or all gray birds are males, most or all brown birds females. Both Friedmann (1950) and Brown and Amadon (1968) mentioned that the females' primaries are more reddish than the males', and Brown and Amadon (1968) further mentioned the females' narrower tail bars. Immatures in any plumage have more bars on the tail than do adults of the same sex or morph (Friedmann 1950, Smith and Temple 1982). Thus, the flock of 25 birds consisted of 20 light-phase adult males, 3 light-phase adult females, and 2 dark-phase adults; there were no immatures present. Not only the size of the flock but the sex and age ratios seem unusual. On the following day we saw two gray birds, presumably males, soaring together 4 km south of Ortiz, Guárico, Venezuela.

Haverschmidt (1964) stated that he had not seen the dark phase in Suriname, where it was much rarer than the light phase, although 3 of 14 Suriname specimens in the Leiden Museum were dark-phased. Brown and Amadon (1968) called the dark phase "uncommon." I have been unable to find other statements concerning the relative frequency of the morphs.

Apparently the Hook-billed Kite has not been considered a flocking bird, although it is well known as a soarer. Brown and Amadon (1968) stated that it is "encountered singly or in groups of two or three. At times it soars freely." Ridgely (1976) wrote "soars occasionally, usually not very high." It is possible that this species is more social than indicated in the literature, as it generally is not common and is not very well known. The related *Rostrhamus sociabilis,* as its name implies, is one of the more social kites, and the snails on which it feeds are, of course, patchily distributed because of their dependence on water. The tree snails on which *C. uncinatus* feeds are doubtless also patchy, and this species could respond by aggregating at food-source areas. The six nests found by Smith (1982) within 5 km of one another imply some concentration of resources. This would not entirely explain the flock described herein, however.

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Tree Swallows Cross a Polygyny Threshold

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Orians (1969) and von Haartman (1969) noted that polygyny is more widespread in passerine species whose nest sites are limited. The importance of resource distribution in influencing mating systems is now well documented. The Verner-Willson-Orians model (Verner 1964, Verner and Willson 1966, Orians 1969) emphasized that polygyny is expected when the distribution of resources is sufficiently inequitable that a female mating with an already paired male on a territory of superior quality will have reproductive success equal to or better than that of a female mating with an unpaired male occupying a territory of poorer quality. The difference between territories sufficient to favor polygyny has been termed the polygyny threshold, and a species is considered regularly polygynous when the incidence is 5% or greater (Verner and Willson 1966). Emlen and Oring (1977) added that polygyny occurs only when the operational sex ratio ("the average ratio of fertilizable females to sexually active males at any given time") deviates from unity in conjunction with some minimum degree of inequity in territory quality. Inequity in territory quality explains the occurrence of polygyny in several species, and differential food availability has been emphasized as the most important factor selecting for polygyny in these examples (Verner 1964, Willson 1966, Orians 1972, Wittenberger 1980). Male characteristics (Weatherhead and Robertson 1977, 1979) and predator defense (Elliott 1975) have also been identified as potentially important factors in the evolution and maintenance of polygyny.

I have been studying the breeding performance of two nest-box populations of Tree Swallows (*Tachycineta bicolor*). Resources are distributed in a manner that would predict the occurrence of polygyny, namely, limited nest sites in both populations in association with differential food abundance between

TABLE 1. Nest-box occupancy, 1977–1982.

	Sewage Lagoon		Backus Field	
Year	Boxes occupied / Boxes available	Percentage occupied	Boxes occupied / Boxes available	Percentage occupied
1977	28/36	78	11/15	73
1978	37/40	98	19/25	76
1979	40/40	100	27/29	93
1980	48/48	100	45/49	92
1981	48/48	100	49/49	100
1982	48/48	100	47/49	96

populations. Herein, I describe the appearance of facultative, resource-defense polygyny (Emlen and Oring 1977) in the Tree Swallow population with the superior food supply.

The two populations are 3 km apart, near Long Point, Ontario (42°30′N, 80°01′W), and are found in areas known as (1) Backus Field and (2) Sewage Lagoon (Port Rowan's secondary waste treatment ponds). Backus Field and the Sewage Lagoon have been occupied by nesting Tree Swallows for 7 and 6 yr, respectively. Nest boxes are 24 m apart in both areas, and they are arranged in a single row around the perimeter of the two ponds at the Sewage Lagoon and in two rows at Backus Field. All nest boxes are fitted with metal collars that exclude terrestrial predators. Two stationary, aerial tow nets (designed by D. J. T. Hussell) at each area provide a method of obtaining an index of aerial insect abundance. Commonly, a nest box is occupied and defended by one pair of birds. A female lays her eggs daily and incubates her 4–7-egg clutch alone, but both parents feed their offspring, which fledge at about 3 weeks of age. Tree Swallows are single brooded, but replacement clutches are laid. Adults were sexed by the presence of a brood patch or cloacal protuberance and, if not previously banded, were banded with standard U.S. Fish and Wildlife Service bands.

All nest boxes at the Sewage Lagoon and 90% of the boxes at Backus Field have been occupied since 1979 (Table 1). Tow-net trapping showed that the numbers and biomass of aerial insects were 10-times greater on average at the Sewage Lagoon than at Backus Field during the breeding season (Quinney unpubl. data). High insect productivity at waste treatment ponds is well documented (Swanson 1977). Differences in food abundance have coincided with differences in clutch sizes and growth of nestlings between areas. Although 6 eggs has been the modal clutch size in both locations, about 25% of the females at the Sewage Lagoon lay 7-egg clutches, but only 4% of the females at Backus Field do so. The distribution of clutch sizes is different between these two locations ($P < 0.001$, χ^2 test). Sewage Lagoon nestlings grow more quickly, reach heavier maximum weights, and have longer primaries at fledging than do young at Backus Field (Quinney unpubl. data).

During the 1980–1982 breeding seasons, I found seven nest boxes at the Sewage Lagoon (5% of the total) that contained 10–15 eggs in a single nest cup after laying was completed. Two females were found simultaneously on the nest cup in six of these nest boxes during late incubation and/or the early nestling period. For example, females 016 and 017 were found together in 1980 in nestbox 18 on 5 June (11 eggs present), 6 June (10 eggs, 1 young), 8 June (4 eggs, 7 young), and 11 June (1 egg, 8 nestlings). Females 047 and 495 were seen simultaneously in nest box 50 in 1982 on 27 May (12 eggs present), 1 June (12 eggs), 3 June (12 eggs), 10 June (4 eggs, 3 young), and 11 June (4 eggs, 3 young).

I did not capture two females simultaneously in the seventh nestbox. I trapped female 023 in this nestbox on 11 June 1981, when it contained 5 eggs and 6 nestlings; on 17 June, I captured female 416 delivering food to the 7 nestlings present. I had captured female 023 with a different female (582) 1 yr earlier during late incubation (10 eggs present) in a nest box 200 m distant from the one in which she nested with 416 in 1981. Females 047 and 495 also nested polygynously in more than one year. In 1982, these females nested 72 m from the nest box where both had nested in 1981. I do not know whether the male was the same in each year. None of the females nesting

TABLE 2. Breeding performance of females in relation to mating system. Means are given ±1 SD, with ranges in parentheses.

		Years	*n*	Per female: Eggs laid	Per female: Young hatched	Per female: Young fledged
Monogamy (exclusively)	Sewage Lagoon	1977–1979	62	6.0 ± 0.7 (5–8)	5.1 ± 1.3 (1–7)	4.8 ± 1.5 (0–7)
	Backus Field	1977–1979	52	5.6 ± 0.7 (3–7)	4.8 ± 1.2 (2–7)	4.0 ± 1.7 (0–7)
Monogamy (bigamous at some time)		1978–1982	12	6.2 ± 0.58 (5–7)	4.9 ± 2.23 (0–7)	4.7 ± 2.35 (0–7)
Bigamy		1980–1982	14	5.9 ± 0.79 (5–8)	3.6 ± 1.69 (1–6)	4.2 ± 2.50 (0–4)

in the seven nest-boxes with 10–15 eggs was ever found in a different nest box during the same breeding season, despite my having trapped monogamously breeding females in virtually all other nest boxes at both the Sewage Lagoon and Backus Field.

In three nest boxes that were watched closely, 12 eggs were laid in 11 days (two nests) and 11 eggs laid in 12 days. I subsequently observed these three pairs of females and one male per box delivering food to their nestlings. In 6 of the 7 polygynous matings, the first 5 eggs were laid daily, indicating that the second female (hereafter, secondary) moved into an already occupied nestbox after the first female (hereafter, primary) had laid most of her clutch. The remaining nest was not examined daily but contained six eggs 6 days after the appearance of the first egg. The spread in hatch dates was determined in six of these nest-boxes, and it averaged 6 days (range 2–12 days). Hatch spread for young from monogamous matings was 1–3 days. Only 1 of the 11 females involved in these 7 cases of polygyny was a yearling; the ratio of yearlings to older females breeding monogamously at the Sewage Lagoon from 1980 to 1982 was about 1:10. Female 582 hatched at the Sewage Lagoon in 1979 as 1 of 6 young in the nest box beside the one in which she nested polygynously in 1980. Her mother and sisters have not mated polygynously at the Sewage Lagoon. Her father and brothers were not among the two polygynous males that I captured.

I have breeding data on 7 of the 11 polygynous females when they bred monogamously. Four of these females bred at the Sewage Lagoon before mating polygynously. Two females nested at the Sewage Lagoon and one at Backus Field after mating polygynously. Monogamy is the most productive mating system, on average, for females (4.7 vs. 2.1 young fledged per female, $t = 2.626$, $P < 0.01$; Table 2). I excluded data from the years 1980–1982 for exclusively monogamous females, because I altered clutch and brood sizes for breeding performance experiments. It is noteworthy that 15% of the monogamous, older (not yearling) females at Backus Field and 6% at the Sewage Lagoon fledged 2.0 or fewer nestlings between 1977 and 1979 (Hussell and Quinney unpubl. data). Females who mated polygynously were more successful, on average, than these monogamists. Polygynous males were just as successful at fledging young as monogamous males at either Backus Field or the Sewage Lagoon (4.2 vs. 4.0 young fledged per male at Backus Field, $t = 0.276$, $P > 0.1$, and 4.2 vs. 4.8 young fledged per male at Sewage Lagoon, $t = 1.447$, $P > 0.1$). Polygynous males also had an additional female to assist them in raising their offspring. Nestlings in large broods from polygynous matings grew almost as well as smaller broods raised monogamously. The mean maximum weight was 24.8 g, and the length of the outermost primary at 16 days was 51.6 mm for nestlings in broods of six young raised monogamously at the Sewage Lagoon in 1980; the nestlings in the brood of eight raised by three parents reached a mean maximum weight of 24.4 g and the outermost primary averaged 48.8 mm at 16 days of age.

Forbush (in Bent 1942: 387) noted "occasionally three birds, usually two males and one female, engage in preparing a nest, incubating the eggs and feeding the young." Others have also seen more than two Tree Swallows feeding young in a nest [Wetherbee 1933, Lewis (in Bent 1942)]. De Steven (1980) suggested that there may be occasional polygyny in this species. Several times she trapped males feeding nestlings at two different nests (usually in adjacent nest boxes). Sheppard (1977) found three confirmed and four probable cases of nesting trios in 1972–1973. All of these involved at least one yearling female, but no clutch sizes were given, and none of the nests was more successful than average. Sheppard suggested that these trios were not polygynous but were cases of helpers at the nest (Skutch 1961). In 1974, Sheppard found one clutch of 11 eggs and one of 10 eggs. Differences in size, shape, and color of the eggs led her to conclude that each clutch had been produced by two females laying in a single nest. The 11-egg clutch was covered by new nesting material and replaced by a clutch of 3 eggs. Five young were "produced" from the 10-egg clutch. Her study area was, presumably, good Tree Swallow habitat when she observed these 10- and 11-egg clutches, because, not only were 98% of the nest boxes in Colony I occupied, but 25% of the females laid 7-egg clutches.

A combination of limited nest sites (causing the operational sex ratio to deviate from unity in favor of females) and a superior supply of food apparently has led to the appearance of polygyny at the Sewage Lagoon. Nest-site saturation occurred in one year at Backus Field also, but the poorer food supply apparently prevented the birds from becoming polygynous. Secondary females breed polygynously at the Sewage Lagoon, because they can occupy Sewage Lagoon sites only by breeding with already mated males. Wittenberger (1976) pointed out that the Verner-Willson-Orians model requires only that polygyny be advantageous to unmated females. Polygyny is advantageous to secondary females at the Sewage Lagoon if these females could not breed otherwise. Primary females at the Sewage Lagoon also appear to have little choice but to breed with a polygynous male, as most of their eggs have been laid by the time a secondary female appears. Thus, a primary female can either attempt to prevent the secondary female from nesting in her box or abandon her eggs. If she chooses the latter option, where would she renest? All nest boxes at the Sewage Lagoon and greater than 90% at Backus Field were occupied. The disappearance of some eggs and/or very young nestlings from all of the nest boxes where polygyny occurred suggests that females attempt to prevent other females from sharing one nest. For example, when mated monogamously, 0.45 eggs per female disappeared, were broken, or failed to hatch, and 0.09 young per female disappeared or died. The corresponding numbers for females mated polygynously were 2.34 eggs and 1.29 young per female.

Females who mated polygynously were less successful than monogamous birds breeding in nest boxes at the Sewage Lagoon. This would not necessarily be the case in the natural nesting habitat of tree cavities. Cavities could be distributed such that one male would defend more than one cavity and each cavity would be occupied by one female. Tree Swallows can defend more than one nest box when they are close together. Harris (1979) placed eight pairs of nest boxes so that each member of a pair was 1 m apart. Seven of these pairs of boxes were each defended by one pair of birds. Thus, I predict that I can increase both the incidence of polygynous matings at the Sewage Lagoon and the nesting success of the individuals involved by manipulating the number and arrangement of nest boxes.

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