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Floating Populations of Female Tree Swallows

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A floating population is a surplus of nonbreeding individuals during the breeding season that are able and willing to establish a territory and breed if the necessary resources become available (Brown 1969). Floaters often are excluded from breeding due to competition for limited breeding resources. Floating populations of males have been reported for many bird species (e.g. Hensley and Cope 1951, Stewart and Aldrich 1951, Delius 1965, Watson and Jenkins 1968, Power 1975, Smith 1978, Rutberg and Rohwer 1980, Weatherhead and Robertson 1980), but there are relatively few reports of female floating populations (Watson and Jenkins 1968, Harris 1970, Knapton and Krebs 1974, Smith 1978, Hannon and Zwickel 1979, Saether and Fonstad 1981, Hannon 1983). One reason for this bias is that intrasexual competition for breeding opportunities tends to be very intense among males relative to females (Selander 1972). Intense competition among females would be expected in hole-nesting species, where populations are limited by the availability of suitable nest sites (Holroyd 1975). If nest sites are limiting breeding opportunities, then females that are excluded from breeding may form a floating population. The purpose of this study was to estimate the extent and composition of female floating populations in a hole-nesting species, the Tree Swallow (*Tachycineta bicolor*). One-year-old female Tree Swallows have a distinct brown-blue subadult plumage, whereas older females have a blue adult plumage (Hussell 1983). This allows for a comparison of the proportion of one-year-old females in the breeding and floating populations.

The study was conducted during 1983 and 1984 at the Queen's University Biological Station, near Chaffey's Lock, approximately 50 km north of Kingston, Ontario. Two Tree Swallow populations were studied, both of which have been established for at least 5 yr. These appear to be 2 separate breeding populations, since only 2 out of 50 individuals that have been captured in the last 2 or 3 consecutive years are known to have moved between populations. One study site, the New Land (NL), was about 10 ha in size and consisted of several hay fields and two small ponds. The area was bordered by deciduous forest and was less than 1 km from open water. All nest sites were plywood nest boxes, and most were mounted on aluminum posts. The other study site, the Northeast Sanctuary (NES) of Lake Opinicon, was 10 km from the NL. Nest sites were distributed over approximately 5 ha of open, shallow water and consisted of both nest boxes and natural hollow stumps. The size of both populations increased between 1979 and 1981, but has remained stable since 1982. In May 1982, there were 54 breeding pairs in the NL and 30 pairs in the NES.

As an alternative to creating nesting opportunities by removing breeding females, we provided a surplus of nest boxes late in the season to attract females that had been excluded from breeding during May. Most females with nest sites had laid eggs by this time, so these females were not expected to be attracted to the new nest sites and prevent surplus females from settling. An attempt was made to band and individually color-mark all breeding females before erecting new boxes. Between 29 May and 16 June in 1983, 53 additional nest boxes were erected throughout the NL and NES (Table 1). In 1984, 45 new boxes were erected between 5 and 14 June. All new boxes were more than 15 m from existing nest sites, and were erected a few at a time to permit general observation of the activity around newly provided nest sites. The boxes were checked every 3–4 days

TABLE 1. Total number of boxes erected, number of available nest sites, and number of occupied nest sites early (before 1 June) and late (after 1 June) in the breeding season for the NL and NES study sites over two years.

	1983		1984	
	Early	Late	Early	Late
NL				
Total no. erected	81	38	78	32
No. available sites	63	45	61	34
No. occupied (%)	51 (81)	19 (42)	56 (92)	19 (56)
NES				
Total no. erected	46	15	43	13
No. available sites	37	19	35	14
No. occupied (%)	33 (89)	10 (53)	34 (97)	10 (71)

for signs of nesting. Nesting females were defined as those females that laid eggs. First-egg date was used to indicate the relative timing of nest initiation and occupancy.

The percentage occupancy of available nest sites was calculated to estimate the extent to which nest sites limited breeding. The percentage occupancy ranged from 81 to 97% early in the season and from 42 to 71% late in the season (Table 1). The total number of boxes in place is not an accurate indication of the number of available nest sites. Tree Swallows defend an area of approximately a 15-m radius around their nest site, and can defend more than one nest site within that area (Harris 1979, Robertson and Gibbs 1982). Therefore, nest sites that were less than 15 m from sites already occupied by breeding Tree Swallows were considered to be unavailable. Nest sites occupied by other species, such as Eastern Bluebirds (*Sialia sialis*), Common Grackles (*Quiscalus quiscula*), and European Starlings (*Sturnus vulgaris*), were discounted both early and late in the season. Nest sites unoccupied by 1 June were included as available nest sites after 1 June, since they represented potential nest sites for nonbreeding birds.

The number of females nesting late in the season, in either newly provided boxes or available original boxes, was used to estimate the relative size of the floating population that was present during the peak of the nesting activity in May. The proportion of ultimately nesting females that nested after 1 June in the NL was 27% (19/70) in 1983 and 25% (19/75) in 1984 (Table 2). In the NES, 23% of the nesting females bred after 1 June in both years (10/43, 10/44). The results for the two populations and two years were treated separately to examine the consistency of the floating populations. These estimates assume that females that nested after 1 June had not nested earlier in the breeding season. At least 80% of the early-nesting females were banded and individually marked by 1 June. All the late-nesting females were unmarked, so it is unlikely that any had bred previously in these study areas. The general shortage of nest holes and the absence of other large breeding populations of Tree Swallows nearby reduce the likelihood that late-nesting females bred earlier outside these study areas.

The proportion of subadults in the floating population (47–79%) was higher than in the early-breeding females (4–18%, Table 2). This was true for both study areas and in both years [NL (1983): $\chi^2 = 34.96$, df = 1, $P < 0.001$; NL (1984): $\chi^2 = 18.38$, df = 1, $P < 0.001$; NES (1983): $\chi^2 = 7.47$, df = 1, $P < 0.01$; NES (1984): $\chi^2 = 11.04$, df = 1, $P < 0.001$].

From general observations, it was clear that the floaters responded quite rapidly to newly erected boxes, as individuals often began defending new boxes within hours. Without detailed observations of each pair, it was difficult to estimate when floaters became established at a nest site. The interval between time of box erection and first-egg date was 9.7 ± 3.3 days over both years and study sites. Although first-egg date may not be a good indicator of the time of establishment, it represents a maximum response time to new nesting opportunities.

This paper focuses on female floating populations in Tree Swallows, but there was also an opportunity to examine surplus males, since nest sites are limiting for both males and females. Except for two cases of polygyny in 1984, all the late-nesting females were mated monogamously with males that were not known to have bred previously. None of the late-nesting males was marked, but the origin of these males is uncertain since only about 30% of the early-breeding males were marked when the new boxes were erected. There was no evidence that early-nesting males were leaving their mates to breed with late-nesting females. It appears likely that there was a floating population of males as well as females.

A major assumption of the hypothesis that floating females are expected is that the availability of suitable nest sites prevents some females from breeding early in the season; therefore, one would expect the percentage occupancy to be 100%. Although the percentage occupancy in this study was high early in

TABLE 2. The number of adult and subadult females nesting early (before 1 June) and late (after 1 June) during the 1983 and 1984 breeding seasons in the NL and NES populations.

	1983		1984	
	Early	Late	Early	Late
NL				
Adult	48	4	54	10
Subadult	3	15	2	9
Total	51	19	56	19
NES				
Adult	27	3	30	3
Subadult	6	7	4	7
Total	33	10	34	10

the season, it did not reach 100% in either study area (Table 1). Why are some available nest sites left vacant even though there is a substantial floating population? Possibly the area defended by Tree Swallow pairs varies both individually and between populations. Some of the empty boxes could have been defended by adjacent pairs even though they were outside the 15-m range. Another alternative is that females were limited from breeding by a shortage of males (Leffelaar and Robertson 1984). However, there appeared to be a surplus population of males during the breeding season, and hence no shortage of mates.

We have shown that a surplus of females existed in two populations of Tree Swallows, for two consecutive years, and that these females would breed when nest sites were provided. There was a high level of intruder activity by females during May (Stutchbury 1984), which suggests that surplus females were present throughout the breeding season. It is important to establish that females that nested late in the season did so because they were prevented from breeding earlier, and not because they were not ready to breed early in the season. In 1982, the year prior to our experimental provision of late boxes, 11% (7/61) of the breeding females in the NL nested late. In 5 of the 7 cases, nest sites became available through abandonment of a nest, predation, polygyny, and early completion of clutches by other hole-nesting species, indicating that these late nesters were part of a floating population. We conclude that the total proportion of late-nesting females represents the number of surplus females that were prevented from breeding earlier, and therefore estimates the size of the floating population early in the season.

The extent of the floating population in 1983 and 1984 in both the NL and NES was estimated at 23–27% of the total female population. This could be an underestimate if some surplus females that were willing to breed early in the season were unwilling to breed in the new boxes. After the addition of new boxes late in the breeding season, the percentage occupancy was relatively low, indicating a surplus of nest sites. Although the nest-site limitation was removed, there could be other constraints that prevented some floaters from breeding. Breeding late in the season may have high costs in terms of lower reproductive output, and decreased amount of time to accumulate energy reserves for molt and migration (DeSteven 1978).

Surplus individuals that are excluded from breeding do not necessarily have to stay in the breeding area and form a floating population. Surplus female Tree Swallows may remain in a saturated habitat because of the opportunity to obtain nest sites that become available during the breeding season. The existence of a female floating population has several implications for the breeding biology of Tree Swallows. Not only must females compete intensely to obtain nest sites early in the season, but they may have to defend them from intruding females throughout the breeding season (Leffelaar and Robertson 1985). A high level of female-female aggression during the breeding season has been observed in both populations (Stutchbury 1984). A surplus of potentially breeding females means that males can easily replace their mates. Females may be selected to resist cuckoldry attempts since males could replace their mates if they had reason to suspect that cuckoldry had occurred (Leffelaar and Robertson 1984).

The proportion of subadults in the floating population was significantly higher than in the original breeding population. The presence of subadults in the floating population was unlikely to be a result of their inability to breed, since some subadults did breed early in the season. Floating populations with a large proportion of yearlings have been found in nonpasserine species (Watson and Jenkins 1968, Zwickel 1980, Hannon 1983). This is harder to document in passerines because subadult plumages are less common, especially for females (Rohwer et al. 1980). The large proportion of subadult floaters may reflect their competitive inferiority to older females. We are currently investigating the possibility that subadult plumages of one-year-old females are related to their role as floaters.

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Predation in Relation to Spacing of Kingbird Nests

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Western Kingbirds (*Tyrannus verticalis*) and Cassin's Kingbirds (*T. vociferans*) usually breed in different habitats, but both species nest together in open habitats with tall trees (Hespenheide 1964, Ohlendorf 1974, Blancher and Robertson 1984). We noted previously that breeding success of Cassin's Kingbirds was higher in habitats where they nested alone than in habitats where Western Kingbirds also nested (Blancher and Robertson 1984). Here we test the hypothesis that a negative relation between predation rate and the spacing of kingbird nests is responsible for lower breeding success where both species nest together (i.e. predation rate is higher because nests are close together).

Several studies have shown a positive correlation between density and predation rate on birds' nests (e.g. Krebs 1970, 1971; Fretwell 1972; Goransson et al. 1975; Dunn 1977; Weatherhead and Robertson