging effectiveness of females before laying should reduce their ability to gain resources and cause them to delay clutch initiation and decrease clutch size. Because it involves altering the foraging ability of birds beyond the natural range of variation, the timing and severity of any condition differences that arise also should help us evaluate the importance of condition

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TABLE 1. Summary of numbers of females in each treatment group in 1993 and 1994, and numbers that progressed to each stage of breeding episode.

Treatment	*n*	Initiated clutch	Hatched young	Fledged young
		1993		
Clipped	11	10	8	8
Control	8	8	7	5
		1994		
Clipped	15	9	9	7
Control	12	10	10	10
		Both years		
Clipped	26	19	17	15
Control	20	18	17	15

differences among females to reproductive decisions in this species. The dichotomy between species for which condition is most important and those for which a strategic adjustment to environmental changes is most important closely parallels the dichotomy proposed by Drent and Daan (1980) of "capital breeders" versus "income breeders," and tests of the importance of condition to egg laying can indicate whether a species is a capital breeder. Impairment of foraging efficiency in capital breeders would either not affect egg laying or would affect it only if the impairment in foraging took place early enough to result in significant condition differences before laying. By contrast, handicapped income breeders should show the effects of reduced foraging efficiency through delayed laying and smaller clutches without necessarily displaying any intervening changes in body condition. Finally, although our principal focus is on egg laying, we will consider the effects of feather clipping on female parental care, as well as on the subsequent survival of clipped females.

METHODS

We experimentally manipulated Tree Swallows breeding in 1993 and 1994 at a study site 10 km north of the campus of Cornell University near Ithaca, New York (42°30'N, 76°28'E). The site contained a grid of 105 nest boxes (for a map, see Winkler 1994), each 20 m from its nearest neighbor, around a series of 41 experimental ponds (0.08 ha each) and a 4.8-ha lake. Each nest box was a standard bluebird box (with a floor about 13 cm square, walls 25-30 cm high and an entrance hole 3.8 cm in diameter) and was fitted with a conical metal predator guard. Nest boxes were cleaned of old nesting material prior to each season.

Beginning the third week of April each year, we inspected nest boxes every other day to monitor the amount of nest material in each box. "Target nests" were those nest boxes containing an amount of nesting material between about 25 grass strands and the equivalent of about one-half of a complete nest. Each morning, between 0230 and 0400 EST, we checked target nests to locate and capture roosting females. Capturing females that were in the early stages of nest building helped assure that they were not going to be laying within the next few days, but had already settled to breed at our site. (A nest ceased to be a target nest once a female was captured there or when the amount of nest material exceeded that of about one-half of a completed nest.) All captured birds were released inside the same box in which they were captured after about 10 min of processing. Most birds caught were returning adults that had been sexed and banded previously. Unbanded birds (18% [9 of 49] of those captured) were assumed to be females because we encountered few males (20% [8 of 40]) among captured birds of known sex. Known males were released without manipulation. Females generally were assigned alternately to the clip treatment or the control treatment in the order they were captured. The only purposeful exceptions to this protocol involved five individuals caught in 1994 that also were part of this experiment in 1993; they were put in the opposite group to which they belonged in 1993. These exceptions, as well as several others caused by imperfect communication between researchers capturing birds in the dark, early morning hours, resulted in unbalanced numbers of birds in the control and experimental groups (Table 1).

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 carpal joint to tip of longest primary feather) was measured to the nearest millimeter using a metal ruler with a wing stop. We recorded the condition of the captured females as measured by mass and several subjective fat scores. In 1993, two subcutaneous fat deposits were scored (the claviculo-coracoid [henceforth "furcular"] deposit and composite abdominal deposit) and, in 1994, birds were scored on each of seven subcutaneous fat deposits (Winkler and Allen in press) plus medio-ventral abdominal deposit and ischio-pubic deposit (King and Farner 1965). In 1993 and 1994, birds assigned to the clip treatment had every third primary feather (i.e. primaries 3, 6, and 9) from each wing removed near its base with scissors. In 1994, every third secondary feather (i.e. secondaries 1, 4, and 7) also was removed from birds in the clip treatment. All clip-treatment birds in 1994 and some clip-treatment birds in 1993 also had every third tail feather (i.e. rectrices 1 and 4) removed from each side of their tail. In 1993, some birds (26% [5 of 19]) were trapped at target nests with mist nets or nest traps later in the day (between 0630 and 1400). These birds were treated using the same protocol as birds caught in the early morning. Dates of initial captures at target nests in both seasons ranged from 22 April through 8 May. (The earliest clutches in our overall study population in 1993 and 1994 were initiated on 6 and 7 May, respectively.)

Clutch initiations were recorded during the nest checks when we noted nest-material levels. Nests containing a single egg when first encountered were assumed to have been initiated on the day the egg was found. Since egg dumping is virtually unknown in this population (Winkler unpubl. data), nests found with two eggs were assumed to have been initiated on the day before the eggs were found. Once a clutch was initiated, the eggs were weighed, and the nest was visited daily to record the mass of each new egg. We standardized clutch-initiation dates each year by subtracting the mean initiation date of all nonexperimental nests that year from the initiation date for each nest.

We captured females a second time either late in their egg-laying period (1993) or soon after clutch completion (1994) and measured condition again. Beginning with this second capture, an additional condition measure, the combined thickness of the pectoralis major and supracoracoideus muscles (henceforth "breast muscles") was added to the standard set of measurements recorded. This was measured with a Krautkramer-Branson Model USL 48 ultrasound thickness instrument using a 10 MHz contact transducer (cf. Newton 1993). An additional replicate of condition measurements was taken the third time females were captured, within one day of their eggs hatching (i.e. within one day of hatching of first egg). The final, fourth female capture occurred on the 11th day after first hatch, and all condition measurements were taken at that time. If the final female capture was unsuccessful on the scheduled day, then trapping attempts were continued until successful or were abandoned after the 14th day posthatching.

On the eighth day after hatching of the eggs, nestlings were weighed, were banded, and had their wing lengths measured. Nests with chicks were visited every two to three days to monitor the number of nestlings alive, and nests with fledging-age young were checked daily without opening the box until all living chicks had fledged. The total number of chicks fledged from a nest was adjusted by the number known to have died during the nestling stage and by the number of dead chicks found in the nest after fledging.

We performed a 1-h behavioral observation of parental care at each nest on the tenth day after hatch. (Visitation rates are near their maximum on day 10, and 1-h observation periods provided the best compromise between precision and limited observer hours available [Winkler 1991, unpubl. data].) Observations were made from an automobile or blind 10 to 15 m from the focal nest box, and the arrivals and departures of each parent were recorded on a laptop computer running an event-recorder program. We later calculated the total number of visits and the amount of time spent inside the nest box. When adverse weather conditions (i.e. light showers or worse) were encountered during an observation, we rescheduled the observation to later in the same day or on the following day, since bad weather can affect the foraging behavior of aerial insectivores. Observations were made only from 0430 to 0930 and 1230 to 1730, with the majority being completed in the morning. Throughout both seasons, observations on nests were balanced so that approximately equal numbers from each experimental group were completed within each 1-h segment of the daily observation period. In order to distinguish better between the parents at nests during behavioral observations in 1994, females were painted with a patch of light-colored acrylic paint on their back feathers or permanent felt-tip markers on their underparts at the capture when their eggs hatched.

We used SYSTAT (1992) for statistical analyses, except for Fisher's exact test, which was run using StatXact (CYTEL 1991). In conducting t-tests, we used tests based on separate variances because there were *a priori* reasons to expect that the variances of the control and treatment groups would be different. P-values are for two-tailed tests unless indicated otherwise. To evaluate the proportion of variance explained by our analyses of variance (ANOVAs), we report the adjusted multiple R^2 for each. ANOVAs were run with MGLH, and the P-values are based on Type III sums of squares, which reflect the effect of a predictor when the effects of all other predictors are controlled statistically.

RESULTS

Effects on female condition.—Clipping had a significant effect on the condition of females. Because we trapped females on several occasions during their nesting attempts, we have time trajectories of mass for each bird. These measurements are not independent and, thus, are not amenable to analysis by ANOVA. To reduce this interdependence problem, we calculated a separate regression of female mass on trapping date for each individual and then did ANOVAs on the slopes and intercepts of these regressions across females. In the ANOVA, on the slopes of female mass loss ($R^2 = 0.414$, $n = 34$) with year, treatment, and a year-by-treatment interaction as predictors, both year ($P = 0.001$) and treatment ($P = 0.025$) had significant effects, with no effect of the interaction ($P =$

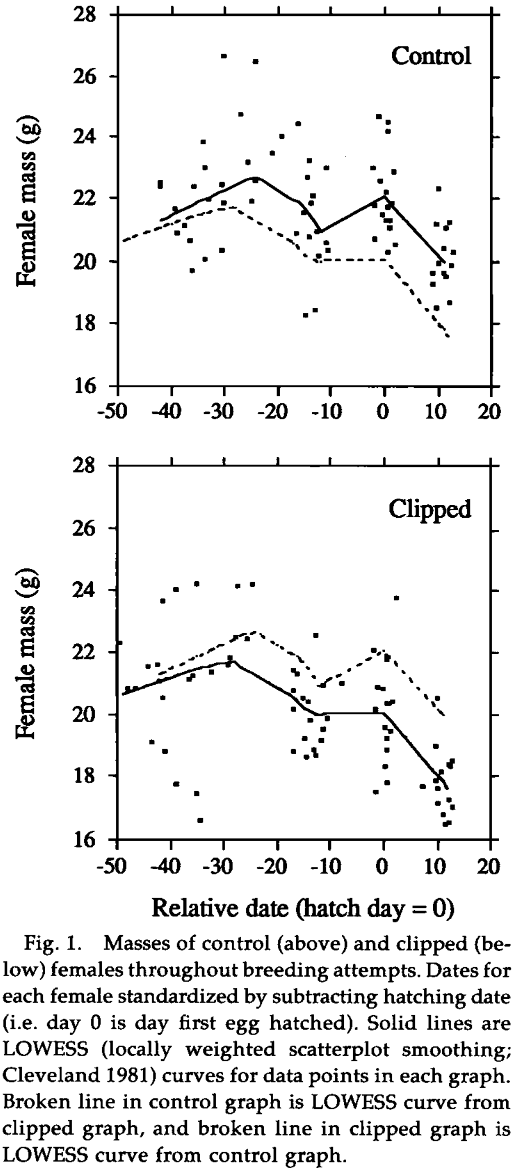

Fig. 1. Masses of control (above) and clipped (below) females throughout breeding attempts. Dates for each female standardized by subtracting hatching date (i.e. day 0 is day first egg hatched). Solid lines are LOWESS (locally weighted scatterplot smoothing; Cleveland 1981) curves for data points in each graph. Broken line in control graph is LOWESS curve from clipped graph, and broken line in clipped graph is LOWESS curve from control graph.

0.826). In the ANOVA on the intercepts ($R^2 = 0.340$, $n = 34$) with year, treatment, and a year-by-treatment interaction as predictors, year had the only significant effect ($P = 0.001$), with no significant effect of treatment ($P = 0.137$) or the interaction ($P = 0.267$). Thus, females that had been clipped were not different in mass at their first capture and lost mass faster over the season than did control females (Fig. 1).

Given the more rapid mass loss in clipped females, we were interested in determining which body components decreased most strongly. The breast muscles of females in both experimental groups decreased in thickness over the reproductive season. Clipped females tended to have thinner breast muscles, and experimental groups showed significant or nearly significant differences at captures when the eggs hatched ($t_{17,15} = 3.485$, $P = 0.002$) and when the chicks were 12 days old ($t_{13,14} = 1.909$, $P = 0.068$). However, analyses of the individual regression slopes and intercepts of breast-muscle thickness analogous to the mass analysis above revealed no significant effects of treatment. The ANOVA on the slope of breast-muscle thickness ($R^2 = 0.171$, $n = 32$) revealed year ($P = 0.030$) as the only significant effect, while treatment ($P = 0.535$) and the year-by-treatment interaction ($P = 0.611$) were not significant. Similarly, the ANOVA on the intercept of breast-muscle thickness ($R^2 = 0.199$, $n = 32$) revealed year ($P = 0.017$) as the only significant effect, while treatment ($P = 0.705$) and the year-by-treatment interaction ($P = 0.540$) were not significant.

Because our fat measures were categorical scores rather than measurements, we could not perform the within-individual regressions for this body component as we did for mass and muscle thickness. To analyze total-visible fat stores, we summed all scores for an individual at a given capture and tested whether the birds in the treatment groups had different rank sums. Because of the different fat deposits scored in 1993 and 1994, there were two data sets that could be used for this analysis: one for females from both 1993 and 1994, but incorporating only composite abdominal and furcular fat scores; and a second, using females only from 1994, but incorporating all nine fat scores. For both data sets and all breeding stages, clipped females averaged lower fat scores than did control females. However, the first data set revealed no significant differences in the fat scores of females just beginning to incubate (Mann-Whitney $U_{37} = 108.5$, $P = 0.051$) or at hatching (Mann-Whitney $U_{34} = 111.5$, $P = 0.236$), but it showed a difference when the chicks were 12 days old (Mann-Whitney $U_{28} = 35.0$, $P = 0.003$). The second data set, which had a smaller sample size but more comprehensive fat measures, also revealed no differences in the fat scores of females when they were just beginning to incubate (Mann-Whitney $U_{19} = 52.0$, $P = 0.567$) or at hatching (Mann-Whitney $U_{19} = 61.5$, $P = 0.170$), but did show a difference when the chicks were 12 days old (Mann-Whitney $U_{16} = 55.0$, $P =$

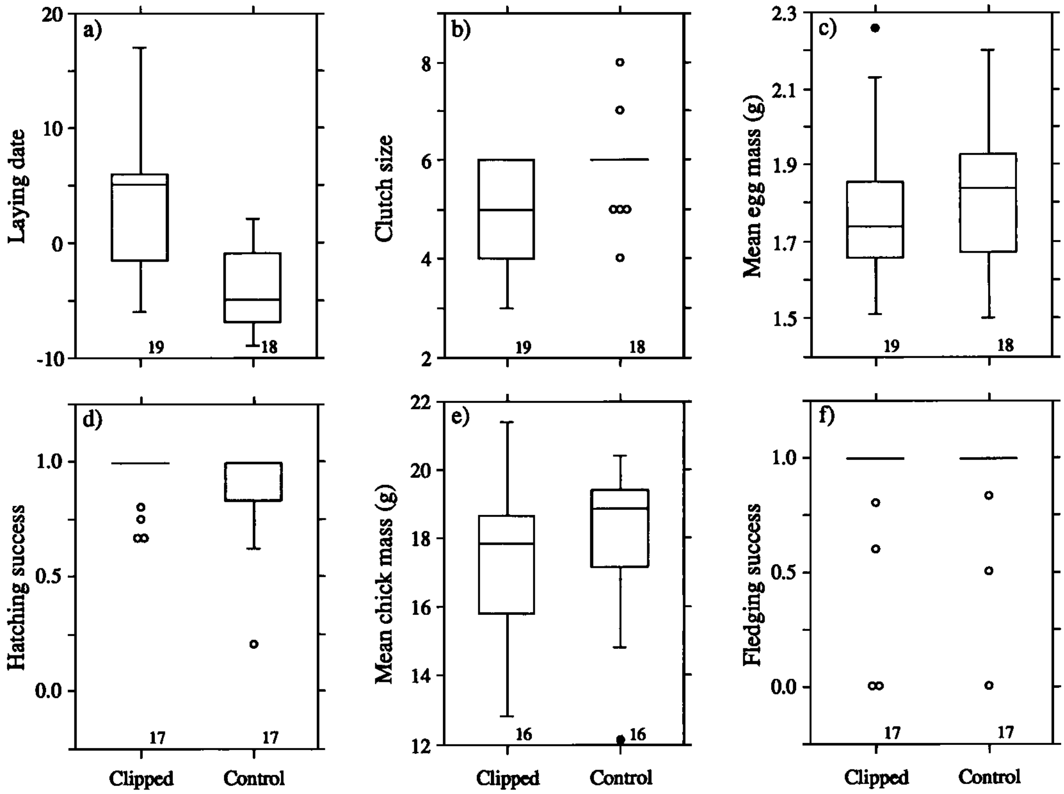

Fig. 2. Comparisons of clipped and control females for: (a) standardized laying date, (b) clutch size, (c) mean egg mass of clutches, (d) hatching success (no. eggs hatched/clutch size), (e) mean chick mass of broods measured eight days after hatching, (f) fledging success (no. chicks fledged/brood size). Figures plotted are Tukey box plots (see Velleman and Hoaglin 1981) with sample sizes beneath each plot. Horizontal line bisecting each box is median (not the mean), and upper and lower edges of each box are midpoints of those data above and below overall median (i.e. box encompasses central half of data, or interquartile range). Whiskers above and below boxes extend to most extreme data value that is still within 1.5 times interquartile range either side of median. Values more than 1.5 times the interquartile range above or below median plotted as filled circles, and those more than 2.5 times interquartile range above or below plotted as open circles. Extreme data points with tied values outside interquartile range are displaced slightly to allow all data to be seen.

0.013). Even though this analysis did not correct for the temporal interdependence of the data from the same females, we feel that the results indicate an effect of clipping on fat stores that parallels its effects on mass (Fig. 1).

Effects on egg laying.—Of the 26 females clipped in 1993 and 1994, 19 (73%) were known to have laid eggs during the season they were clipped (Table 1). Of the 20 control females in both years, 18 (90%) laid eggs. Although this is a suggestive difference, it was not significant (for both years pooled, $X^2 = 0.221$, $P = 0.638$). Females with their feathers clipped before egg laying laid later in the season than did control females (Fig. 2a; $\bar{x}_{\text{clipped}} = 21.63$ days, $\bar{x}_{\text{control}} = 14.27$ days; $t_{19,18} = 3.468$, $P = 0.002$). Clipped females also laid significantly smaller clutches (Fig. 2b; $\bar{x}_{\text{clipped}} = 4.74$ eggs, $\bar{x}_{\text{control}} = 5.89$ eggs; $t_{19,18} = 3.510$, $P = 0.001$), but the masses of the individual eggs that they laid were not significantly smaller than those of control females (Fig. 2c; $\bar{x}_{\text{clipped}} = 1.78$ g, $\bar{x}_{\text{control}} = 1.83$ g; $t_{19,18} = 0.753$, $P = 0.456$).

Because there is a strong correlation between clutch size and laying date in this species (Stutchbury and Robertson 1988, Winkler and Allen in press), we tested whether the smaller clutches of clipped females were due entirely to their later laying dates. In an ANOVA of clutch size ($R^2 = 0.464$, $n = 37$) with standardized laying date, year, treatment, and year-by-treatment interaction as predictors, year ($P = 0.026$) was the only significant effect, and treatment ($P = 0.062$) and laying date ($P = 0.093$) were nearly so. Because the clipped birds laid later than the controls, this ANOVA compared clutch sizes of the treatment groups over largely nonoverlapping ranges of one important predictor, laying date. Thus, we checked this result using the entire pool of unmanipulated females in both years as controls. (There were no significant differences between the clutch sizes of the females in the original control group and these other unmanipulated birds.) An ANOVA ($R^2 = 0.188$, $n = 292$) of clutch size, testing for the effects of laying date, year, treatment (clipped vs. all unmanipulated instead of clipped vs. control), and a year-by-treatment interaction revealed significant effects of laying date ($P < 0.001$), year ($P = 0.040$), and treatment ($P = 0.045$), but not of the year-by-treatment interaction ($P = 0.099$). Thus, when we compared clutch sizes among clipped and unclipped birds across the entire range of clutch initiation dates, clipping had a direct effect on clutch size in addition to its influence on laying date.

We analyzed the direct effects of condition on reproduction with ANOVAs using laying date and clutch size as dependent variables, and wing length, head-bill length, mass, furcular fat, composite abdominal fat, and breast muscle thickness as predictor variables (cf. Winkler and Allen in press). (Small sample sizes for these analyses precluded using all of the fat measures taken in 1994.) Using data from females captured at or near clutch completion, the ANOVA for laying date ($R^2 < 0.001$, $n = 34$) had no significant predictors, and the ANOVA for clutch size ($R^2 = 0.301$, $n = 34$) had laying date ($P = 0.004$) and mass ($P = 0.038$) as significant predictors. Thus, even though differences in the condition of clipped and control females may have begun to appear by the time of clutch completion, there was no indication that condition differences near the time of laying had any effect on laying date. The effect of mass on clutch size was much weaker than the effect of laying date, and none of the measures of specific body components known to be important in reproduction in other species had significant effects.

Effects on postlaying reproductive success.—Clipping had few effects on breeding performance after egg laying. Of all the females that laid eggs, only three failed to hatch any eggs (Table 1). One of these was a female accidentally included in another experiment after she had completed laying, but which caused her eggs to be spoiled (Winkler unpubl. data). Of the two females that abandoned during incubation, one was a control and one was clipped. Leaving these three females out of the analysis, the clipped and control groups did not differ in the proportions (Fig. 2d) or numbers of eggs that the females hatched. In an ANOVA of the numbers of chicks hatched ($R^2 = 0.551$, $n = 34$) with clutch size, standardized laying date, treatment, and year as predictors, only clutch size had a significant effect ($P < 0.001$) and the treatment effect was far from significant ($P = 0.663$).

Neither the proportions (Fig. 2f) nor numbers of chicks fledged differed between clipped and control groups; in an ANOVA ($R^2 = 0.687$, $n = 35$) of the effect of brood size, standardized laying date, treatment, and year as predictors of the numbers of chicks fledged, only brood size had a significant effect ($P < 0.001$) and the treatment effect again was far from significant ($P = 0.653$). Of the four pairs that hatched young and failed to fledge any chicks (Table 1), two were controls and two were clipped.

Treatment groups did not differ in the masses of chicks weighed on day 9 of their development (Fig. 2e); an ANOVA ($R^2 = 0.454$, $n = 35$) with year, treatment, standardized laying date, and brood size as predictors revealed only brood size as a significant ($P = 0.003$) predictor of mean chick mass; treatment was the worst predictor ($P = 0.522$). Qualitatively, this conclusion remains even if the low-mass chicks of the outlying control nest in Figure 2e are excluded from the analysis.

Effects on parental care.—Clipped females made fewer visits to the nest than control females (Fig. 3a). This difference, based on those nests where the sex of the adult was identified more than one-half of the time during parental-care observations, was significant ($\bar{x}_{\text{clipped}} = 6.54$ visits, $\bar{x}_{\text{control}} = 12.91$ visits; $t_{13,11} = 3.284$, $P = 0.006$) when the analysis was not controlled for other factors. In an ANOVA ($R^2 = 0.401$, $n = 24$) with treatment, brood size, hatching date, and year as predictors of the rate of female visits to the nest, treatment was no longer significant ($P = 0.069$); however, it was the only predictor with a P-value less than 0.25. We place greater em-

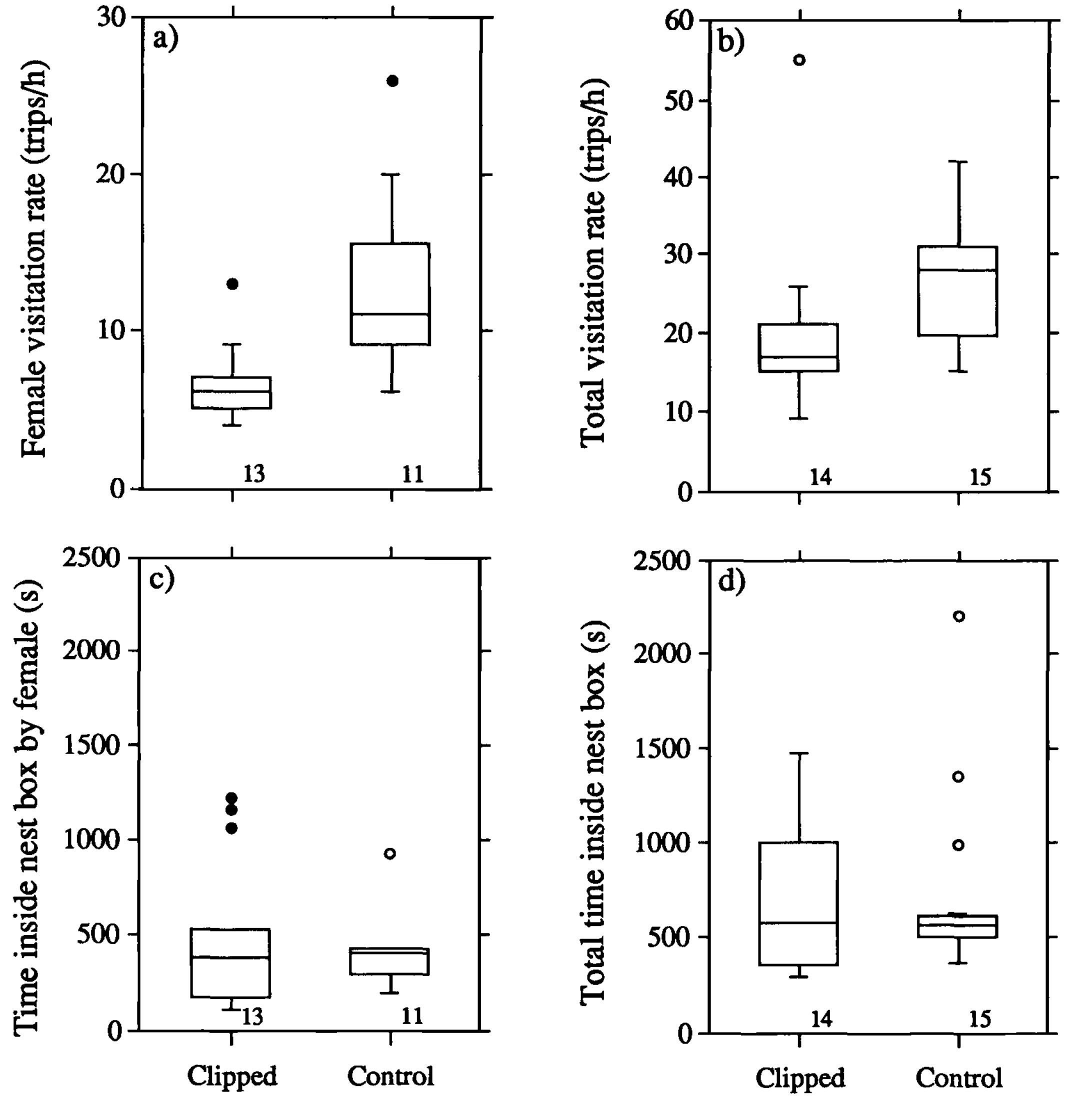

Fig. 3. Comparisons of clipped and control females for: (a) female visitation rate, (b) sum of visitation rates for female and her mate, (c) time spent inside nest box by female, and (d) total time spent inside nest box by both adults. All measures derived from observations 10 days after hatching. Sample size noted beneath each plot. Different vertical scales used in panels *a* and *b*. Only those nests in which adults sexed on more than one-half of nest visits during observation are included in panels *a* and *c*. All other conventions for data plotting as in Figure 2.

phasis on the *t*-test in this case because of the limited degrees of freedom available for the ANOVA.

Pairs of swallows with clipped females averaged fewer feeding trips to their nest boxes during our observation than did control pairs (Fig. 3b); however, these differences were significant only if the extreme outlier in the clipping group (Fig. 3b) was excluded from the analysis. The ANOVA ($R^2 = 0.446$, $n = 29$) with year, hatching date, treatment, and brood size as predictors of the total visitation rate for the pair revealed brood size ($P = 0.043$) and treatment ($P = 0.011$) as the only significant effects. If the outlier in Figure 3b was included, the ANOVA P-value for treatment drops to 0.130 and no other predictors retained any significant effect.

Treatment effects on the time spent inside the nest box were weaker, both for females (Fig. 3c) and pairs (Fig. 3d). An ANOVA ($R^2 = 0.326$, $n = 23$) with year, hatching date, treatment, and brood size as predictors of total time the female spent inside the box showed a significant effect only of brood size ($P = 0.035$) and no effect of treatment ($P = 0.487$). Similarly, an ANOVA ($R^2 = 0.343$, $n = 30$) with year, hatching date, treatment, and brood size as predictors of total time the adults spent inside the box showed significant effects of hatching date ($P = 0.022$) and brood size ($P = 0.004$), and a nearly significant effect of year ($P = 0.055$), but no effect of treatment ($P = 0.952$). Thus, there is no indication that clipped females or their mates spent more time inside their boxes because of fatigue resulting from feeding a brood with one handicapped parent. Neither is there any indication that clipped females or their mates spent less time in their box because of increased time spent foraging.

Effects on female return rates.—Pooling data from returns of females in 1994 and 1995, 5 (19%) of 26 clipped females were known to survive to the following breeding season. Control females returned at a much higher rate; 11 (48%) of 21 were captured in the subsequent season. This difference was significant with a one-tailed test (Fisher's exact test statistic = 4.192, $P = 0.031$).

DISCUSSION

Our experiments are the converse of those done on many other species (reviewed in Meijer et al. 1990) in which food has been supplemented prior to laying. Even though we did not manipulate food directly, it seems safe to conclude that altered foraging success leads to altered laying dates. One of the advantages of delaying rather than advancing laying dates is that most birds are being altered so as to breed at the same time as other, unmanipulated birds in the population. It also has the advantage that one need not worry about the appropriateness of the supplemental food or the possibility that supplemented birds may be constrained by some unmeasurable factor and unable to lay larger clutches. In this context, our study revealed significant effects of reduced foraging success on both laying date and clutch size, paradoxically, a result found in few food-supplementation experiments (see Meijer et al. 1990:table 1). It would be interesting to attempt handicapping experiments on other species of varying ecologies, since it may be that, as aerial foragers, swallows are much more sensitive to such manipulation than would be foliage gleaners or ground foragers.

We need to consider an alternative interpretation of the results discussed so far. The observed delay in laying date may not be due to a depression in foraging ability, but rather to a reduction in attractiveness to potential mates or effectiveness in other social interactions caused by clipping. Similar effects have been observed when males of other passerines have been handicapped (e.g. Lifjeld and Slagsvold 1988, Slagsvold and Lifjeld 1988, Møller 1994:fig. 4.4), but we feel that there are not likely to be problems in obtaining mates for handicapped female Tree Swallows. Even if altered social interactions could explain the delay in clutch initiation of the clipped females, it could not explain the decrease in the relative condition, clutch size, and subsequent parental care of the clipped females.

Another problem in interpretation arises when we compare our study with those of Slagsvold and Lifjeld, who have clipped the feathers of female Pied Flycatchers (*Ficedula hypoleuca;* 1988) and tits (1990) during incubation of their first clutch to study the sizes of replacement clutches. They found a decrease in replacement clutch size of clipped females in three of the four species studied and a difference in relaying date in two. They ascribed these results to an adjustment by the female of her replacement clutch to reductions in her capacity to feed chicks. We have argued (Winkler and Allen in press) that the seasonal decline in clutch size in Tree Swallows can be seen as a strategic response to variation in laying date, and our analyses indicate that much of the decrease in clutch size observed in our clipped birds is due to their later laying dates. Because Slagsvold and Lifjeld (1990) conducted their manipulations during incubation, their birds were laying their replacement clutches during periods of relative food abundance. By contrast, the swallows in our study were attempting to form eggs during the early nesting season, when food is quite limited (Winkler unpubl. data). This difference in protocol may well explain our observation of a large effect of clipping on laying date that Slagsvold and Lifjeld detected in only one-half their studies. However, the presence of a treatment effect on clutch size, even when laying date is controlled for in the analysis, suggests that there is more to be explained. The reduction in clutch size beyond the laying-date effect could be due, as Slagsvold and Lifjeld have suggested, to a reduced self-assessment of chick-rearing ability by the clipped females. However, we think it is more parsimonious at present to explain this further reduction in clutch size as a direct physiological consequence of the reduction in foraging efficiency caused by clipping.

We also interpret the declines in mass and condition observed in our study as physiological consequences of reduced foraging efficiency. However, mass declines of passerines during the breeding season must be interpreted with caution; several authors have suggested that such declines, at least in part, can be explained as the result of an optimization of mass and wing loading associated with efficient foraging for a brood of hungry offspring (Freed 1981, Norberg 1981), perhaps compounded by predation risk (e.g. Lima 1987). Such arguments are especially strong in a bird that spends as much time flying as does the Tree Swallow. It is difficult to know whether the greater mass decline of clipped birds is a reflection of the birds regulating their mass at an alternative optimal level or the reflection of simple physiological stress. In any event, the loss of mass will affect the clipped females' abilities to adjust to short-term adversities in weather or food supply, and the fact that clipped females had significantly lower probabilities of returning the following year indicates that the reductions in condition in the clipped females were indeed costly.

Our data showing that the mass and fledging success of chicks reared by clipped females were not reduced relative to those of controls indicate that the clipped females (and possibly their mates) were bearing the brunt of their reduced foraging efficiency, rather than passing any of these costs on to their offspring. It is difficult to reconcile these observations with the lower visitation rates of clipped females to their chicks. Perhaps clipped females were bringing larger loads of prey to their young in response to their increased travel and foraging costs.

No matter what the costs of clipping, our results provide strong support for an intrinsic biological linkage between clutch size and laying date (e.g. Daan et al. 1988, Price et al. 1988, Tinbergen and Daan 1990, Rowe et al. 1994). However, the results of the present study, together with those from a parallel study of unmanipulated birds (Winkler and Allen in press) indicate that the physiological condition of the female does not play a primary role in this biological linkage. In the present study, we detected no direct effect of the female's condition near the time of clutch completion on laying date. Although there was a significant effect of mass on clutch size, it is imprudent to interpret this mass effect alone as a very strong indicator of a bird's condition. This effect could include aspects of body size that are not captured by the wing and head-bill measurements, as well as variation in resources that were not detected in our measures of other components of the body (i.e. muscle and fat). In any event, the effect of mass on clutch size was much weaker than the effect of laying date, and this suggests that a very large part of the clutch-size decision is being made independent of the dictates of the female's condition (cf. Winkler and Allen in press). Feather clipping eventually did have a strong effect on female condition, but much of this effect was not manifested until well after the eggs were laid. Clipping presumably impaired foraging efficiency immediately after the manipulation, and the change in foraging efficiency alone appears to be adequate to explain the delay in laying and a large amount of the reduction in clutch size. The availability of aerial insects at the Ithaca site increases throughout the laying period (Winkler unpubl. data), and clipped females appear to be waiting to lay until the increase in food availability compensates, in part, for their decreased foraging efficiency. These results from clipping experiments thus reinforce the suggestion from our work on unmanipulated birds (Winkler and Allen in press) that Tree Swallows are essentially income breeders (sensu Drent and Daan 1980), basing their early-season reproductive decisions largely on their success in foraging rather than large somatic stores of energy and resources.

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