

Size, condition, and territory ownership in male tree swallows (*Tachycineta bicolor*)

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Male tree swallow (*Tachycineta bicolor*) territory owners and floaters were compared in terms of size and nutritional condition to test the resource holding potential hypothesis. Owners were larger than floaters when compared using six morphological measurements. There were no differences in dry mass, ash, or fat content, but territory owners were heavier and had larger protein reserves than floaters. Territory owners may be those individuals who win intrasexual conflicts for the possession of nest boxes, or those who, because of their better nutritional condition, can arrive at the breeding grounds earlier to secure a territory.

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Dans le but de tester l'hypothèse du potentiel d'accapement des ressources, la taille et les réserves nutritives ont été comparées chez deux catégories de mâles de l'Hirondelle bicolor (*Tachycineta bicolor*), les mâles territoriaux et les reproducteurs non cantonnés. Une analyse basée sur six mesures corporelles a révélé que les mâles territoriaux étaient de plus grande taille que les reproducteurs non cantonnés. Les deux catégories de mâles ne différaient pas quant à la quantité de gras ou de cendres ou quant à la masse sèche, mais les mâles territoriaux étaient plus lourds et possédaient une plus importante réserve de protéines. Il est possible que les mâles territoriaux soient ceux qui remportent les conflits intrasexuels afin d'obtenir l'accès aux nichoirs, ou alors leur meilleure condition physique leur permet d'arriver plus tôt sur les lieux de nidification et d'accaparer ainsi les territoires.

Introduction

Many species of birds require territories for reproduction; potential breeders unable to obtain territories are referred to as floaters (Brown 1969). The resource-holding potential (RHP) hypothesis (Parker 1974) proposes that certain individuals become territory owners because they are intrinsically better competitors. However, several studies comparing territory owners and floaters have failed to find the morphological (Hannon and Roland 1984; Eckert and Weatherhead 1987a; Shutler and Weatherhead 1991) or behavioural (Yasukawa 1979; Shutler and Weatherhead 1991) differences predicted by the RHP hypothesis.

Tree swallows (*Tachycineta bicolor*) are well suited to an examination of this hypothesis. The availability of nest sites severely limits their populations (Kuerzi 1941; Holroyd 1975), and swallows readily nest where nest boxes are provided. The colony used in this study was located around two sewage lagoons, where the high abundance of aerial insects (Quinney et al. 1986; Hussell and Quinney 1987), the main food source of swallows, might increase the competition for the available nest sites and make it more likely that clear differences between territory owners and floaters could be obtained. In this study, male tree swallows were used to test the idea that territory owners were larger and in better condition than floaters.

Methods

The study was carried out in 1990 at a tree swallow colony surrounding two sewage lagoons near Tweed, Ontario (44°29'N, 77°26'W); this colony has been occupied since 1983. Fifty-three nest boxes (14 × 14 × 33 cm, 3.85 cm diameter entry hole) were available.

Each box was fitted with a bird trap and stood approximately 1.5 m above ground, attached to a metal or wooden pole. The boxes were placed around the lagoons at approximately 20-m intervals, with the entrance holes all facing south.

Starting in late April all boxes were monitored daily for the first signs of nest building. As soon as nest building had begun at a nest box, beginning in early May, the resident male was removed, and his replacement was removed within the following 2 days. Three second replacements and two third replacements were also included in the sample. Neighbouring males were not observed breaking pair bonds or taking possession of boxes from which males were removed, so all replacements were considered former floaters. The birds were killed, weighed, and frozen (Canadian Wildlife Service scientific kill permit No. EK0624).

All birds obtained were measured and analyzed to determine if the original nest box occupants were larger and (or) in better nutritional condition (in terms of mass, fat, protein, and ash) than floaters. The following structural measurements were taken from each bird: wing chord length (mm), ninth primary feather length (mm), left tarsus length (0.01 mm), keel length (0.01 mm), body length (mm), and middle rectrix length (mm). The birds were then weighed to the nearest 0.01 g; they were reweighed after being plucked, and again after the reproductive organs and contents of the intestinal tract had been removed. The carcass and reproductive organs were dried to a constant mass. The dry carcass was weighed to obtain the dry mass, and its lipid content was determined by extraction with petroleum ether in a Soxhlet apparatus. The residue of this extraction, the lean dry mass (LDM), was then burned in a muffle furnace overnight to determine the amount of ash. This value was subtracted from the LDM to determine protein content (Dobush et al. 1985).

To test for differences in size a MANOVA was carried out using all six morphological measurements. A canonical discriminant analysis (CDA) (Pimentel 1979) was used to determine how the two groups were separated with respect to the six variables. To try to account for body size when comparing condition, a principal components analysis (PCA) was performed on the correlation matrix of the six morphological measurements and then each body-composition variable was regressed against the resulting first principal

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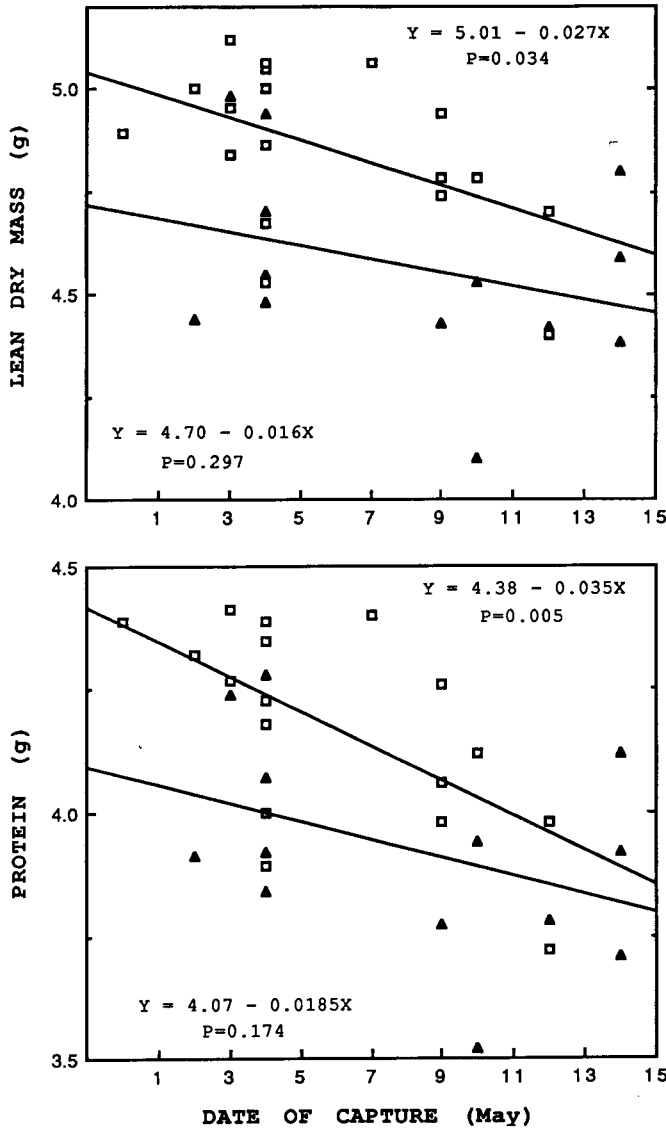


FIG. 1. Mean lean dry mass and protein content of territory owners and floaters with respect to date of capture. Included are the regression lines and the respective *P* values; □, owner; ▲, floater.

component (PC1), taken to be a measure of size (Rising and Somers 1989). Because food abundance changes during the season (Quinney et al. 1986), the effect of date of capture has to be taken into account when comparing nutritional condition. An ANCOVA with territory ownership as the grouping variable, date of capture as a covariate, and the territory ownership – date of capture interaction was used to test for differences in condition between territory owners and floaters. The interactions and date of capture effects were removed from the model if they were not significant. Despite the fact that not merely differences but rather directional predictions were being tested, all tests were kept conservative by using two-tailed tests.

Results

From April 30 to May 14, 1990, 31 males were collected: 18 original territory owners and 13 floaters. Two individuals were excluded from all multivariate analyses because of missing data. Territory owners were larger than floaters (MANOVA, *P* = 0.003); univariate *F* tests (Table 1) revealed that this was due to a difference in tarsus length. This is

TABLE 1. Size of territory owners and floater tree swallow males

| Variable | Owners | Floaters | <i>P</i> |
|------------------------|--------------|--------------|----------|
| Wing chord * | 122.4 (0.11) | 120.6 (0.93) | 0.212 |
| Ninth primary feather* | 95.2 (0.72) | 93.8 (1.18) | 0.359 |
| Keel* | 21.4 (0.196) | 21.4 (0.208) | 0.756 |
| Tarsus | 12.4 (0.08) | 11.8 (0.09) | 0.000 |
| Body* | 154.4 (0.82) | 152.8 (1.06) | 0.365 |
| Rectrix | 47.3 (0.34) | 46.5 (0.42) | 0.223 |

NOTE: A MANOVA using all the variables yielded a *P* value of 0.003. All values shown are the mean length in millimetres, with the standard error in parentheses, and two-tailed *P* values from univariate *F* tests; *N* = 31 (18 initial occupants and 13 floaters).

**N* = 30; in one bird the keel and vertebrae were broken and in another the wing feathers were worn.

TABLE 2. Loadings of PC1 and standardized discriminant function coefficients resulting from PCA and CDA, respectively

| Variable | PC1 | CDA |
|-----------------------|--------|--------|
| Wing chord length | 0.916 | 0.562 |
| Ninth primary feather | 0.872 | 0.170 |
| Tarsus length | -0.038 | 1.119 |
| Keel length | 0.040 | -0.381 |
| Body length | 0.738 | -0.167 |
| Rectrix length | 0.731 | -0.003 |
| Variance explained | 44.7% | 100% |

confirmed by the standardized coefficients of the first discriminant function resulting from a CDA (Table 2). Tarsus length had the lowest loading on PC1 but the highest standardized coefficient of the canonical discriminant function, meaning that tarsus length contributes little to the total variance but is the most useful variable for differentiating the two groups. Using canonical discriminant function scores, 25 out of 29 (86.2%) individuals were correctly classified as either territory holders or floaters.

To account for body size when comparing nutritional condition, a PCA was performed on the correlation matrix of the six morphological measurements and then each body-condition variable was regressed against the resulting PC1. PC1 was highly and positively loaded with all morphological variables except tarsus and keel length (Table 2), but none of the regressions of condition measures against PC1 was significant. Therefore, subsequent body-composition comparisons do not merely reflect differences in size.

There were no significant interaction effects between territorial status (owner or floater) and date of capture in any of the analyses; this means that territory ownership effects did not depend on the date of capture. Only for lean dry mass and protein content was the effect of date of capture significant (ANCOVA, *P* = 0.028 and 0.004, respectively). For both these variables there was a significant decrease (linear regression, *P* < 0.05) with later date of capture for territory owners, but not for floaters (Fig. 1). The lean dry mass and protein content of territory holders were significantly (ANCOVA, *P* = 0.004 and 0.008, respectively) greater than those of floater males (Fig. 1). Territory owners were heavier than floaters in terms of thawed mass, but not when carcass masses were compared (Table 3). There were no significant differences in dry mass, ash, or testis mass,

TABLE 3. Nutrient reserves and gonad development of territory owners and floaters

| Variable | Owners | Floaters | P |
|---------------|---------------|--------------|-------|
| Thawed mass | 21.2 (0.256) | 20.4 (0.257) | 0.029 |
| Carcass mass* | 18.3 (0.220) | 17.8 (0.286) | 0.112 |
| Dry mass | 6.29 (0.170) | 6.00 (0.158) | 0.249 |
| Fat | 1.43 (0.154) | 1.44 (0.134) | 0.979 |
| Ash | 0.674 (0.015) | 0.64 (0.015) | 0.109 |
| Testis (wet) | 0.554 (0.031) | 0.48 (0.025) | 0.094 |
| Testis (dry) | 0.079 (0.005) | 0.08 (0.005) | 0.892 |

NOTE: $N = 31$ (18 owners and 13 floaters). All values are given in grams. Shown are the means, with the standard error in parentheses, and two-tailed P values resulting from ANOVAs.

* Excluding feathers, gonads, and contents of alimentary tract.

although, except for fat, the means for territory owners were always greater than those for floaters (Table 3).

Discussion

Replacement male tree swallows were lighter (Table 3) and slightly smaller (Table 1) than the first occupants; the differences in mass were due to differences in protein content (Fig. 1). The regressions of body mass and other condition indexes on size (PC1) were not significant; this shows that, even controlling for size, territory owners are heavier than floaters. Although it may seem intuitively obvious that territory owners should be larger and in better condition than floaters, only one previous study has specifically reported size differences between territory owners and floaters in passerines (Hogstad 1989).

There are several possible interpretations of my findings. It is conceivable that replacement birds were not floaters at all, but birds from adjacent habitats that moved into optimal areas when opportunities became available. However, this is unlikely. It takes several years for a newly established colony of nest boxes to become fully occupied (Chapman 1935; Kuerzi 1941). Also, even when two colonies are located a mere 10 km apart, individuals seldom move between colonies (Stutchbury and Robertson 1985). Finally, some replacement males were observed taking possession of nest boxes within 30 min after the previous owner had been removed, and when extra nest boxes are provided (Stutchbury and Robertson 1985) individuals start defending the new boxes within hours. All this indicates that tree swallows concentrate their search for nesting cavities around very specific areas; replacement males were therefore almost certainly floaters from the same colony.

The larger size and better condition of territory owners could be the result of larger birds winning intrasexual confrontations for possession of nest boxes. In tree swallows the existence of a large floating population (Stutchbury and Robertson 1985) ensures keen competition for available nest sites, manifested by the high frequency of nest intrusions (Kuerzi 1941; Leffelaar and Robertson 1985). Large size can be an advantage in agonistic interactions (Searcy 1979; Watt 1986; Eckert and Weatherhead 1987b; Björklund 1989), and it might be sufficient to explain why territory holders are larger if all males arrived at the breeding grounds simultaneously or if prior ownership had no effect on challenges for territory ownership.

Site dominance associated with territory ownership has been found in other species (e.g., Davies 1978; Krebs 1982). Perhaps because of the limited availability of nest sites, male tree swallows are among the earliest spring arrivals, and this results in many dying because of cold weather (Chapman 1935; Dence 1946; Anderson 1965; Whitmore et al. 1977). This seems to indicate that although residents are sometimes evicted by intruders (Kuerzi 1941; Leffelaar and Robertson 1985), initial occupancy is important, or males would simply arrive a week or two later, as females do (Chapman 1935, Kuerzi 1941), when the weather is slightly better, and simply challenge earlier arrivals for the possession of nest boxes. If site dominance plays a role in territorial disputes among swallows, the larger size of territory owners could be the result of differences in arrival time, rather than the result of differences in success at intrasexual confrontations for available nest sites.

Under this more likely scenario, large size and good condition allow some birds to withstand harsh weather conditions. Low temperatures during April decrease the population density and activity of flying insects (Taylor 1963) and put swallows under thermal stress (Chapman 1935; Dence 1946; Anderson 1965; Whitmore et al. 1977). Under these conditions, large body size and large nutritional reserves would certainly be an advantage (Blem 1990) and would allow some individuals to arrive sooner and secure a territory. Accordingly, Arvidsson and Neergaard (1991) found that early-arriving willow warbler males were not bigger, but were in better condition, as determined by the ratios $\text{mass}^{1/3}/\text{tarsus}$ length and $\text{mass}^{1/3}/\text{wing chord length}$, than later arrivals.

Larger males might also be older birds. In willow warblers (*Phylloscopus trochilus*), Hogstad (1989) found that replacement males had shorter wing chords than the initial territory holders in one of the two sites he studied. Because the wing chord length of willow warbler males increases with age (Hogstad 1985), Hogstad (1989) concluded that his results were caused by differences in age. Other studies have also found that territorial birds are generally older (e.g., Zwickel 1980; Hannon 1983; Arcese and Smith 1985; Smith and Arcese 1989). However, except in a life-history context, territory ownership cannot be explained by age per se; we must instead seek specific age-related differences in behaviour or morphology to explain patterns of territory ownership. Without necessarily discarding age as a factor, this study presents evidence of tangible morphological differences in size and condition between territory owners and floaters.

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