

## CAUSES AND CONSEQUENCES OF TREE SWALLOW (*TACHYGINETA BICOLOR*) DISPERSAL IN SASKATCHEWAN

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**ABSTRACT.**—Poor breeding success often increases dispersal, but there is conflicting evidence about the putative adaptive benefits of dispersal behavior. Thus, observational and experimental data were analyzed to test whether breeding success (number of young fledging) influenced breeding and natal dispersal by Tree Swallows (*Tachycineta bicolor*), using information from 1,302 nests over 12 years. Success was experimentally altered at 291 randomly selected nest boxes by adding or removing three eggs (representing  $\pm 50\%$  of modal clutch size). Finally, we tested whether dispersal distance, controlling for antecedent breeding success, had consequences for subsequent breeding success.

Contrary to predictions, (1) adult and natal dispersal distances were not significantly influenced by breeding success, and (2) manipulating success had no effect on either breeding or natal dispersal. Moreover, after controlling for antecedent breeding success, dispersal distance had no influence on subsequent breeding success. In most years of our study,  $>85\%$  of nest initiations produced at least one fledgling, and individual boxes did not consistently have low or high fledgling production. Hence, swallows may have little to gain by dispersing out of our nest-box grid, and box-specific success did not provide a reliable cue about where to disperse within the grid. Thus, remaining in the grid for subsequent breeding attempts, regardless of fledgling production, could be interpreted as adaptive. Nonetheless, most adults remained close to the nest they had used in previous years, which suggests that some unmeasured influence, such as social interactions among neighbors, led to nonrandom dispersal. Received 27 September 2002, accepted 22 April 2003.

**RÉSUMÉ.**—Un faible succès de reproduction augmente souvent la dispersion, mais les bénéfices d'un tel comportement adaptatif peuvent sembler conflictuel. Par conséquent, les données d'observations et expérimentales ont été analysées pour tester si le succès de reproduction (nombre de jeunes à l'envol) influençait la dispersion au moment de la reproduction et à la naissance chez l'Hirondelle bicolor (*Tachycineta bicolor*). Ces analyses ont utilisé l'information recueillie à partir de 1 302 nids et ce pendant une période de 12 ans. Le succès de reproduction était expérimentalement altéré dans 291 nichoirs sélectionnés aléatoirement en ajoutant ou en retirant 3 œufs (soit  $\pm 50\%$  de la taille modale de couvée). Finalement, nous avons testé si la distance de dispersion avait des conséquences sur le succès de reproduction futur tout en contrôlant pour le succès de reproduction passé.

Contrairement aux prédictions, (1) les distances de dispersion à l'âge adulte et à la naissance n'étaient pas significativement influencées par le succès de reproduction, et (2) la manipulation du succès de reproduction n'avait pas d'effet sur la dispersion aussi bien au moment de la reproduction qu'à la naissance. De plus, après avoir contrôlé pour le succès de reproduction passé, la distance de dispersion n'avait pas d'influence sur le succès de reproduction futur. Pour la plupart des années de l'étude,  $>85\%$  des nids initiés ont produit au moins un jeune à l'envol, et les nichoirs isolés n'étaient pas toujours caractérisés par une faible ou une forte production de jeunes à l'envol. Par conséquent, les hirondelles semblent avoir peu à gagner en se dispersant en dehors du réseau de nichoirs. De plus, le succès de reproduction de nichoirs identifiés ne constituait pas un signe fiable pour savoir où se disperser dans le réseau. Donc, le comportement qui consiste à rester dans le réseau de nichoirs pour de nouvelles tentatives de reproduction, sans porter attention à la production de jeunes à l'envol, pourrait être interprété comme adaptatif. Pourtant, la plupart des adultes restaient proches du nid qu'ils avaient utilisés les années précédentes, suggérant que des influences non mesurées, telles que les interactions sociales entre voisins, conduisaient à une dispersion non aléatoire.

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By LEAVING AN area, dispersers forego knowledge they have acquired about local resource distribution, may expose themselves to unfamiliar environments where they are more likely to be caught by predators, or may leave behind productive mates. On the other hand, dispersers may find richer resources, leave behind predators or parasites, or find fewer competitors and better or genetically unrelated mates (Clobert et al. 2001). Adult birds often have greater breeding dispersal (i.e. movements between successive breeding sites) following relatively poor breeding success (Greenwood and Harvey 1982, Anderson et al. 1992). However, such apparently adaptive responses are not always observed (Newton and Marquiss 1982, Lindberg and Sedinger 1997), which suggests that some dispersal either imposes high costs or provides few benefits (Switzer 1993, 1997; Powell and Frasch 2000). Regardless, the balance between costs and benefits should govern dispersal decisions at all scales. We used both observational and experimental data to test whether fledgling production (number of young leaving a nest) influenced dispersal, and whether dispersal influenced subsequent fledgling production in Tree Swallows (*Tachycineta bicolor*). We examined both breeding dispersal and natal dispersal—that is, movement between fledging and first breeding sites (Greenwood and Harvey 1982, Johnson and Gaines 1990); those measures are the inverse of site fidelity and natal philopatry, respectively.

Few studies have considered whether natal dispersal is adaptive (other than in communal breeding systems; Brown 1987), partly because natal dispersal tends to be much greater than breeding dispersal so that the former is poorly sampled. Some birds remember aspects of their natal environment (e.g. Klopfer 1963); if that includes information on relative breeding success for the nests from which they fledge (Oring and Lank 1984, Nur 1988a), or if quality of breeding sites can be assessed in the preceding year (Boulinier and Danchin 1997, Reed et al. 1999), natal and breeding dispersal could have similar patterns relative to antecedent breeding history.

If dispersal is adaptive, dispersers should have greater fitness than individuals showing site fidelity (Greenwood et al. 1979, Nilsson 1989, Spear et al. 1998); whereas if fidelity is adaptive, more sedentary individuals should

have greater fitness (Clobert et al. 1988, Pärt 1994, Bensch et al. 1998). A balance between costs of site fidelity versus costs of dispersal would maximize fitness at intermediate dispersal distances (Bateson 1983, Waser 1985). All of those scenarios should interact with previous breeding success; why disperse from somewhere when you are doing well (Switzer 1993)? Hence, to determine whether dispersal is adaptive, subsequent breeding success needs to be measured against previous breeding success.

Researchers studying costs of reproduction in birds often manipulate breeding success by adding or removing eggs from clutches. If reducing clutch size effectively decreases a bird's perceived breeding success, it might be motivated to disperse greater distances, which would produce lower estimates of survival, not because those birds were dead, but because they had dispersed outside a study area (Nur 1988a, Koenig et al. 1996). On the other hand, birds may not be fooled by manipulations or may perceive extra young as parasitic. Despite the potential influence of clutch manipulations on dispersal, there have been few formal tests of their effects (Nur 1988b and Doligez et al. 2002 are among the exceptions).

Tree Swallows readily make use of nest boxes, facilitating repeated captures of individuals at nest sites and measurements of their inter-nest movements ("ecological" vs. "genetic" dispersal distances, sensu Johnson and Gaines 1990). Although there is substantial literature on Tree Swallow return rates (e.g. Robertson et al. 1992), there are few published data on that species' dispersal.

We tested whether Tree Swallow breeding dispersal was related to breeding success. We also tested for a relationship between relative breeding success at a nest site and natal dispersal. Our third test was whether or not clutch manipulation ( $\pm 3$  eggs = 50% modal clutch size) affected breeding or natal dispersal. Finally, we tested whether breeding success was related to dispersal distance, breeding success in the prior year, and the interaction between those variables.

#### METHODS

*Field methods.*—Our study site was the 385 ha St. Denis National Wildlife Area, 40 km east of Saskatoon, Saskatchewan, Canada. The study site consists of small groves of small trees, mainly aspen

(*Populus tremuloides*), separated by much larger areas of cropland, native and planted grasslands, shrubs, and wetlands (Sugden and Beyersbergen 1984). Large diameter trees and concomitantly natural nest cavities are at lower densities than in forested areas (R. G. Clark pers. obs.). Anecdotal evidence based on recapture rates of adults (see below), of occurrence of Tree Swallows in areas of southern Saskatchewan (Shutler et al. 2000), and on an absence of natural cavities detected in 12 years of field research, suggests that at most 20% of the breeding population on the study area uses natural cavities. If so, our nest-box grid is an island of suitable habitat surrounded by areas with much lower nesting density.

We completed erecting our grid of 115 boxes by 1993 (Table 1); the irregular arrangement (Fig. 1) affected how dispersal distances would be distributed. Boxes were placed a minimum of 30 m apart, were cleaned each year to reduce variation in ectoparasite populations, and were oriented with their openings facing southeast and placed primarily in locations that were at least 10 m from the nearest tree copses to reduce microclimatic variation among boxes (Austin 1974, Facemire et al. 1990).

Beginning in mid-May, boxes were checked daily for clutch initiation date (day on which the first egg was laid); thereafter visits were timed to observe clutch completion date, hatch date (of first egg), number of eggs hatching, and fledgling production (number of nestlings at 12 days minus young found dead in the nest at 20 days).

Approximately 15% of nests were depredated (primarily by House Wrens [*Troglodytes aedon*]) or abandoned, usually before hatch, which meant we seldom had attempted to capture the associated adults. Where we captured adults for the first nest and the re-nest, only 8 of 24 captures involved the same individuals. Hence, our tests on causes and consequences of breeding dispersal were based on the final nest attempt of the year for a given bird. Our conclusions are essentially unchanged if we restrict analyses to only first nests.

Breeders in the population were captured opportunistically by hand in nest boxes, or trapped (Stutchbury and Robertson 1986) shortly after eggs hatched. Adults were banded with numbered Canadian Wildlife Service aluminum bands; nestlings were banded at 12 days of age. Adults were sexed by presence (female) or absence (male) of brood patches. We made no attempt to sex adults captured before nest initiation.

*Clutch manipulations.*—As part of a larger study on costs of reproduction, clutch manipulations were done in 1991, 1992, 1993, 1994, 1996, and 1998. In each of those years, between 18 and 31 trios of clutches that were initiated on the same day were randomly assigned to reduce, control, or add treatments. Three eggs were removed from a reduce clutch and placed in an add clutch. Three eggs in a control clutch were

TABLE 1. Nest box activity and demography of Tree Swallows captured at St. Denis. Active boxes were those in which at least one egg was laid. Numbers captured at boxes include floaters and visitors (see text).

Year	Available boxes	Active boxes	Nestlings banded	Adults						Percent that were female
				Local recruits	Recaptured recruits	Immigrants	Recaptured immigrants	Number captured per active box		
1990	50	26	130	0	0	37	0	1.4	65	
1991	75	70	299	1	0	94	9	1.5	54	
1992	100	94	394	5	0	91	39	1.4	57	
1993	115	111	38	6	1	38	29	0.7	72	
1994	115	100	514	5	2	42	12	0.6	85	
1995	115	111	583	21	8	156	51	2.1	53	
1996	115	108	551	26	16	136	85	2.4	57	
1997	115	113	644	21	18	93	95	2.0	52	
1998	115	114	564	27	13	65	99	1.8	55	
1999	115	115	400	43	10	121	57	2.0	50	
2000	115	111	612	25	24	76	87	1.9	53	
2001	115	115	564	23	21	95	75	1.9	56	
Total	1,260	1,188	5,293	203	113	1,044	638	1.9	56	

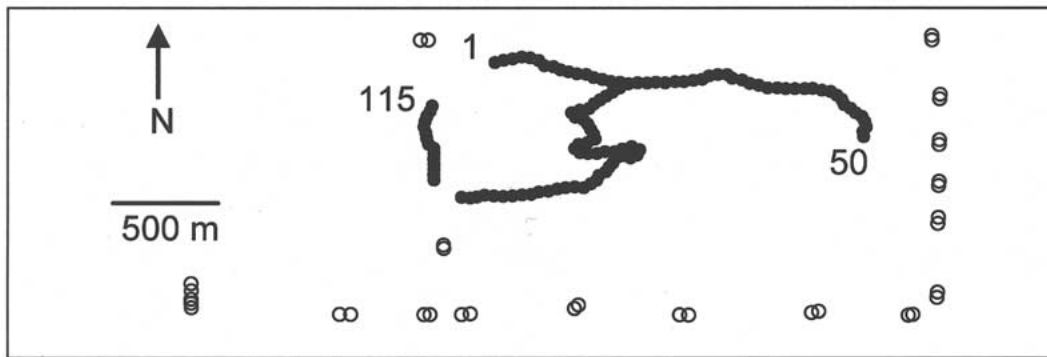


FIG. 1. Arrangement of Tree Swallow boxes at the St. Denis National Wildlife Area, Saskatchewan. The arrangement meant that random dispersal within the grid would not have a simple pattern (see Fig. 4). Nest box numbers 1, 50, and 115 reveal the order in which the grid historically increased in size (see Table 1). The paired boxes (open circles) outside the grid boxes (solid circles) were used only in 2001 to estimate dispersal outside the grid.

picked up and replaced. Not all manipulated clutches within a trio of treatments survived to fledging (usually because of predation); thus, number of clutches among treatments was 145, 150, and 146 for reduce, control, and add, respectively. Analyses include incomplete trios because that did not affect conclusions presented below.

*Missed dispersal.*—Missed dispersal increases the farther one travels from the center of a survey area (Barrowclough 1978, Koenig et al. 2000). Baker et al. (1995) corrected for that error by computing for each dispersal event the probability that an individual had moved to unsurveyed versus surveyed suitable habitat. In our case, because we only actively checked nest boxes and not natural cavities, dispersal to the latter would be missed both on and off our grid. Nor could we experimentally measure a correction factor by monitoring dispersal to newly erected boxes outside the grid (Fig. 1), because creation of vacant breeding sites may artificially reduce dispersal (Shutler and Weatherhead 1994). Moreover, because we have detected no natural nest sites, the empirical correction factor is 0 for all our boxes, although we know it is higher than that. We thus caution readers of that potential bias and note that at peripheral boxes (Fig. 1) erected during the 2001 breeding season, 9% of adults captured were breeding dispersers, and 21% were natal dispersers, which is expected given differences in dispersal distances.

*Data analysis.*—Survival and recapture probabilities ( $\pm$ SE) were estimated with program MARK using Cormack-Jolly-Seber models for live recapture data (White and Burnham 1999). Other analyses were performed in SAS (SAS Institute 1990) and for those means are plus or minus standard deviation ( $\pm$ SD). We used correlations for bivariate analyses, and general linear models where we had multiple explanatory variables.

Our tests on causes of breeding dispersal assumed that adults captured in a nest box were responsible for eggs or nestlings contained therein, but that may not always be the case. First, to minimize error arising from early season turnover at boxes, we assigned reproductive effort only to adults captured after eggs had been laid. Second, if two adults of the same sex were captured in a nest box, we designated those individuals caught before nest initiation date as floaters, or after nest initiation those caught as the second individual of the same sex. If, however, adults were found breeding in another box in the same year, they were designated as visitors at the nest box in which they probably did not breed. Birds that bred in natural cavities should be classified as visitors, so some misclassification was possible. Dispersal analyses were based only on putative breeders. Because >50% of Tree Swallow nests typically have extrapair young (e.g. Lifjeld et al. 1993, Barber et al. 1996), a male's breeding success often is not the same as the clutch in his nest. Because DNA fingerprinting was not done on that population, caution is necessary in interpreting male breeding success. For females, however, intraspecific brood parasitism (inferred if more than one egg was laid on any day) has been observed in only 1 of 1,302 nests at St. Denis (also see Lombardo 1988, Lifjeld et al. 1993). Hence, nest success reliably indicated the associated female's exact breeding success. Fourth, we experimentally added eggs to some individuals' clutches. Thus, analyses of effects of natural breeding success on dispersal were performed on unmanipulated nests only. Similarly, for tests of the consequences of dispersal on breeding success, we could not use data from manipulated nests on fledgling production.

Because capture effort and success varied among years, and because our grid of nest boxes was not

complete until 1993, apparent dispersal could have varied among years. Hence, we tested whether year was a significant covariate in general linear models.

## RESULTS

*Demographics.*—Excluding the first year of the study, an average of 96% of our boxes attracted at least one Tree Swallow pair to nest in them (Table 1). In 1,188 nest-box-years combined, we observed 114 (8.7% of the 1,302 total) second nests. Since 1995, when consistent capture effort began (estimates given below), 927 different adults were captured breeding; of those, 20.0% were initially banded as nestlings (local recruits) and remaining individuals were immigrants. More than 95% of adults were captured only once in any year. We calculated the proportion of nestlings that attained breeding status following Koenig et al. (2000). Using data after 1995 (because of consistent capture effort), and including only up until 2000 (because birds banded in 2001 had not had an opportunity to recruit), 3,354 nestlings were banded (Table 1). Of those, 3,190 disappeared, and 165 recruited locally. Meanwhile, 586 new, unbanded immigrants recruited. Thus, assuming that immigration equals emigration (which is the best we can do without knowledge of dispersal outside the study area), 586 of 3,189 (18.4%) of young dispersed to breed, and 165 of 3,354 (4.9%) young recruited locally to breed, so that in total during that interval, 23.3% of nestlings survived to breed. The latter figure changes by at most 6% if different five-year intervals are considered. No birds that we captured had initially been banded anywhere but at St. Denis; we are not aware of any other banded Tree Swallow population within 35 km. Of 1,942 adult capture events (i.e. counting each adult once for each year in which it was captured) since the start of the study, 70 floaters were female and 20 were male, and 36 visitors were female and 24 were male; the remaining 92% were putative breeders at a single nest box per year.

Disregarding manipulation effects, annual variation, or other factors influencing survival (R. G. Clark unpubl. data), Program MARK estimated virtually identical apparent survival probabilities for female and male adults ( $\phi = 0.51$ , 95% CI = 0.48–0.54). Recapture probability (probability that a bird is alive and is captured breeding in a nest box on the study area) varied among years because of differences

in capture effort and weather. In particular, unusually cold, rainy weather in 1993 caused almost complete nest failure (Table 1; R. G. Clark unpubl. data), and recapture probabilities in that year were  $0.48 \pm 0.07$  for females and  $0.20 \pm 0.05$  for males because adults were not entering nest boxes to feed young (which is when we normally captured them). From 1995 to 2001, more intensive, systematic capture effort resulted in recapture probabilities of 0.79 (95% CI = 0.71–0.85) for females, and 0.85 (95% CI = 0.78–0.91) for males. Those values are still lower than for most years because significant chick mortality also occurred in 1999, again making adults difficult to capture.

*Breeding dispersal.*—We exclude dispersal events that followed clutch manipulations in the following analysis. Breeding dispersal was not normally distributed (Fig. 2), so we used nonparametric tests for univariate analyses. Male breeding dispersal was significantly less than that of females (Fig. 2; median distance moved by females = 129 m or roughly four boxes, by males = 28 m or roughly one box; Wilcoxon  $Z = 5.3$ ,  $P < 0.001$ ). In a general linear model, year was not a significant predictor of breeding dispersal (for females,  $F = 1.2$ ,  $df = 10$  and 156,  $P = 0.29$ ; for males,  $F = 1.4$ ,  $df = 9$  and 147,  $P = 0.18$ ), so it was eliminated from analysis. Within the preceding data, there are multiple dispersal events for 25 of 134 females and for 24 of 127 males (Fig. 2). Also, breeding dispersal distance tended to decrease as adults aged (female  $r_s = -0.24$ ,  $P = 0.002$ ; male  $r_s = -0.23$ ,  $P = 0.004$ ; also see Robertson et al. 1992). To limit effects of age, and so that each

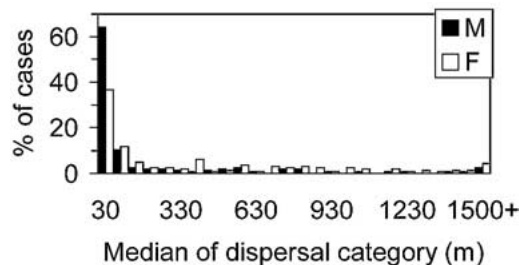


FIG. 2. Median breeding dispersal was shorter for 154 male (M) than for 161 female (F) Tree Swallows. Those data include multiple dispersal events for some individuals (see text). Data are pooled for 60 m intervals; adjacent nest boxes were at least 30 m apart (Fig. 1).

individual appeared only once in an analysis, we randomly selected one dispersal event for each individual, and repeated that resampling of our data 1,000 times (Westfall and Young 1993). Higher previous fledgling production was only weakly associated with decreased female breeding dispersal (mean  $r_s \pm 95\%$  CI from the 1,000 repetitions =  $-0.15 \pm 0.002$ ,  $P = 0.10$ ) and not associated with male breeding dispersal (mean  $r_s \pm 95\%$  CI =  $0.06 \pm 0.003$ ,  $P = 0.45$ ). There was also no evidence of curvilinear pattern to dispersal (Fig. 3; neither the square or cube of number of fledglings was significant in general linear models,  $P > 0.40$ ).

**Natal dispersal.**—We judged that distribution of natal dispersal data (Fig. 4) was sufficiently normal to be analyzed parametrically; results were comparable when analyses were nonparametric. Of 4,730 nestlings banded before 2001, 4.3% were detected as recruits (Table 1; including young from manipulated nests). Assuming an equal sex ratio at banding, and excluding eight birds that were not sexed, females ( $n = 73$ ) tended to recruit within the grid at a lower rate than did males (binomial test,  $n = 122$ ,  $P = 0.0002$ ; Robertson et al. 1992 found no difference). Nonetheless, natal dispersal detected within the grid did not vary by sex (data mean for females =  $853 \pm 521$  m, males =  $812 \pm 492$  m;  $F = 0.3$ ,  $df = 1$  and  $193$ ,  $P = 0.59$ ), so we pooled sexes and included individuals of unknown sex in subsequent analyses.

Of recruits, 84 were seen one year after, 81 were not seen until two years after, 34 were not seen until three years after, 3 were not seen until four years after, and 1 was not seen until seven years after fledging. If those delays are consistent among years, they lead to a revised, projected recruitment of 4.8% for birds banded before 2001. Regardless, natal dispersal distance within the grid was unrelated to the interval between banding and recapture ( $r = 0.03$ ,  $P = 0.72$ ). Moreover, in analyses that follow, interval was not significantly associated with previous or subsequent breeding success.

The distribution of natal dispersal distances (mean =  $826 \pm 496$  m) was broadly similar to that on the basis of all possible interbox dispersal distances (Fig. 4). Because of the irregular arrangement of nest boxes (Fig. 1), an individual's dispersal distance was not directly comparable to all those possible. To deal with that potentially confounding factor, we randomly chose

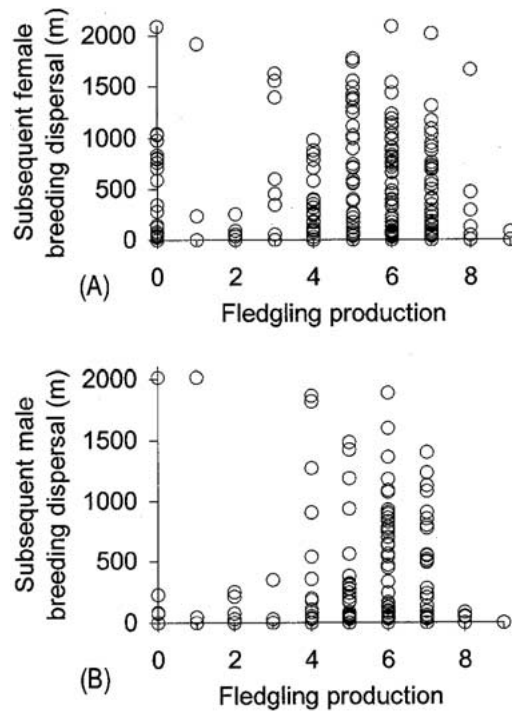


FIG. 3. Tree Swallow fledgling production for females (top) and males (bottom) was not significantly associated with subsequent breeding dispersal.

an eventual breeding nest box for each nestling, compared those random dispersal distances with actual dispersals, and repeated that 1,000 times (Westfall and Young 1993). Observed dispersal distance averaged 26 m more than randomly generated dispersal distances, but only 27 of 1,000 tests were significant versus 50 expected by chance.

Neither year ( $F = 1.2$ ,  $df = 10$  and  $108$ ,  $P = 0.30$ ) nor the (unmanipulated) number of siblings leaving the nest ( $F = 2.3$ ,  $df = 1$  and  $108$ ,  $P = 0.13$ ) were associated with natal dispersal distance ( $n = 120$ , model  $F = 1.3$ ,  $df = 11$  and  $108$ ,  $R^2 = 0.11$ ,  $P = 0.25$ ). There was no evidence of a curvilinear pattern to dispersal (again, square and cube of number fledging were not significant in general linear models;  $P > 0.50$ ).

**Clutch manipulations and dispersal.**—Removing or adding eggs did not influence subsequent female (median = 253, 310, and 305 m for 53 reduce, 63 control, and 61 add clutches, respectively; Kruskal-Wallis test,  $\chi^2 = 1.0$ ,  $P = 0.62$ ) or male breeding dispersal (median = 125, 114, and 215 m for 39 reduce, 52 control, and 53 add clutches, re-

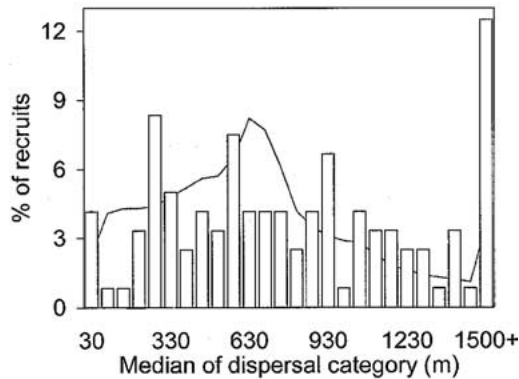


FIG. 4. Natal dispersal (bars) by 203 Tree Swallows was approximately random when compared to the distribution of all 13,110 possible interbox distances (solid line). Data are pooled for 60 m intervals; adjacent nest boxes were at least 30 m apart (Fig. 1).

spectively;  $\chi^2 = 0.2$ ,  $P = 0.90$ ). (Those dispersal distances are higher than from unmanipulated nests [see above], even if comparisons are restricted to controls. That implicates clutch manipulation years rather than clutch manipulations as the probable explanation.) Manipulations also did not significantly affect natal dispersal (mean [m] for 16 reduce =  $940 \pm 464$ , for 29 controls =  $779 \pm 472$ , for 36 add =  $783 \pm 471$ ;  $R^2 = 0.02$ ,  $F = 0.7$ ,  $df = 2$  and  $78$ ,  $P = 0.49$ ).

*Consequences of dispersal for subsequent breeding success.*—Because of variation in reproductive success among years caused by inclement weather (see above), year was a significant predictor of breeding success for females (Table 2); but female breeding dispersal, previous fledgling production, and interaction between dispersal and previous fledgling production were not significantly related to subsequent fledgling production. Results were similar for males (Table 2).

Fledgling production following natal dispersal from and to 86 unmanipulated nests was not significantly related to year, dispersal distance, previous fledgling production, or interaction between dispersal and previous fledgling production (Table 2). If we included natal dispersal from manipulated nests ( $n = 142$ ), year became a significant predictor of fledgling production ( $F = 3.8$ ,  $df = 9$  and  $130$ ,  $P = 0.0003$ ) largely because the bad weather in 1993 also occurred when manipulations were done; other variables were not significant in the latter model. Even

if dispersal within the grid was not associated with significant variation in subsequent breeding success, it is possible that local recruits might have an advantage over immigrants. However, there was no evidence of a difference for either females (244 immigrants produced a mean of  $4.9 \pm 1.6$  fledglings per breeding attempt, and 42 local recruits produced  $4.5 \pm 1.9$  fledglings;  $F = 2.4$ ,  $df = 1$  and  $284$ ,  $P = 0.12$ ) or males (186 immigrants,  $5.0 \pm 1.4$  fledglings, 81 local recruits,  $5.0 \pm 1.9$  fledglings;  $F = 0.0$ ,  $df = 1$  and  $265$ ,  $P = 0.97$ ).

*Cues about where to disperse.*—Given the weak associations between reproductive success and dispersal, and between dispersal and subsequent success, we asked whether there were cues that could aid Tree Swallows in deciding where to nest. One useful predictor would be nest success at a particular nest box, which might relate to a variety of factors, such as microclimate or predator home ranges (in our case, House Wrens). We computed correlations between number of young fledging in successive years (i.e. 1990 with 1991, 1991 with 1992, etc.) within specific boxes, excluding second attempts and manipulated clutch sizes. That resulted in 11 correlations, none of which was significant (all  $P > 0.11$ ).

#### DISCUSSION

*Breeding dispersal.*—Contrary to many studies, greater breeding dispersal following poor breeding success (Greenwood and Harvey 1982, Robertson et al. 1992, Clark and Shutler 1999) was not observed. Several studies have found no relationship between previous breeding success and breeding dispersal (e.g. Delius 1965, Wiklund 1996). For breeding dispersal to be adaptive, there needs to be variability in breeding success at different locations. Also, breeding success should be predictable among years (Boulinier and Danchin 1997). In support of that, Bollinger and Gavin (1989) found that, at a high-quality Bobolink (*Dolichonyx oryzivorus*) breeding site, dispersal of failed and successful nesters was not significantly different; whereas at a poor quality breeding site, dispersal was much greater for failed nesters. Similarly, Haig and Oring (1988) found that Piping Plover (*Charadrius melodus*) breeding dispersal was not influenced by breeding success at a high-quality site. In contrast, in most

TABLE 2. Previous dispersal, previous fledgling production, and interaction between those variables were not related to subsequent fledgling production. Response variables are given above results of separate ANCOVAs where year was a class covariate.

Explanatory variable	df	F	P
<b>Female fledgling production following breeding dispersal (n = 69)</b>			
Year	7	4.7	0.0003
Previous breeding dispersal	1	0.0	0.92
Previous fledgling production	1	0.1	0.72
Previous dispersal × previous fledgling production	1	0.0	0.84
Overall model ( $R^2 = 0.38$ )	10	3.6	0.001
<b>Male fledgling production following breeding dispersal (n = 82)</b>			
Year	8	2.5	0.02
Previous breeding dispersal	1	0.7	0.42
Previous fledgling production	1	0.0	0.99
Previous dispersal × previous fledgling production	1	0.5	0.47
Overall model ( $R^2 = 0.30$ )	11	2.8	0.005
<b>Fledgling production following natal dispersal (n = 86)</b>			
Year	9	1.8	0.08
Previous dispersal	1	1.4	0.30
Previous fledgling production (of parents)	1	1.4	0.24
Previous dispersal × previous fledgling production	1	1.8	0.18
Overall model ( $R^2 = 0.21$ )	12	1.6	0.10

years, >85% of our nests produced fledglings, and that high success rate may be unattainable by dispersing off of the grid. Moreover, we observed that breeding success was not predictable at specific nest boxes. Also, Tree Swallows do not defend foraging areas, so dispersal does not affect access to food. Nor does population density appear to affect the proportion of nests containing extrapair young (Conrad et al. 2001). Hence, two conditions promoting adaptive dispersal, variable and predictable breeding-site quality (Switzer 1993, Doligez et al. 2002), were absent on our grid. In addition, cleaning of nest boxes may lower ectoparasite loads, or nest boxes may be larger than natural cavities, so that our nest boxes could be of higher quality than natural cavities (see Robertson and Rendell 1990). Low densities of natural cavities would further constrain dispersal. On the other hand, we observed lower box fidelity (percentage of recaptured birds breeding in the same box in successive years; 101 of 387 females = 21% and 139 of 335 males = 41%) than did Robertson et al. (1992; 33% fidelity for females, and 66% for males). Because, recapture probabilities for our adults were close to 80%, that suggests that <20% of swallows in our population used natural cavities whereas most move among boxes. Lower fidelity at our nest boxes could

indicate that competition for (and consequently turnover) was greater than in the Ontario study site. That is supported by our occupancy rate of 94% versus the 50–60% observed at many other locales. However, N. Wheelwright (pers. comm.) has found comparably low box fidelity (24% of 91 females) with ~50% occupancy on Kent Island. Thus, reasons for low box fidelity are unclear.

Aside from nest-box quality, one would predict greater fidelity to mates with a history of high breeding success. However, despite high reproductive success within our grid of nest boxes, we found only 17% ( $n = 125$  pairs where both survived and were recaptured) of individuals kept the same mate in successive years, which is consistent with Robertson et al. (1992). Consequences of switching mates have been assessed particularly well in seabirds; divorces may result in short-term declines in breeding success but may provide higher lifetime reproductive success (Coulson 1972, Ollason and Dunnett 1978). However, most passerines may be too short-lived to substantially improve their lifetime breeding success via divorce. More importantly, the high frequency of extrapair paternity in Tree Swallows suggests that pair bonds are poor indices of mate fidelity. Opportunities for extrapair copulations may further reduce

costs associated with dispersal, because no matter where an individual breeds, it may be able to find a quality mate (also see Ramsay et al. 1999).

Female Tree Swallows had greater breeding dispersal than males, which is the typical pattern for birds (Greenwood and Harvey 1982). Sex-biased dispersal is usually ascribed to resource defense; in monogamous species where one sex defends resources to attract mates, the other sex usually disperses longer distances (Greenwood and Harvey 1982). Because high population density is also predicted to provoke greater dispersal (but see Hines 1986), we could possibly explain our female-biased dispersal as being because of higher female than male density (Spear et al. 1998). However, we have no reliable estimates of floater population size.

*Natal dispersal.*—Larger brood size has been positively related (Fleischer et al. 1984, Nilsson 1989) or, as we found, unrelated to natal dispersal distance (Nilsson 1989, Wheelwright et al. 1991). High fledgling production may be indicative of quality breeding sites, but that could be balanced by costs of more intense local competition, leading to an ideal free distribution (Fretwell and Lucas 1970, Greenwood et al. 1979, Nilsson 1989). Unfortunately, population density is difficult to measure when almost all boxes are occupied each year, and where size of the floater population is unknown.

Twenty-nine pairs of siblings accounted for 58 of the 203 (29%) natal returns we recorded. In a given year, an average of 440 fledglings are produced from an average of 99 nests on our grid, for an average of 4.44 fledglings per nest. There are thus  $440 \times 439$  possible pairs of nestlings; of those  $4.44 \times 3.44 \times 99$  pairs would be siblings, or ~1.5% (binomial test,  $P < 0.001$ ; also see Morton 1992, Brown and Brown 1996, Shutler et al. 2004). The high proportion of siblings in the natal returns could relate to genetic predispositions for low dispersal (Greenwood et al. 1979, Fleischer et al. 1984, Johnson and Gaines 1990), high survival because of high-quality parents (Oring and Lank 1984), factors relating to the nest environment that are independent of relatedness (Brown and Brown 1996, Fleischer et al. 1984), or a combination of those.

*Study design.*—Given the artificial nature and spatial distribution of nest boxes, it is worth remarking that our data revealed both breeding and natal dispersal patterns comparable (i.e. shapes of the distributions) to those reported

for natural populations of other avian species (Barrowclough 1978, Clark and Shutler 1999, Shutler and Weatherhead 1994, Daniels and Walters 2000, Koenig et al. 2000). Other aspects of Tree Swallow breeding biology are also broadly similar between natural and nest box studies (Robertson and Rendell 1990, Barber et al. 1996). Thus, the same costs and benefits of dispersal in natural populations likely apply to nest-box studies.

*Clutch manipulations and dispersal.*—Most of our understanding of dispersal comes from observational studies; few studies have experimentally manipulated conditions that could affect dispersal. For example, Bollinger and Gavin (1989) compared between-year return rates of Bobolinks that lost nests to haying versus unmanipulated controls and found lower return rates in the haying treatment. Shutler and Weatherhead (1994) increased density of available Red-winged Blackbird (*Agelaius phoeniceus*) territories by removing territory owners and found that natal dispersal (movements by floaters before they began breeding) was decreased by creation of vacancies. Doligez et al. (2002) increased dispersal by experimentally decreasing reproductive success. Those results suggest that experimental manipulations can mimic natural influences on dispersal, and researchers studying costs of reproduction should ensure that if they do clutch manipulations, that those do not affect dispersal. Manipulations could also affect natal dispersal for other reasons. If clutch reduction increases nestling growth rates (e.g. Cronmiller and Thompson 1980), those birds may either stay closer to home because they are better equipped to establish social dominance (Murray 1967, Nilsson 1990), or they may disperse farther because they have more opportunity for prospecting (Drilling and Thompson 1988, Reed et al. 1999). Opposite effects would be predicted for nestlings from clutch additions. Doligez et al. (2002) observed increased breeding dispersal for experimentally enlarged broods that had low growth rates. In our case, manipulations affected neither breeding nor natal dispersal. Thus, it appears that differential dispersal (and hence probability of recapture) following clutch manipulations does not explain the lack of evidence for costs of reproduction in Tree Swallows (De Steven 1980, Wheelwright et al. 1991, Murphy et al. 2000).

*Consequences of dispersal.*—Many researchers

have found that the distance traversed in response to influences such as breeding success had no significant effect on subsequent fitness (Drilling and Thompson 1988, Badyaev and Faust 1996, Robinson and Oring 1997). It may therefore be unclear why dispersal patterns persist, because no obvious selective advantages have been identified (e.g. Spear et al. 1998). A problem with simply comparing breeding success relative to dispersal distance is that that fails to take into account the potential interaction between dispersal distance and antecedent breeding success. Optimal dispersal is facilitated by cues about future fitness (Jackson et al. 1989). In some situations, an area's previous breeding success may predict its future breeding success (e.g. Blancher and Robertson 1985, Sonerud 1985), but in others, there may be little predictability (Filliater et al. 1994, Clark and Shutler 1999, this study). That may explain why we found no negative consequences to breeding dispersal within our grid, and why we found no significant interaction. However, prospecting should not be expected when there is little variation in quality among breeding sites (Boulinier and Danchin 1997, Reed et al. 1999), and yet that behavior has been reported for Tree Swallows using nest boxes (Lombardo 1987); that may relate to differences among more distantly separated breeding sites. Alternatively, prospecting is an innate behavior that retains its adaptive value in populations using natural cavities.

In some studies, higher breeding success or higher survival (a strong correlate of breeding success) has been observed in immigrants versus locally produced birds (Clobert et al. 1988, Nilsson 1989); immigrants would primarily be natal dispersers. In our study, fledgling production did not differ between local recruits versus newcomers. Additional studies are needed to identify causes of those disparate results, although data on antecedent breeding success for immigrants will often be lacking.

*Conclusion.*—We cannot completely assess fitness consequences of dispersal because we could not follow all individuals (Koenig et al. 1996); consequences will be influenced by the surrounding habitat matrix that is incompletely characterized. However, our results suggest that the majority of breeding dispersal is within our grid, whereas the majority of natal dispersal is off the grid, meaning conclusions for young birds need to be treated more cautiously.

Our grid of nest boxes is likely an island of exceptional breeding habitat, and dispersal within that grid probably has few fitness costs, whereas dispersal from the grid potentially has many (Bensch and Hasselquist 1991). Grid (as opposed to box) fidelity (Fig. 2) we observed is consistent with Switzer's (1993) predictions under those constraints. However, breeding success alone fails to explain why breeding dispersal is so short within the grid. We recommend that the analytical approach used here, especially with respect to analyzing consequences of dispersal after controlling for antecedent breeding success, be attempted where there is a gradient in breeding conditions, and where there is more site-specific predictability.

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