

THE INFLUENCE OF FOOD ABUNDANCE ON NEST-BOX OCCUPANCY AND TERRITORY SIZE IN THE TREE SWALLOW, A SPECIES THAT DOES NOT DEFEND A FEEDING TERRITORY

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Abstract. In species that defend all-purpose breeding territories, territory size is usually inversely related to food abundance, but it is unclear whether this relationship results from reduced need to defend a large territory if food is abundant or from greater competitive pressure from conspecifics. Although studies of both breeding and winter territories suggest that competitive pressure is the proximate determinant of territory size, with food abundance acting indirectly by increasing the density of competitors, results are often equivocal because competitor density and food abundance tend to be positively correlated. In the Tree Swallow (*Tachycineta bicolor*), an aerial insectivore that defends only nest sites, defense of a food supply is not a determinant of territory size. I describe two series of experiments involving manipulation of nest-box spacing and measurements of insect abundance at four sites at and near Long Point, Ontario, Canada. Rates of occupancy of nest boxes spaced 24 m apart (beyond the normal range of territorial defense) were high at all sites (75–100%) and positively correlated with insect abundance. Occupancy of nest boxes placed 3 m apart (within the range Tree Swallows defend) was 28% to 100%, and the effect of close spacing on occupancy (attributable to territorial behavior) was also positively correlated with insect abundance. I conclude that the latter relationship must result from variation in competitive pressure because the food resource is not defended. Food abundance acts indirectly on occupancy and territory size by influencing the level of competitive pressure for nest boxes.

Key words: breeding, competition, food abundance, *Tachycineta bicolor*, territory, Tree Swallow.

Influencia de la Abundancia de Alimento en la Ocupación de Cajas Nido y en el Tamaño del Territorio en *Tachycineta bicolor*, una Especie que No Defiende un Territorio de Alimentación

Resumen. En las especies que defienden los territorios de cría multipropósito, el tamaño del territorio está usualmente inversamente relacionado con la abundancia de alimento, pero no está claro si esta relación es el resultado de una baja necesidad de defender un gran territorio si el alimento es abundante o de una presión competitiva mayor de aves de la misma especie. Aunque los estudios de los territorios de cría e invernada sugieren que la presión competitiva es la causa directa del tamaño del territorio, con la abundancia de alimento actuando indirectamente al incrementar la densidad de los competidores, los resultados son usualmente equívocos debido a que la densidad de los competidores y la abundancia de alimento tienden a estar positivamente correlacionados. En *Tachycineta bicolor*, una especie insectívora aérea que defiende sólo los sitios de nidificación, la defensa de una fuente de alimento no es determinante del tamaño del territorio. Describo dos series de experimentos que involucran la manipulación del espaciamiento de cajas nido y mediciones de la abundancia de insectos en cuatro sitios en y cerca de Long Point, Ontario, Canadá. Las tasas de ocupación de las cajas nido distanciadas a 24 m (más allá del rango normal de defensa del territorio) fueron altas en todos los sitios (75–100%) y estuvieron positivamente correlacionadas con la abundancia de insectos. La ocupación de las cajas nido distanciadas a 3 m (dentro del rango de defensa de *T. bicolor*) fue de 28% a 100% y el efecto del espaciamiento cercano en la ocupación (atribuible a comportamiento territorial) estuvo también positivamente correlacionado con la abundancia de insectos. Concluyo que esta última relación debe resultar de una variación en la presión competitiva, debido a que no se defiende el recurso alimenticio. La abundancia de alimento actúa indirectamente en la ocupación y en el tamaño del territorio influenciando el nivel de presión competitiva por las cajas nido.

INTRODUCTION

A territory has been broadly defined as “any defended area” (Hinde 1956). The typical passerine’s breeding territory is

a “large breeding area within which nesting, courtship and mating and most food-seeking usually occur” (Hinde 1956). This corresponds to the Type A “all-purpose” territory of both Hinde (1956) and Nice (1941). Nice described several other

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types of territory including Type B, “reproduction” (“Mating and Nesting, but Not Feeding Ground”), and Type D, “nest-site” (“restricted to narrow surroundings of nest”) territories. She categorized some swallows, of both colonial and less colonial species, as defending nest-site territories. Nice indicated that her categories are not rigid and suggested that the foregoing three types merge into each other. Nevertheless, all-purpose territories clearly differ from reproduction and nest-site territories because the former encompass the occupant’s main feeding ground, whereas the latter two do not.

The functions of territories were much debated in the 1940s and 1950s (Nice 1941, Hinde 1956, Tinbergen 1957, and references therein). One question that was raised and investigated then and later, but never fully resolved, was whether the size of an all-purpose territory is determined primarily by the abundance of food within the territory relative to the food requirements of the occupants (Stenger 1958), leading to smaller territories where food is abundant. Hixon (1980, 1987) developed models indicating that sexual selection should favor large territories under certain conditions, leading to the alternative hypothesis: high-quality territories should be larger, because their occupants can devote more time and energy to their defense when food is easy to get. However, several studies have shown sizes of breeding territory to be inversely related to food resources in both passerines (Stenger 1958, Cody and Cody 1972, Zach and Falls 1975, Seastedt and MacLean 1979) and raptors (Newton et al. 1986, Village 1987, Dunk and Cooper 1994). Moreover, an inverse relationship between food resources and territory size has been demonstrated in a shorebird and three other raptors in winter (Myers et al. 1979, Village 1982, 1987, Temeles 1987) and in hummingbirds and sunbirds defending local food resources (Gill and Wolf 1975, Eberhard and Ewald 1994). Also, attempts to find support for Hixon’s hypothesis in a passerine were unsuccessful, except under experimental conditions when supplementary food, hidden from intruders, was available at the time of territory establishment (Askenmo et al. 1994, Arvidsson et al. 1997).

Although these studies demonstrated that the sizes of feeding territories are often inversely related to food abundance within the territory, most did not provide evidence concerning the mechanism determining territory size. The relative importance of food abundance and population density (competitor abundance or intrusion pressure) on territory sizes has been investigated via multivariate analyses of observational data in wintering Sanderlings (*Calidris alba*) (Myers et al. 1979), Northern Harriers (*Circus cyaneus*) (Temeles 1987), and Common Kestrels (*Falco tinnunculus*) (Village 1982), and in breeding White-tailed Kites (*Elanus leucurus*) (Dunk and Cooper 1994). The weight of evidence from these studies supports the hypothesis that intruder pressure is the proximate factor influencing territory size and that prey abundance acts indirectly on territory size via intruder pressure. Nevertheless, “without experimental data, it was impossible to establish cause and effect” (Village 1982). Manipulations

of intrusion rates or food abundance in experiments with the Black-chinned Hummingbird (*Archilochus alexandri*) (Norton et al. 1982), Anna’s Hummingbird (*Calypte anna*) (Eberhard and Ewald 1994), and Spotted Towhee (*Pipilo maculatus*) (Franzblau and Collins 1980) were consistent with the hypothesis that intrusion rate was the primary proximate determinant of territory size, but these studies did not unequivocally exclude other explanations.

Studies of species that defend only their nest sites eliminate defense of a food resource as a determinant of territory size. Western Gulls (*Larus occidentalis*) defend breeding territories and forage elsewhere (Pierotti and Annett 1994). In a low-density colony, intrusion rate per unit area best explained variation in territory size (Ewald et al. 1980), but variation in food abundance could not have caused variation in territory size, directly or indirectly, because similar resources were available to all breeders.

Presumably, colonial or semi-colonial species like the Western Gull and swallows do not defend food resources for one or more reasons: (1) nest sites are limited and more important for successful breeding than is exclusive access to food, which may be distant from the nest site, (2) the food resource is difficult to defend in a relatively featureless 3-dimensional environment, and (3) the food supply is ephemeral, so defense of a larger territory provides no assurance of long-term exclusive access to food (Hinde 1956).

In this paper, I describe a study of the Tree Swallow (*Tachycineta bicolor*) that provides the first evidence that food abundance can also influence territory size in a species that does not defend a feeding territory. Tree Swallows are convenient research subjects (Jones 2003) because they are abundant and will nest close together in nest boxes. Both sexes defend a small area around a nesting cavity and forage for flying insects with other conspecifics in the surrounding undefended air space (Robertson et al. 1992). Resident pairs perch on or near their nest boxes and display to or vigorously chase intruders and any swallows flying by within a range of 10–15 m, especially those of the same sex (Robertson et al. 1992). Both sexes may concurrently defend two or more adjacent nest boxes or natural cavities (Robertson et al. 1992). Territory sizes can be manipulated by varying the distances between nest boxes. When available nest boxes are far apart, there are few, if any, interactions between adjacent pairs, but with closer spacing territorial behavior comes into play, and Tree Swallows prefer to nest as far as possible from conspecifics (Muldal et al. 1985). Moreover, cavity availability can limit opportunities to nest, and in many areas there are floating populations of nonbreeders ready to move into any new sites that become available (Holroyd 1975, Stutchbury and Robertson 1985, D. J. T. Hussell unpublished data). In southern Ontario, the region of my study, Tree Swallows are nearly always single-brooded (Hussell, 1983, 2003a), and territory establishment and egg laying are highly synchronous at any one site (Hussell and Quinney 1987). Therefore, competition

for territories (nest cavities) is also highly synchronous, making it possible to examine territory characteristics through manipulation of nest-box spacing. To investigate the effects of food abundance on the size of the Tree Swallow's "nest-site" territory, I describe the effects on occupancy (and territory sizes) of two series of different experimental manipulations of nest-box spacing at four sites at which I measured aerial insects' abundance.

METHODS

STUDY SITES

The four study sites and some of their characteristics have been described more fully by Hussell and Quinney (1987) and Hussell (2003b); all are in the vicinity of Port Rowan, Ontario, Canada (42° 37' N, 80° 27' W). The Sewage Lagoon site (SL) is ~0.5 km west of Port Rowan; nest boxes were on a wide grassy bank around two lagoons separated by an embankment 10 m wide (Fig. 1, 2). Backus Field (BF) is 3.25 km north-northwest of Port Rowan; nest boxes were on strips of uncultivated land planted with young trees among three cultivated fields (Fig. 1). Mud Creek (MC) is 1 km east of BF, in similar habitat; nest boxes were in and along the sides of a creek valley and adjacent to a hay field (Fig. 2). The Long Point site (LP) is about 33 km east of Port Rowan and 1 km from the eastern tip of the Long Point peninsula in Lake Erie; nest boxes were on grassy dunes with shallow ponds and scattered cottonwoods (*Populus deltoides*; Fig. 2). The LP, BF, SL, and MC sites were first occupied by Tree Swallows in 1969, 1976, 1977, and 1987, respectively.

Plywood nest boxes were ~1.5 m above the ground (or sometimes above water at LP) on steel poles in lines or grids

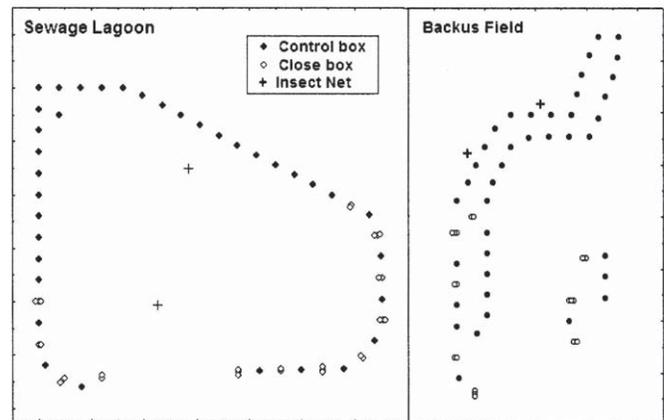


FIGURE 1. Arrangement of regular (control) and experimental (close) boxes and insect-sampling nets at Sewage Lagoon and Backus Field in 1984. Minor changes were made from 1985 to 1988 (see text). Control boxes were 24 m from their nearest neighbors. Close boxes were in groups of two or three and each box was 3 m from its nearest neighbor within its group.

(Fig. 1, 2). All nest boxes were of similar dimensions with a floor measuring 140 × 140 mm and an entrance 35 mm in diameter centered 155 mm above the floor. Except in the experiments described below, each nest box was ~24.4 m (hereafter 24 m) from its nearest neighbor.

The inter-box distance of 24 m was chosen when the LP site was established in 1969, following earlier casual observations that adjacent pairs did not interfere with each other at that distance. Consistent with that observation, the radius of Tree Swallow territories was estimated at 6–8 m, on the basis

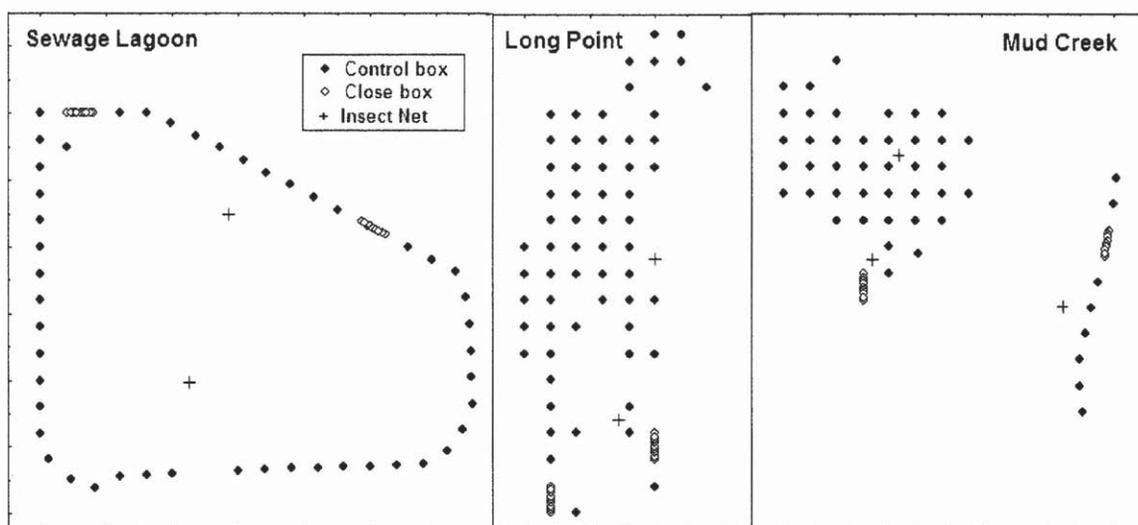


FIGURE 2. Arrangement of regular (control) and experimental (close) nest boxes and insect-sampling nets at Sewage Lagoon, Long Point, and Mud Creek in 1991. Minor changes were made in 1992 and 1993 (see text). Control boxes were 24 m from their nearest neighbors. Experimental close boxes were in two groups of nine boxes at each site and each box was 3 m from its nearest neighbor in a single straight line within each group.

of responses to models of conspecifics (Robertson and Gibbs 1982), or at least 10–15 m, presumably on the basis of general observations (R. J. Robertson in Robertson et al. 1992). Also, Tree Swallows nesting in groups of boxes 1–19 m apart tended to occupy boxes as far as possible from each other, but when their nearest neighbors were ≥ 36 m away they did not show any preferences for spacing (Muldal et al. 1985). Visibility of adjacent nest boxes can also affect occupancy rates (Mitchell and Robertson 1996). My nest boxes were all clearly visible from adjacent nest boxes, so visibility could not have influenced occupancy rates in my study.

EXPERIMENTS

Because territorial behavior occurs only in the immediate vicinity of the nest site, occupancy rates of closely spaced nest boxes are reliable indicators of the sizes of territories that Tree Swallows can successfully defend, provided that a population of floaters is available to move into unoccupied nest boxes (Stutchbury and Robertson 1985; unpublished data for SL and MC from 2001 to 2007 indicate large floating populations). Two series of experiments involving closely spaced nest boxes (3.05 m apart; hereafter 3 m) in 1984–1988 and 1991–1993 elucidated the effects of food abundance on “nest-site” territory size. The first series was not designed for that purpose, but the results indicated a positive relationship between food and occupancy rate (the inverse of territory size). The object of the second series was to determine whether the relationship between territory size and food abundance could be confirmed with a different nest-box arrangement.

In experiment 1 (1984–1988 at BF and SL), Terry Quinney set up one or two extra nest boxes 3 m from existing boxes and perpendicular to the existing lines of boxes spaced at 24 m, thereby forming groups of two or three closely spaced boxes (Fig. 1). His purpose was to induce polygyny by making it easier for a male to defend two nest boxes simultaneously. [Polygyny occurred occasionally in regular boxes at SL and LP, with two females occupying the same box simultaneously, but has never been recorded at BF or MC (Quinney 1983, D. J. T. Hussell, unpubl. data)]. With close spacing we expect adjacent boxes to be occupied by different pairs only via aggressiveness of intruders forcing previously established residents to reduce the sizes of their defended areas. In 1984, there were five “double” and three “triple” groups of boxes at BF, and six of each at SL. I have no record of when the extra boxes were added, but it was no later than 25 April, when regular nest checks started. In the following years, the numbers of closely spaced boxes available to swallows varied because of addition of new boxes, loss or disrepair of a few old ones, and, at BF, occupation of some boxes by other species, the Eastern Bluebird (*Sialis sialis*), House Wren (*Troglodytes aedon*), and House Sparrow (*Passer domesticus*). All boxes were removed from BF prior to the 1987 breeding season, but most of the “double” and “triple” groups remained at SL until 1988.

The number of closely spaced nest boxes (nearest neighbor 3 m away) available at BF in 1984, 1985, and 1986 was 19, 19, and 14, respectively; and at SL in 1984, 1985, 1986, 1987, and 1988 it was 30, 30, 29, 29, and 25, respectively. The number of nest boxes available as controls (24 m apart) varied from 34 to 36 at SL and from 33 to 37 at BF. Trapping of adults indicated that polygyny may have occurred infrequently (but was not rigorously confirmed) at SL but not at BF. At SL more than 90% of boxes that had nests appeared to be occupied by socially monogamous pairs.

In 1991, I set up 18 closely spaced nest boxes each at SL, MC, and LP (experiment 2). I randomly selected two locations in different parts of each site at which I placed seven new nest boxes at 3-m intervals in a straight line between two existing nest boxes (24 m apart) to make a total of nine closely spaced boxes at both locations at each site (Fig. 2). The extra boxes were added on 1 May at SL, on 2 May at MC, on 9 May at one LP location, and on 13 May at the second LP location. All of these closely spaced boxes remained in place in 1992 and 1993. In all years there were 48 regularly spaced controls at SL, 47–49 at MC, and 59–61 at LP. However, in 1991 many of the “control” boxes were used in another experiment that precluded their use for determining dates of clutch initiations. This reduced the number of controls used to determine timing of laying in 1991 to 24, 25, and 31, at SL, MC, and LP, respectively.

NEST-BOX OCCUPANCY AND TERRITORY SIZE

Because Tree Swallows that lack near neighbors normally defend only the airspace within a maximum of 10–15 m of their nest cavities (Robertson and Gibbs 1982), the defended area can be compressed permanently only when suitable nest cavities are closer than 20–30 m apart. It follows that occupancy rates of nest boxes spaced at 3 m must be influenced by territorial behavior and will be inversely related to territory size. Therefore, I used occupancy rates of closely spaced boxes as a surrogate for territory size. I sought additional support for this view by testing whether occupancy of closely spaced boxes was nonrandom, with the birds tending to nest as far apart as possible. I did not expect occupancy of my regularly spaced boxes to be significantly influenced by territory size because their spacing (24 m apart) was greater than the normal range of territorial behavior; instead, their occupancy rate may primarily reflect the quality of the site and motivation of the birds to nest there, in the absence of territorial constraints.

I considered a box occupied if a nest was built and at least two eggs were laid in it. (Single eggs sometimes appear to be “dumped” so I excluded them as evidence of occupancy.) I calculated the occupancy of regularly spaced control boxes or of closely spaced boxes as (number of occupied boxes)/(total number of available boxes), the relative occupancy of closely spaced boxes as (occupancy of closely spaced boxes)/(occupancy of regularly spaced boxes). To express occupancy rates as percentages, I multiplied occupancy and relative occupancy

by 100. Relative occupancy measures the proportion of occupied closely spaced boxes relative to what it would have been if they were occupied at the same rate as regularly spaced boxes, at the same site in the same year. For statistical analyses, I transformed occupancy rates to $\arcsin(\text{occupancy})^{1/2}$ and $\arcsin(\text{relative occupancy})^{1/2}$.

To study the relationship between territory size and food abundance, I defined site- and year-specific time periods during which I judged competition for nest boxes to be intense. Competition for nest boxes starts as soon as the swallows return in late March or April, is weather-dependent particularly early in the season (Robertson et al. 1992, D. J. T. Hussell unpubl. data), and becomes more intense as the height of nest building approaches. Nest-box defense continues intensively throughout the egg-laying and incubation stages but starts to wane once the young are hatched and both adults are occupied with feeding their nestlings (Robertson et al. 1992). Some vacancies were filled late in the season when early broods had fledged, or were close to fledging, and competition for nest boxes was greatly reduced. From the phenology of egg laying in regularly spaced control boxes, I chose to study the period starting 10 days before the 20th percentile of clutch initiations and ending 20 days after the 80th percentile of clutch initiations. Basing this period on 20th and 80th percentiles excluded extreme outliers. Nevertheless, this period always started on (rarely) or before the day that the first egg was laid in any nest and ended several days before the earliest broods fledged. Tree Swallows usually laid one egg per day, the most frequent clutch sizes were five and six eggs, and hatching usually started 12–14 days after clutch completion. Consequently about 80% of adults were feeding nestlings by 20 days following the 80th percentile of clutch initiations. I considered that clutch initiations within this interval represented relevant occupancy of a territory in both the closely spaced and control boxes. I used the same period to determine site- and year-specific measures of insect abundance.

INSECT ABUNDANCE

I trapped flying insects in two suspended conical nets near or among the nest boxes at each site, except at MC, where I used three nets in the more diverse habitat at that site (Fig. 1, 2). Nets were 2 m above ground (except one net 2 m above water at the edge of a pond at LP) and rotated in the wind so that the mouth always faced upwind. Insects were collected in a jar of 70% ethanol at the rear of each net; for more details see Hussell and Quinney (1987). The nets were operated for 8.86–15.67 hr per day (mean 12.00, SD 1.21, $n = 1109$) for samples used in this paper, from a maximum of approximately 16 hr of daylight foraging time in mid-June. I calculated the dry biomass of insects (between 1 and 13 mm in body length) in each net catch by the methods described by Hussell and Quinney (1987). I calculated daily estimates of the density of insect biomass in the air at net height at each site by dividing

the sum of the dry biomass of insects captured in the nets by the total km of wind estimated to have passed those nets (by a method similar to that described in Hussell and Quinney 1987) and expressed it as mg dry biomass/100 km wind. (The wind adjustment converts the daily capture rate into an index of the average density of dry biomass of insects in the air at the net sites.)

Tree Swallows forage at high altitudes, often venturing above 13 m and sometimes over 30 m (Holroyd 1972). Timed observations at LP during the breeding season showed that Tree Swallows spent 47% of their foraging time below 4.6 m and 53% between 4.6 and 13.7 m (Holroyd 1972). At SL and LP they usually they foraged above the nest boxes, or over adjacent ponds, and rarely went elsewhere except when foraging conditions were extremely poor (D. J. T. Hussell, unpubl. obs.). Although my nets are below the swallows' average foraging height, insect biomass indices (IBIs) derived from the net captures are positively correlated with mean clutch sizes (Hussell and Quinney 1987) and growth rates of young (Quinney et al. 1986) and negatively correlated with intensity of nestlings' begging (Hussell 1988). Moreover, the nets trap many of the same insects that the swallows feed to their nestlings (Quinney and Ankney 1985). These findings indicate that IBIs measured at my nets are relevant measures of food available to swallows at my sites.

IBIs for the site- and year-specific periods of territory defense, defined above, were calculated as the means of $\ln(M + 0.1)$, where M is the daily measurement of insect biomass in mg dry biomass/100 km wind. I used this "geometric mean" IBI because daily measurements of insect biomass were skewed to the right (Hussell and Quinney 1987). All statistical analyses were done in the transformed scale, but for presentation of results, I reconverted mean IBIs to the original scale by taking the exponent of mean $\ln(M + 0.1)$ and subtracting 0.1.

Times of operation of the insect nets at SL and BF were missing for 1985, so it was impossible to estimate the daily total wind that passed through the nets during their hours of operation. However, total biomasses of net captures were available for 53 days between 28 April and 27 June at SL and for 16 days between 28 April and 10 June at BF. Also, the total wind at the nets was available for an arbitrary period of 16 hr (04:20–20:20 Eastern Standard Time) corresponding approximately to daylight hours in mid-June. I used these data to estimate IBIs for 1985, assuming that the average time of operation of the nets was similar to that in 1984 and 1986, i.e., 12.73 hr, the mean time that the nets were operated on equivalent seasonal dates in those two years. The known IBIs for those dates in 1984 and 1986 were predicted accurately ($R^2 = 0.996$, $P < 0.001$, $n = 134$) with the following regression: $I = a + b_1 \ln B + b_2 (\ln B)^2 + b_3 (\ln B)^3 + b_4 (\ln B)^4$, where I is the known IBI [i.e., $\ln(M + 0.1)$, as defined previously], $B = 100 \times (m/w) \times (16/12.73)$, m is the daily total dry biomass of captures, and w is the estimated 16-hr total km of wind at

the two or three nets at each site. I used the regression estimates of a , b_1 , b_2 , b_3 , and b_4 to estimate daily IBIs for days with total biomass data at BF and SL in 1985.

After the preceding estimation of IBIs for 1985, there were still 45 site-days missing insect data on the relevant dates in 1984–1986 at BF and 1984–1988 at SL (mean 2.4 missing days per site-year, except BF in 1985, which was missing 28 of 40 days), and there were 20 site-days missing insect data on relevant dates in 1991–1993 (mean 2.2 days per site-year). I estimated missing IBIs from a covariance analysis of known IBIs, in which site-years were factors and site-specific date variables (date and date²) were covariates. Third-order site–date variables and several weather variables were available for stepwise inclusion at $P < 0.05$. Because they include the effects of year, season date, and weather, these models provide better estimates of daily insect abundance than do any simpler models (such as the average of all nonmissing values for the site-year). To estimate the missing insect data for 1984–1988, I used all IBIs measured from 28 April to 21 June 1978–1986 at BF and 1982–1990 at SL, including as “measured” the accurate estimates for BF and SL in 1985 ($R^2 = 0.65$, $n = 845$, $P < 0.0001$). To estimate IBIs missing for 1991–1993, I used all measured IBIs between 28 April and 21 June 1989–1995 ($R^2 = 0.56$, $n = 1009$, $P < 0.0001$).

RESULTS

OCCUPANCY OF CONTROL NEST BOXES

Occupancy of regularly spaced control nest boxes was $\geq 75\%$ at all sites in all years. At sites with high insect abundance (LP and SL),

occupancy was always $\geq 98\%$, but it varied between 75% and 96% at sites with relatively low insect abundance (Tables 1, 2). Occupancy rate was positively correlated with insect abundance (occupancy versus mean IBI, Spearman rank correlation, $r_s = 0.80$, $P = 0.001$, $n = 17$). Therefore it is necessary to use relative occupancy (not occupancy) to assess the effect of insect abundance on territory size at the closely spaced nest boxes, because relative occupancy excludes the effects of between-site differences in occupancy that are consequences of the different attractiveness (occupancy densities) of the sites, unrelated to territorial behavior.

SPACING OF OCCUPANTS OF CLOSELY SPACED NEST BOXES

Experiment 1. At SL only 2 of 143 opportunities for occupancy (summed over the 5 years, 1984–1988) were unused, both in 1984. Therefore, there was little opportunity to detect evidence of spacing behavior, and the distribution of occupied boxes did not differ from random ($\chi^2 = 0.1$, $P > 0.75$, Table 3).

Over the 3 years at BF, there were 54 opportunities for occupancy in 31 pairs of closely spaced boxes. Twenty-six of the 54 opportunities were unused. Distribution of occupancy among the pairs of boxes was not random, with a preponderance of only one of the two boxes occupied and a deficiency of pairs in which none or both boxes were occupied ($\chi^2 = 7.9$, $P < 0.01$, Table 3), indicating that at BF swallows tended to avoid each other in closely spaced boxes.

Experiment 2. The 18 closely spaced boxes at each site yielded 16 pairs of adjacent boxes spaced 3 m apart, in each of the 3 years, or 48 pairs at each site over the 3 years.

TABLE 1. Dates, nest-box occupancy, and insect biomass indices (IBI) for experiment 1. Means for all years at each site are shown in boldface.

Site and year(s)	Dates ^a	Occupancy		Relative occupancy ^d %	Mean IBI mg/100 km
		Control boxes ^b % (<i>n</i>)	Close boxes ^c % (<i>n</i>)		
Sewage Lagoon					
1984	10 May–13 Jun	100 (34)	93 (30)	93	20.63
1985	3 May–6 Jun	100 (34)	100 (30)	100	42.93
1986	4 May–7 Jun	100 (35)	97 (29)	97	45.76
1987	4 May–7 Jun	100 (35)	100 (29)	100	12.02
1988	5 May–9 Jun	100 (36)	100 (25)	100	21.76
All		100	98	98	28.62
Backus Field					
1984	13 May–16 Jun	92 (36)	53 (19)	57	2.41
1985	3 May–11 Jun	88 (33)	53 (19)	60	3.18
1986	3 May–7 Jun	75 (37)	50 (19)	66	2.07
All		85	52	61	2.55

^aInterval during which occupancy and insect abundance were determined, 10 days before the 20th percentile to 20 days after the 80th percentile of clutch initiations.

^bControl boxes were 24 m from their nearest neighbor; n = total number available.

^cClose boxes were 3 m from their nearest neighbor; n = total number available.

^d $100 \times (\text{occupancy of close boxes}) / (\text{occupancy of control boxes})$.

TABLE 2. Dates, nest-box occupancy, and insect biomass indices (IBI) for experiment 2. Means for all years at each site are shown in boldface.

Site and year(s)	Dates ^a	Occupancy		Relative occupancy ^d %	Mean IBI mg/100 km
		Control boxes ^b % (n)	Close boxes ^c % (n)		
Sewage Lagoon					
1991	5 May–6 Jun	100 (48)	67 (18)	67	13.97
1992	3 May–5 Jun	100 (48)	78 (18)	78	10.63
1993	30 Apr–3 Jun	100 (48)	83 (18)	83	5.69
All		100	76	76	10.10
Mud Creek					
1991	5 May–6 Jun	96 (47)	28 (18)	29	5.01
1992	3 May–7 Jul	92 (47)	39 (18)	43	5.18
1993	30 Apr–5 Jun	80 (49)	50 (18)	63	2.64
All		89	39	45	4.27
Long Point					
1991	7 May–11 Jun	100 (61)	61 (18)	61	7.51
1992	9 May–12 Jun	100 (59)	72 (18)	72	3.93
1993	5 May–13 Jun	98 (60)	89 (18)	90	5.90
All		99	74	75	5.78

^aInterval during which occupancy and insect abundance were determined, 10 days before the 20th percentile to 20 days after the 80th percentile of clutch initiations.

^bControl boxes were 24 m from their nearest neighbor; n = total number available.

^cClose boxes were 3 m from their nearest neighbor; n = total number available.

^d100 × (occupancy of close boxes)/(occupancy of control boxes).

At SL, 12, 14, and 15 of the 18 closely spaced boxes were occupied in 1991, 1992, and 1993, respectively. Again, singly occupied pairs of adjacent boxes outnumbered both doubly occupied and doubly unoccupied pairs, but the difference from a random distribution was nonsignificant ($\chi^2 = 3.4, 0.10 > P > 0.05$; Table 4).

At LP, 11, 13, and 16 of the 18 closely spaced boxes were occupied in 1991, 1992, and 1993, respectively. The pattern of occupancy of pairs of adjacent boxes did not differ from that expected if the boxes were occupied at random ($\chi^2 = 0.5, P > 0.25$, Table 4).

At MC, 5, 7, and 9 of the 18 closely spaced boxes were occupied in 1991, 1992, and 1993, respectively. In this case, occupancy

of only one of the pair of boxes was significantly greater than expected from a random distribution of swallows among the closely spaced pairs of boxes ($\chi^2 = 5.1, P < 0.05$, Table 4), indicating that at MC Tree Swallows tended to avoid nesting close to each other.

OCCUPANCY OF CLOSELY SPACED NEXT BOXES

Experiment 1. In the 1984–1988 experiment, occupancy rates of closely spaced boxes were higher at SL than BF and were associated with insect abundance: annual IBIs averaged over

TABLE 3. Distribution of breeding Tree Swallows among pairs of closely spaced nest boxes in experiment 1.

Site	No. occupied ^a			Totals
	2	1	0	
Sewage Lagoon (1984–1988)				
Observed	83	2	0	85
Expected	82.64	2.32	0.04	85
Backus Field (1984–1986)				
Observed	5	24	2	31
Expected	7.89	16.38	6.73	31

^aThe body of the table shows observed and expected numbers of pairs of closely spaced nest boxes that were occupied by 2, 1, or 0 pairs of swallows.

TABLE 4. Distribution of breeding Tree Swallows among pairs of closely spaced nest boxes in experiment 2, 1991–1993.

Site	No. occupied ^a			Totals
	2	1	0	
Sewage Lagoon				
Observed	23	24	1	48
Expected	27.33	18.22	2.44	48
Long Point				
Observed	26	18	4	48
Expected	26.00	19.11	2.89	48
Mud Creek				
Observed	2	31	15	48
Expected	6.44	24.44	17.11	48

^aThe body of the table shows observed and expected numbers of pairs of closely spaced nest boxes that were occupied by 2, 1, or 0 pairs of swallows.

10 times greater at SL than at BF (Table 1). Both sites and all years considered together, relative occupancy was positively correlated with IBI ($r = 0.87$, $P = 0.005$, $n = 8$).

Experiment 2. In the 1991–1993 experiment, rates of occupancy of closely spaced boxes were again positively associated with insect abundance. There was no overlap in annual occupancy or insect abundance between SL and MC, the sites with consistently the highest and lowest occupancy and insect abundance, respectively (Table 2). LP was intermediate in mean IBI but overlapped with both of the other sites in different years. All three sites and three years considered together, relative occupancy was positively, but not significantly, correlated with IBI ($r = 0.18$, $P = 0.64$, $n = 9$).

Both experiments. With data from both experiments combined, relative occupancy was positively correlated with IBI ($r = 0.72$, $P = 0.001$, $n = 17$; Fig. 3).

I examined whether the experimental treatment (experiment 1 vs. experiment 2) or year influenced the relationship between relative occupancy and IBI, via an analysis of covariance, with relative occupancy as the dependent variable, year and treatment as factors, and IBI as a covariate. IBI was forced into the ANCOVA and treatment and individual year factors were made available for inclusion in a stepwise procedure. Because of the large number of variables and the small sample size ($n = 17$), I entered or retained year and treatment factors only if $P < 0.01$. The results were the same regardless of whether a backward or forward (stepwise) procedure was used.

As noted above, IBI alone was positively related to relative occupancy ($r = 0.72$, $R^2 = 0.52$). Treatment (experiment 1 versus experiment 2) did not explain additional variation in relative occupancy. Only the year variable representing 1991 entered or was retained in the analysis. When it was included, R^2 increased from 0.52 to 0.74, and the P value of IBI decreased from 0.001 to 0.0001, indicating a stronger positive relationship between relative occupancy and IBI, but that relative occupancy was lower in 1991 than predicted by the data for other years (Fig. 3).

DISCUSSION

SPACING OF NEST-BOX OCCUPANTS

My experiments provided evidence that Tree Swallows avoided each other when nesting in closely spaced nest boxes at sites with less food (BF in experiment 1 and MC in experiment 2): occupied nest boxes were farther apart than expected from a random distribution. This result is consistent with other studies of occupancy relative to nest-box spacing (Muldal et al. 1985). At sites where food was more abundant, the pattern of occupation of my closely spaced boxes was not significantly different from random, probably because high overall occupancy at those sites limited opportunities for spacing.

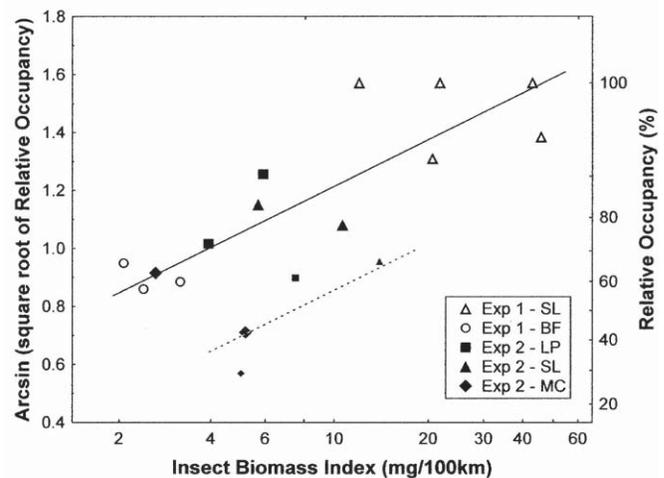


FIGURE 3. Relationship between relative occupancy of closely spaced nest boxes and local insect biomass index in experiments 1 (open symbols) and 2 (solid symbols). Small symbols represent 1991 results from experiment 2, large symbols results from all other years. SL = Sewage Lagoon, BF = Backus Field, LP = Long Point, MC = Mud Creek. The solid and dashed lines represent the covariance regression: $\arcsin(\text{relative occupancy})^{1/2} = 0.674 + 0.234 \times \ln(\text{insect biomass index} + 0.1) - 0.358 \times Y91$, where $\arcsin(\text{relative occupancy})^{1/2}$ is expressed in radians, insect biomass index is the seasonal geometric mean of the daily values of M (mg dry biomass/100 km wind), and $Y91 = 1$ for 1991 and zero for other years. The dashed line represents the regression prediction for 1991, the solid line the prediction for all other years ($R^2 = 0.74$, $P < 0.0001$, $n = 17$).

NEST-BOX OCCUPANCY, TERRITORY SIZE, AND FOOD ABUNDANCE

Occupancy rates of regularly spaced, control nest boxes differed by site and were positively correlated with insect abundance. Also, relative occupancy was positively related to insect abundance, providing unequivocal evidence that insect abundance influenced occupancy (the inverse of territory size) of closely spaced boxes independently of the sites' effects.

The relationship between relative occupancy and insect abundance was strongly positive in experiment 1. In experiment 2, the relationship was again positive but was not significant. The range of IBIs in experiment 2 (Table 2) was much narrower than in experiment 1 (Table 1). Therefore, the swallows were subjected to a narrower range of insect abundances in experiment 2 than in experiment 1 and consequently a significant effect of insect abundance on nest-box occupancy was more difficult to achieve in experiment 2.

My analysis of results for the two experiments combined showed that the arrangement of the closely spaced nest boxes, although very different in the two experiments, did not influence the relationship between relative occupancy and insect abundance (Fig. 3). However, in 1991 relative occupancy of the closely spaced nest boxes was lower than expected from the relationship between relative occupancy and insect

abundance in all other years in both experiments. I attribute that difference to placement of the experimental nest boxes after territory establishment was well under way in 1991, the first year of experiment 2 (12, 9, 6, and 2 days before the first eggs were laid in control boxes, at MC, SL, and two groups of boxes at LP, respectively; see Methods for dates). Alternatively or additionally, there may have been an increase in the numbers of floaters available to occupy closely spaced boxes over the 3 years of experiment 2. Relative occupancy of closely spaced boxes increased at all three sites from 1991 to 1993 (Table 2), but only 1991 differed from the other years. That the relationship between IBI and relative occupancy of closely spaced nest boxes was the same regardless of experimental arrangement of the nest boxes, site, or year (except 1991) adds support for the hypothesis that occupancy is strongly influenced by insect abundance.

In summary, my results show a strong positive relationship between mean insect abundance and relative occupancy of closely spaced nest boxes. It follows that success in defense of extra nest sites (Rendell and Robertson 1994) is likely to vary, not only with nest-box spacing, but with local food resources and the resulting pressure of competition from conspecifics. Elsewhere in Ontario, Muldal et al. (1985) reported occupancy averaging only 45% in one study and commented on the very high occupancy rates reported in some earlier studies, despite close spacing of nest boxes. Those authors suggested that population pressure may have resulted in closer spacing of nests, but they did not mention the possibility that population pressure itself may be dependent on insect abundance or other aspects of the quality of the sites. It is evident from my study that a "preferred" spacing determined at one site (Muldal et al. 1985) is unlikely to be duplicated at another site with different food abundance.

FOOD AND COMPETITORS

The nest-site territories of the Tree Swallow are smaller where food is abundant. I interpret this result as indicating that competition for nest sites is stronger where food is abundant. The alternative explanation, that competitive pressure is relaxed where food is abundant, seems untenable because evidence indicates that reproductive success is lower at low-food sites: clutch sizes and growth rates of nestlings are lower (Quinney et al. 1986, Hussell and Quinney 1987) and predation rates may be higher because nestlings vocalize more (Hussell 1988). Consequently there are clear fitness advantages to nesting at high-food sites. In my study rates of occupancy of widely spaced control boxes were positively correlated with food abundance, indicating that high-food sites are more attractive to swallows. All of these factors imply strong competition to nest at high-food sites rather than relaxation of competition.

Potential benefits of increasing territory size to encompass more than one nest box include, for males, increasing the

probability of attracting a second female, for females, enabling them to prevent polygyny, and, for both sexes, providing a site for re-nesting if the first nest fails (Robertson et al. 1992). Incubation is by the female alone, providing the male greater opportunities for polygyny at this stage. Nevertheless, in one population the incidence of polygyny varied only from 0 to 8% (Robertson et al. 1992). At SL, from 1980 to 1982, 5% of the nest boxes were occupied simultaneously by two females and attended by one male (Quinney 1983). Presumably this situation arose because there were strong potential benefits to females to nest polygynously but no unoccupied boxes available.

Although at high-food sites territory holders are likely to spend less time foraging and have more time for territorial defense, they do not thereby gain larger territories and increase the distance of neighboring pairs, indicating that competitive pressure must be intense. Evidently, at high-food sites, the costs of fighting to exclude swallows from nearby nest boxes are greater than the benefits. Conversely, the benefits to intruders of claiming a closely spaced nest box at a high-food site must be greater than the costs of establishing the territory and defending the nest box. By contrast, territory holders at low-food sites presumably spend more time foraging and have less time for territory defense. Nevertheless, they appear to exclude competitors from nearby boxes and thereby gain larger territories around their nest boxes than do swallows at high-food sites. This implies that the benefits of fighting to establish a territory close to other swallows at a low-food site are insufficient to offset the cost of competition. High occupancy of closely spaced boxes at high-food sites indicates that density per se is not a deterrent to nesting close to conspecifics. Therefore other factors, including the influence of food abundance on the numbers of swallows seeking to establish territories at a site and on the strength of their competitive interactions, must be responsible for the observed patterns of next-box occupancy.

Because Tree Swallows do not defend a feeding territory, my experimental results cannot be explained by a need to defend a food resource. Instead they support the hypothesis that the competitive pressure of intruders is greater where food is abundant and that such pressure directly influences territory sizes. Evidently, intruders assess insect abundance or detect other cues to habitat quality, which in turn leads them to exert more or less pressure, individually or collectively, on existing territory holders. Presumably territory holders make a similar assessment of habitat quality that causes them to offer more or less resistance to intrusions and reductions of their defended areas. The evidence I present indicates that the net effect of the resulting competitive pressure is that at high-food sites Tree Swallows reduce the sizes of their small nest-defense territories below those at low-food sites, as commonly occurs also in species that defend much larger all-purpose territories.

Although additional factors may come into play in all-purpose territories, my results demonstrate that

competition for territories can influence territory size independently of the need to defend a food resource. Therefore, my results add credibility to the equivocal results of other studies that suggested that competitive pressure from conspecifics is the primary proximate driving force behind the inverse relationship between food resources and territory size in species that do defend feeding territories (Myers et al. 1979, Franzblau and Collins 1980, Village 1982, Temeles 1987, Dunk and Cooper 1994, Eberhard and Ewald 1994).

How both initial territory holders and intruders assess habitat quality at the time that Tree Swallows establish territories remains an unanswered question, because early in the season insect abundance varies enormously from day to day and from site to site and is probably an imperfect predictor of insect abundance at key points later in the breeding cycle (Hussell and Quinney 1987: figs. 1, 2). It appears that Tree Swallows must be responding to other features of the habitat as well as to early-season insect abundance, perhaps including any kind of "public information" (Doligez et al. 2002, Valone 2007, Forsman et al. 2008). Floaters and failed breeders may prospect for sites in one breeding season and return to them in the following year. Many of the earliest occupants of territories are returnees that bred successfully at the same site in previous years; the behavior of these birds may provide new arrivals with additional cues to habitat quality carried over from earlier years.

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