

## BREEDING DISPERSAL AND PHILOPATRY IN THE TREE SWALLOW

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**Abstract.** To study the patterns and determinants of philopatry and breeding dispersal in the Tree Swallow (*Tachycineta bicolor*) we analyzed the records of 356 males and 1459 females captured in more than one breeding year around Ithaca, New York. Of these captures, only 4% of male and 14% of female breeders dispersed to a new site for breeding. With our combination of intensive study areas in Tompkins County, New York, and the efforts of volunteer banders throughout New York and surrounding states, we could have detected dispersal in excess of 400 km from the initial breeding site. Randomization tests revealed, however, that breeders dispersed much shorter distances than they could have been detected. Detailed analyses of recaptures in Tompkins County showed that over a 22-km range of distances, the chances of dispersal to a new breeding site declined with the distance from the original breeding site. Females that failed to fledge any offspring were much more likely to disperse than females that reproduced successfully, and the probability of dispersal declined gradually with female age. The spatial scale in which swallows gather and process information appears to be much larger than for passerines that defend all-purpose territories.

**Key words:** adult mortality, breeding success, dispersal, philopatry, spatial scale, *Tachycineta bicolor*, Tree Swallow.

### Dispersión Reproductiva y Filopatría en *Tachycineta bicolor*

**Resumen.** Para estudiar los patrones y los determinantes de la filopatría y la dispersión reproductiva en *Tachycineta bicolor* analizamos los registros de 356 machos y 1459 hembras capturados en más de un año reproductivo en los alrededores de Ithaca, New York. De estas capturas, sólo el 4% de los machos y el 14% de las hembras reproductivas se dispersaron a un nuevo sitio de cría. Con nuestra combinación de áreas de estudio intensivas en el Condado de Tompkins, New York, y los esfuerzos de colaboradores voluntarios que anillaron aves a lo largo de New York y los estados circundantes, pudimos haber detectado eventos de dispersión a más de 400 km desde el sitio de cría inicial. Exámenes aleatorizados revelaron, sin embargo, que las aves reproductivas se dispersaron a distancias mucho más cortas que las que se podrían haber detectado. Análisis detallados de recapturas en el Condado de Tompkins mostraron que en un rango de distancias de 22 km, las probabilidades de dispersión a un nuevo sitio de cría disminuyeron con la distancia desde el sitio de cría original. Las hembras que fracasaron en la cría de pichones presentaron una probabilidad de dispersarse mucho mayor que las hembras que se reprodujeron exitosamente, y la probabilidad de dispersión disminuyó gradualmente con la edad de la hembra. La escala espacial a la que *T. bicolor* recoge y procesa información parece ser mucho más grande que la de aves paserinas que defienden territorios de uso múltiple.

### INTRODUCTION

All organisms are confronted by variable environments. For those organisms that can move,

dispersal is one of the most important life-history responses to unavoidable habitat heterogeneity. Birds have some of the best-developed abilities to move, and the dispersal biology of birds is gradually becoming understood (Paradis et al. 1998, Koenig et al. 2000, Powell and Frasch 2000, Hansson, Bensch, and Hasselquist 2002, Paradis et al. 2002), despite the formida-

Manuscript received 11 December 2003; accepted 11 June 2004.

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ble challenges of following their movements (Koenig et al. 1996, Koenig et al. 2000).

Ornithologists define dispersal as movement to a new breeding site from a natal or previous breeding site and distinguish it from the migrations that take birds to and from often distant wintering areas. Natal dispersal involves a bird's movement to its first breeding site. By definition, it occurs only once in a bird's life, and tends to be of larger spatial scale than the movements between breeding sites, or "breeding dispersal" (Greenwood and Harvey 1982, Harvey et al. 1984, Lebreton et al. 2003; Winkler, in press). In multibrooded species, breeding dispersal can occur more than once in a single breeding season, and all species can undertake breeding dispersal after failed nesting attempts or between breeding seasons. It is unclear whether the underlying behavior and biology of natal and breeding dispersal are really fundamentally different. But surviving adults of breeding age make repeated choices of breeding sites, increasing the opportunities for biologists to understand the kinds of information that are important and the ways that information is used in choosing sites.

The determinants of site choice that have been investigated include declining nest quality with increasing nest age (Gowaty and Plissner 1997, Mazgajski 2003, Stanback and Rockwell 2003), the sex of the bird (Harvey et al. 1978, Drilling and Thompson 1988, Bensch and Hasselquist 1991), and the success of prior nesting, either of the dispersing bird (von Haartman 1949, Harvey et al. 1978, Gavin and Bollinger 1988, Gowaty and Plissner 1997) or its prospective neighbors (Doligez et al. 2002). Another important influence on breeding dispersal has been mate retention or abandonment (Harvey et al. 1978, Bensch and Hasselquist 1991, Beheler et al. 2003). Here, we concentrate on describing the movement patterns and exploring the nonsocial determinants of breeding dispersal in a population of Tree Swallows (*Tachycineta bicolor*) nesting near Ithaca, New York.

## METHODS

Tree Swallows are excellent subjects for studying breeding dispersal. They fly every year between breeding grounds throughout North America and wintering areas in the Gulf Coast of North America, the Caribbean, and Central America (Robertson et al. 1992). Their dispersal

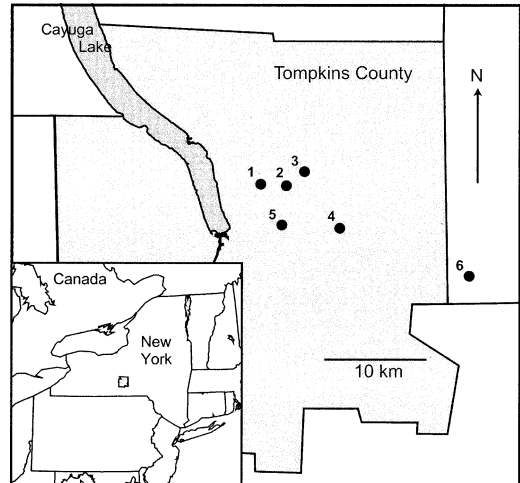


FIGURE 1. Locations of Tree Swallow study sites on Cornell University land to the east of Cayuga Lake (shaded) in Tompkins County, New York. Numerals represent the unit designations for each site. Tompkins County is outlined on the inset map.

distances are thus not constrained by any limitation of patchy habitat availability or vagility, and this expansive potential for dispersal creates a challenge to the researcher that is not present in resident species. Tree Swallows possess a distinctive counteracting advantage: they are secondary cavity nesters that rely on woodpeckers (or humans) to create the tree holes (or nest boxes) in which they nest. Most Tree Swallows in central and western New York nest in boxes erected for Eastern Bluebirds (*Sialia sialis*), and this habit greatly simplifies the researcher's tasks of finding nests, protecting them from predators, and characterizing the distribution of potential habitat. Finally, Tree Swallows are uncommonly resistant to disturbance, making them easy to trap during nesting.

Our studies of Tree Swallows around Ithaca were begun with the erection of 105 nest boxes in 1985 at Cornell University's Experimental Ponds Unit 1 (42°30'N, 76°28'W), about 10 km north of the Ithaca campus. Boxes were established at Experimental Ponds Unit 2 (128 boxes) in 1989, in Unit 3 along roads north of the experimental ponds (95 boxes) in 1991, on Cornell farmland on Mt. Pleasant (Unit 4, 60 boxes) in 1991, along Hanshaw Road (Unit 5, 22 boxes) in 1993, and at Cornell's Harford Animal Science Complex (Unit 6, 131 boxes) in 2001 (Fig. 1). Because of problems with House Sparrow

(*Passer domesticus*) predation, all boxes were removed from Unit 3 after the 1993 nesting season. Boxes at each unit are 20 m from the nearest neighboring box. All nest boxes on the units were cleaned out before each breeding season, so the present study gathered no data on the effect of nest age on breeding dispersal (Gowaty and Plissner 1997, Mazgajski 2003). Tree Swallows in the northeastern U.S. are single brooded (Robertson et al. 1992), and the breeding movements described here are all movements between the breeding locations of one year and the next. We also did not explore fine-scaled movements that birds may have made within units where territorial boundaries were vague. The movements we describe here are thus unequivocally breeding dispersal, but fine-scale movements may be worthy of further exploration in the future.

Analyses are based on the sample of breeding adults captured during 1990–2002, and thus cover potential breeding dispersal over 11 years. In addition to the retrapping efforts conducted on each of our Cornell study sites, we also searched for dispersing breeders throughout Tompkins County, New York, and at many locations throughout New York State with an extensive network (first named the Cornell Nest-box Network and then the Swallow/Bluebird Dispersal Study) of about 60 volunteer bird banders that we trained as subpermites.

To explore the extent to which our extended study area freed the distribution of observed dispersal distances from the constraints of restricted study areas (Baker et al. 1995, Koenig et al. 1996), we conducted randomization tests with S-Plus (S-PLUS 2002) to evaluate the deviation of the observed distribution from dispersal distances expected under uniform and exponentially decaying probabilities of dispersal. Taking the first breeding nest box of each dispersal event as a starting point, we calculated the distance to every other box in the study area at which we captured an adult the following year (henceforth “capture-boxes”). We then conducted randomization tests on the distribution of all capture-boxes (i.e., all the dispersal events that we could have observed) to see whether the observed dispersal-distance distribution differed significantly from it. One draw was taken from the distribution of capture-boxes for each of the nests that was the origin of a breeding dispersal event. This process was repeated 1000 times to pro-

duce an estimate of the median and range of the expected dispersal-distance distribution for all dispersals events.

The uniform null model assumed that potential dispersers were equally able to find and reach all the nesting opportunities in our entire 400-km-radius study circle. One alternative to this null model is that the birds searched for alternative nesting sites starting at their previous site and working outward from there until they found an unoccupied site. Such local searches produce a geometric decline in frequency with distance (e.g., Murray 1967, Waser 1985), and we created a similar exponential null distribution by regressing the overall observed log probabilities of capture on distance and using the slope and intercept of this regression to parameterize the null distribution. This null model thus takes into account the reduction in nest-site availability and detectability with distance and mimics what an animal picking a site at random starting from the previous breeding site would produce.

To test for the nonrandomness of philopatry, we first calculated how many movements would be expected between each of the capture sources (each of the units, nonunit Tompkins County nests, and Swallow/Bluebird Dispersal Study nests) based on the total number of capture-years we logged at each. These expected frequencies were calculated by multiplying the total capture-years in each pair of capture sources, then dividing these products by the sum of all products for all sources. These scaled products were then multiplied by the total number of recaptures to yield an expected frequency of birds recaptured in each cell of the  $8 \times 8$  capture-source matrix. Because some of the resulting expected values were less than five, we lumped cells for Unit 3 with Unit 2, and Unit 4 with Units 5 and 6. The expected movement frequencies under the unconstrained random-movement null hypothesis in the resulting  $5 \times 5$  matrix were compared to the observed with a  $\chi^2$  test with 16 degrees of freedom.

We also used the simple ratio of the observed cell frequency over the expected (henceforth the “frequency ratio”) as a measure of the deviation from random movement for analysis of the effects of distance from the previous breeding site on the chances of dispersal and resettlement. It is very difficult to characterize the distances between the units, Tompkins County nests, and Swallow/Bluebird Dispersal Study nests, so we

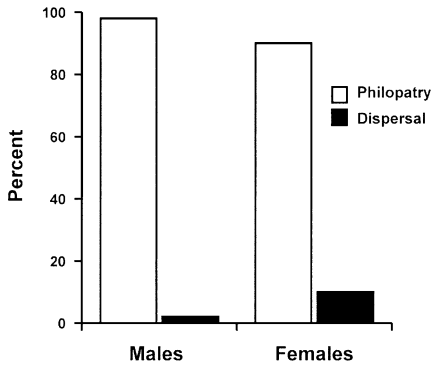


FIGURE 2. The proportion of 356 male and 1459 female Tree Swallows captured in multiple years that dispersed from their initial breeding site vs. remained philopatric.

limited our analysis of distance effects on dispersal to data from the units. Within this subset, we compared the matrix of frequency ratios to a matrix of distances among sites using Mantel's randomization test (Manly 1997b). With the program RT (Manly 1997a), we regressed the frequency ratio matrix on a randomized distance matrix 10 000 times to estimate the probability of observing a more extreme fit of frequency to distance.

Other analyses and scatterplot smoothings were conducted in SYSTAT version 9 (SPSS 1999). We report means  $\pm$  SE unless otherwise noted, and statistical tests are considered significant at  $\alpha = 0.05$ .

## RESULTS

During 1990–2002, we captured 1456 male and 2247 female Tree Swallow breeders at the Cornell units, during which time box occupancy at the units ranged from 13% to 100%, (mean =  $61 \pm 0.03\%$ ). Over the same years, we captured 286 males and 763 females in Tompkins County boxes. Swallow/Bluebird Dispersal Study participants captured 1086 males and 4364 females.

Of 356 males captured in more than one breeding year (Table 1), only 14 (<4%) had moved between breeding sites. Females were less philopatric, and of 1459 females captured in more than one season, 205 (14%) changed sites between breeding seasons (Table 1). This difference between sexes in rates of philopatry and dispersal was significant ( $\chi^2_1 = 22.5$ ,  $P < 0.001$ ; Fig. 2).

To test whether breeding dispersal distances were effectively measured free of study area constraints, we resampled the potential dispersal-distance distribution. The first randomization test was based on a null hypothesis of a uniform distribution, with an equal probability of a breeder moving to breed in any nestbox where an adult was captured the following year. The resulting disparity between observed and null dispersal-distance distributions (Fig. 3a) showed that Tree Swallow breeders dispersed <10 km from the previous breeding site more often than expected. At all larger distances, the observed frequencies of dispersing birds were substantially smaller than those expected under the uniform null hypothesis.

The exponential null hypothesis had an exponentially declining probability of settlement with increasing distance from the previous breeding site. Although the exponential null was much closer to the observed distribution (Fig. 3b), the qualitative mismatch between the observed and null distributions remained: very close dispersals were more common, and more distant ones less common, than would be expected under the null hypothesis.

The fact that the frequencies of birds dispersing at all distances beyond 10 km were smaller than expected by chance indicated that the study area and density of captures were not limiting the detection of dispersing birds and that the dispersal-distance distribution observed (Fig. 3) was a reasonable reflection of how far birds dispersed.

Given the very small number of dispersing males detected, we based the remainder of our analyses on recaptures of females. Using the observed female dispersal frequencies (Table 1), with cells for Units 2 and 3 and for Units 4, 5 and 6 pooled to yield expected values exceeding five, we confirmed nonrandomness in the female recaptures ( $\chi^2_{16} = 7726$ ,  $P < 0.001$ ). Thus, even the more-dispersive females were much more philopatric than would be expected by chance, and the tremendously preponderant diagonal totals in Table 1 indicated strong breeding philopatry of Tree Swallows.

The frequency ratio (observed dispersals:expected dispersals) declined with distance between successive breeding sites, and this decline was captured well with a log smoother in SYSTAT (Fig. 4). The relationship between the frequency ratio and distance was highly signifi-

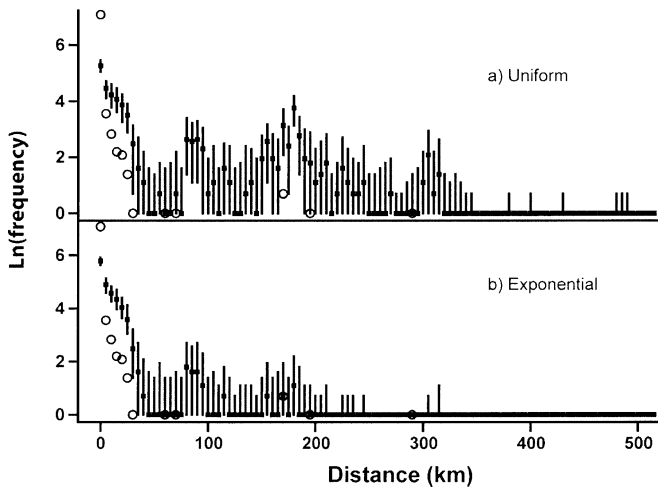


FIGURE 3. The relation between the observed (unfilled circles) and expected (filled squares) distribution of breeding dispersal distances in Tree Swallows. Expected distributions follow null hypotheses of (a) uniform dispersal probability with distance and (b) exponential decline in dispersal probability with distance. For each null distribution, expected values are the median frequency of dispersers in a given distance band using 1000 draws from the detectable distance distribution. The range of all 1000 draws is indicated by a vertical bar.

cant (Mantel test for nonindependent data,  $P < 0.01$ ). Thus, when combined effects of variable nest-box availability and detectability were corrected for (by calculating the frequency ratio), females were less likely to disperse to a more distant site than a closer one.

To evaluate the effect of past experience on movement decisions, we related the probability of dispersal to the breeding success in the previous breeding season. Of 85 failed breeders in the sample, 61 (72%) remained in the same site, and 24 (28%) emigrated. By contrast, of 662 successful breeders (those that fledged at least one young), 632 (95%) stayed and only 30 (5%) emigrated. This higher rate of emigration among failed breeders was highly significant ( $\chi^2_1 = 63.1$ ,  $P < 0.001$ ; Fig. 5). Thus, the generally high rate of philopatry in Tree Swallows can sometimes change in response to poor breeding success.

Finally, we investigated the extent to which the age of the female affected the probability of dispersing (Fig. 6). In a contingency table in which all females at least 5 years old were pooled to produce an expected frequency greater than five, younger females were significantly more likely to disperse ( $\chi^2_4 = 11.0$ ,  $P = 0.03$ ).

## DISCUSSION

This study confirms the fact that Tree Swallows, like many birds (Kendeigh 1941, Austin 1949,

Darley et al. 1971, Harvey et al. 1978, Hansson, Bensch, et al. 2002) are highly philopatric once they begin breeding. Although previous studies have claimed or assumed philopatry, we feel this is the most careful attempt to date, at least in a passerine living in an unconstrained mainland habitat, to locate dispersing birds. As such, we feel the estimated rate of dispersal and philopatry is worthy of note, as breeding dispersal is interesting in its own right as well as being an important source of information for estimates of adult survival rates (Cilimburg et al. 2002).

It is tempting to compare the rates of philopatry and dispersal we discovered with those reported from other studies; however, there are so many differences that such a comparison seems unwise. The first of these differences is the fact that we covered a much larger area than is usually checked. The area covered can have a very large effect on estimates of philopatry and dispersal rates. For example, if we limit our consideration to only the unit records (Table 1), the resulting estimate of dispersal rate is only half that produced by the full data set. A second difference between this and other studies is that we took a rather restrictive definition of dispersal by limiting ourselves to cases of movement to nests in different units or in different sites in Tompkins County and the Swallow/Bluebird Dispersal Study. Studies of breeding dispersal in resident



TABLE 1. Summary of multiyear captures of breeding Tree Swallows in a circle of 400-km radius centered on Ithaca, New York, 1990–2002. Numbers of females are given in each cell, with the number of males beside in parentheses.

Dispersed from:	Dispersed to:							Swallow/ Bluebird Dispersal Study
	Unit 1	Unit 2	Unit 3	Unit 4	Unit 5	Unit 6	Tompkins County	
Unit 1	358 (200)	21	1	2	4	2	5 (1)	5
Unit 2	13 (1)	255 (72)		3	4		2	2
Unit 3	1 (1)	2	5 (2)					
Unit 4		2		72 (20)			4	4
Unit 5	3	1		1	19 (4)		2 (1)	1
Unit 6						27		
Tompkins County	4 (1)	4		4	3		104 <sup>a</sup> (21)	18 (2)
Swallow/Bluebird Dispersal Study	3	3			6	5	12 (1)	472 <sup>b</sup> (29)

<sup>a</sup> Includes 23 females (3 males) that switched sites within Tompkins County.

<sup>b</sup> Includes 35 females (3 males) that switched sites within the Swallow/Bluebird Dispersal Study.

species can often take place over distances as short as the width of a few territories (Harvey et al. 1978), but, given the large distances in undefended space over which Tree Swallows forage, we limited our analysis to shifts between units to ensure that all the movements we studied were biologically significant dispersals events. The movements reported here definitely

placed the birds in a different foraging and social environment with different predators and competitors, but they are difficult to compare to movements reported in other studies.

Female Tree Swallows, like females of other species (von Haartman 1949, Harvey et al. 1978, Freer 1979, Shields 1984, Gavin and Bollinger 1988, Bensch and Hasselquist 1991, Simek 2001), are more likely to disperse away from sites where their breeding attempt failed. This is one of the distinguishing features of breeding dispersal that differentiates it from natal dispersal: experienced breeders can fine-tune their site selection on the basis of actual breeding experience, instead of other site-selection cues.

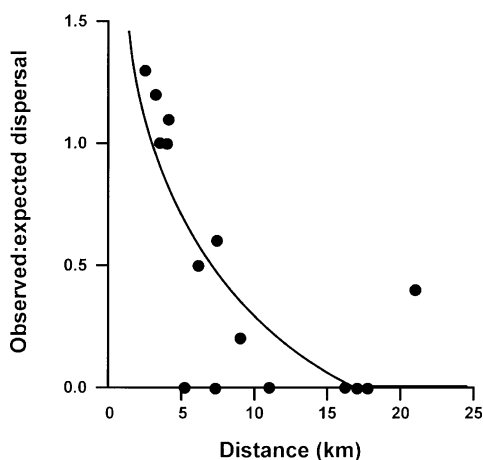


FIGURE 4. Relation between the dispersal frequency ratio and the distance between successive breeding sites (in km) for all breeding female Tree Swallows that dispersed to and from the study units in Tompkins County, New York (Fig. 1). The frequency ratio is the ratio of observed dispersal to that expected under uniform movement among units, so values >1 indicate more dispersers than expected, and values <1 fewer. The curve fit to the data is the result of a log-smoothed plot from SYSTAT.

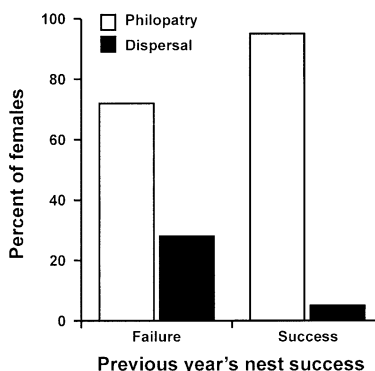


FIGURE 5. The effect of breeding success in one year on the proportion of Tree Swallows dispersing the following season. Breeding success was defined as fledging  $\geq 1$  young.

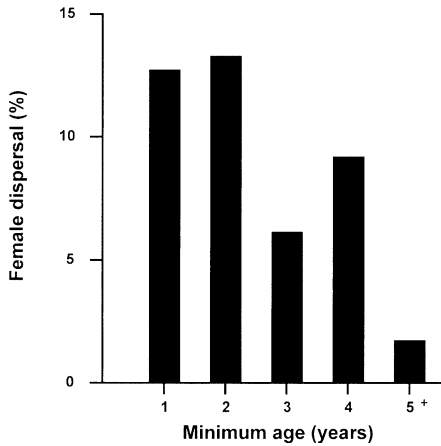


FIGURE 6. The effect of female Tree Swallow age on the probability of female dispersal the following season.

There are many potential determinants of breeding dispersal that we could not explore in our data set. Because nests were routinely cleaned out before each breeding season, we could not test the effect of nest age, and we did not have sufficiently reliable data on all nests to test the effects of more refined success data (e.g., proportion of nestlings fledged, etc.) on breeding dispersal. The results on breeding success do suggest responsiveness; however, that was not apparent in another study of the same species in Canada (Shutler and Clark 2003). Shutler and Clark's study was at a spatial and numerical scale comparable to one of our units, and dispersal movements at the scales studied here may have been unlikely in Shutler and Clark's study because of a paucity of nest sites available elsewhere and an inability to detect them if they occurred.

Although the effect of female age on the probability of dispersing might not be surprising, it is not obvious why the rate of dispersing continues to decline over the females' lifetimes rather than being concentrated in the transition from first-time breeders (second-year females, at least 1 year old) to older birds (Pärt and Gustafsson 1989).

The pattern of observing dispersal increasingly rarely with increasing distance from the previous breeding site is reminiscent of the pattern observed for natal dispersal in this and other species (Paradis et al. 1998, Sutherland et al. 2000; Winkler et al., unpubl. data). This com-

parison raises the interesting question of just how different from each other breeding and natal dispersal really are. Natal dispersal is done only once, by inexperienced birds, but it would be interesting to know if there are other biological differences in the process. Are different sources of information gathered for each? Is information dealt with in different ways by experienced breeders vs. juveniles?

No matter what the answers to these questions, the scale of spatial information available to breeding Tree Swallows is orders of magnitude larger than what we might assume for most passerines, especially if we think of passerines as generally defending all-purpose territories. As in the case of many colonial seabirds, these swallows only really defend the area within a few meters of the nest, spending all their foraging time in undefended space used by many others in their breeding neighborhood. There are tantalizing glimpses of the effects this extended space of activity might have, the most vivid of which is the observation of a polygynous male simultaneously attending nests at both Units 1 and 2 (Ferretti et al., unpubl. data). These sites are separated by approximately 2.5 km, and this bird thus operated daily over a spatial range that most territorial passerines presumably only encounter outside the breeding season. One of the challenges of dealing with the spatial ecology of Tree Swallows is thus to retune our notions of the spatial scales over which information is routinely collected and processed. Thus, the preponderance of philopatry in this species is a result of choices to continue breeding in the same place, not ignorance of other alternatives. And, given the prevalence of breeding philopatry, the landscape-level effects of natal dispersal are likely to be much greater than those of breeding dispersal.

It remains to be seen, however, whether the distances that these birds disperse between seasons are larger than those of territorial passerines. Though Tree Swallows seem to be cognizant of a much larger area during breeding, it is possible that other passerines may have compensating influences (such as the possibility that nocturnal migration is more error prone; Winkler, in press) that more than compensate for their smaller breeding home ranges. We clearly have a great deal still to learn about the spatial ecology and behavior of birds.

## ACKNOWLEDGMENTS

N. Hamm helped us a great deal in searches of the long-term database on Ithaca Tree Swallows, and A. Dhondt, J. Fitzpatrick, and R. Bonney were co-investigators with DWW on the CNBN grant (NSF ESI-9627280) that was an essential precursor to the Swallow/Bluebird Dispersal Study. We thank the following volunteers and assistants in the units, around Tompkins County, and on the Swallow/Bluebird Dispersal Study: J. Abrams, F. Adler, T. Anstey, C. Anstey, D. Ardia, R. Bakelaar, S. Barker, C. Banta, B. Best, R. Biss, K. Boehm, E. Boehm, S. Bonilla, J. Bowe, M. Bowlin, E. Brooks, T. Bruce, J. Buckland, D. Buerk, C. Burney, L. Buttel, L. Carpenter, B. Carter, C. Cassady, B. Christman, B. Cicognani, D. Clark, M. Clark, C. Clews, C. Cliffler, P. Coates, E. Colling, L. Connor, S. Cooper, N. Davis-Ricci, C. DeLong, J. Deobil, A. Dhondt, G. Dingman, W. Dingman, K. Dorsey, D. Edsinger, K. Engel, D. Fancher, A. Finney, W. Fisher, M. Forness, K. Fox, C. Fryer, D. Fryer, L. Gallant, K. Geiger, B. Giles, E. Goetze, G. Graziano, A. Greenwood, T. Greg, F. Griecus, D. Griffin, M. Gunning, B. Habalou, D. Hall, I. Hall, N. Hamm, S. Hartwig, S. Harwood, D. Hauber, J. Henkel, D. Hofer, B. Hohmann, J. Holman, P. Hosner, R. Jensen, T. Kast, E. Kellogg, D. Kelly, S. Kelly, P. Kleinman, E. Klopfer, B. Kozlowski, S. Kozlowski, A. Krakauer, P. Llambías, K. Luther, S. Malone, J. McCarty, S. McCutcheon, D. McDermitt, K. McMahon, D. McNaughton, M. Medler, L. Merrill, S. Mitra, S. Molnich, D. Moore, R. Moore, R. Morantz, G. Nesslage, N. Newcomb, D. O'Neill, E. Ormondroyd, J. Ormondroyd, L. Owens, S. Podulka, M. Quiroga, C. Redinger, D. Robie, J. Rogers, A. Romero, B. Ross, K. Roux, N. Rowe, N. Scalzo, C. Schiefflin, G. Schmieder, S. Schwemmer, J. Sedlacek, P. Senesac, W. Stuart, E. Siemann, L. Siemion, Jr., D. Slavin, D. Smith, P. Smith, K. Smith, L. Smith, J. Smith, L. Sommers, D. Sosnowski, L. Stenzler, B. Taft, A. Terninko, B. Toner, B. Treiber, E. VanderWerf, J. Van Niel, K. Waters, R. Wells, L. Wheeler, D. Whittaker, L. Yang, J. Zamon, J. Zarudsky, C. Zenger, M. Zettel, and the Ontario Bird Banding Association. D. Buerk, J. Holman, S. McCutcheon, and K. Sargianis gave many hours to keeping SDS running on less than a shoestring. The analyses for this paper were supported in part by a cooperative agreement between DWW and the National Center for Environmental Assessment, Environmental Protection Agency, Washington, DC.

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