TABLE 3

STANDARD DEVIATIONS OF THE FOUR VARIABLES IMPORTANT IN THE DISCRIMINANT FUNCTION ANALYSIS (VALUES ARE FROM 36 RANSOM GRID POINTS AND 36 CLUMPED POINTS WITHIN FOUR GRIDS)

		Grid number			
	Random	1	2	3	4
Vegetation height (1 m)	11.2	8.0	9.9	12.8	10.7
Vertical vegetation density	2.2	1.2	0.7	1.5	2.0
% ground cover	28.4	29.7	16.5	46.8	29.0
Horizontal vegetation density	318.4	93.8	145.8	462.2	325.6

respectively. The variability of each of the four variables important in discrimination was similar (Table 3).

Vesper Sparrows were found in areas where the vegetation was short and dense, with a relatively high percentage of ground cover, and not in areas where the vegetation was tall and patchy. In this study vegetation structure in used areas was similar to that found in territories of Vesper Sparrows with high reproductive success as described by Wray and Whitmore (1979). Wray and Whitmore (1979) stated that the higher amount of ground cover may be needed to conceal nests from predators. During the breeding season Vesper Sparrows feed primarily on arthropods (Evans, Am. Midl. Nat. 72:57–75, 1964), and it may be easier for birds to forage in short dense vegetation. Although my results are consistent with previous research, they are based on a small sample size, and caution should be used in generalizing from them.

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Male and female parental care in Tree Swallows.—Often, it is assumed that to maximize their fitness, parental investment by males in raising altricial nestlings is substantial in monogamous species (e.g., Trivers, pp. 136–197 *in* Sexual Selection and the Descent of Man, 1871–1971, E. C. Campbell, ed., Aldine Press, Chicago, Illinois, 1972; Emlen and Oring, Science 197:215–233, 1977; Wittenberger, pp. 271–349 *in* Handbook of Behavioral Neurobiology, Vol. 3, Social Behavior and Communication, P. Marler and J. G. Vandenbergh, eds., Plenum Press, New York, New York, 1979). Although some Tree Swallows (*Tachycineta bicolor*) mate polygynously (Quinney, Auk 100:750–754, 1983), most are monogamous. They are relatively short-lived and almost exclusively single-brooded (but see Hussell, Wilson Bull. 95:470–471, 1983). Plumage characteristics distinguish first year females from males and other females, but the plumage of older birds is monomorphic. Nestlings are brooded by their mothers until they are about 5 days old (Dunn, Wilson Bull. 91:455–457, 1979), they are fed aerial insects, and the fecal sacs produced by the young are

removed from the nest cavities. Thus, if typical assumptions are correct, male assistance in these activities should entail a contribution comparable to that of females. Here, I report the proportion of food deliveries, size of meals delivered and nest sanitation activity by male and female Tree Swallows mated monogamously.

Methods.—I studied a population of Tree Swallows breeding in nestboxes at the Port Rowan, Ontario (42°37′N, 80°27′W) secondary waste treatment ponds (hereafter, Sewage Lagoon). Nesting Tree Swallows have occupied Sewage Lagoon since 1977 when nestboxes were first erected. Plywood nestboxes stood about 1.5 m above ground attached to metal poles. All poles were fitted with large, metal cone-shaped collars that excluded terrestrial predators. Nestboxes were either 5 or 24 m apart, and were placed around the perimeter of the two ponds. Most of the 40–66 boxes have been occupied (minimum of one egg laid) every year, since 1977.

Nestboxes were visited three times daily to determine hatching times. A mean hatch date was calculated for each brood and ninth primary feathers were measured when members of a brood averaged 16 days old. Nestlings fledged at about 20 days but will leave their nests prematurely if handled after they are 16 days old. During the nestling period, adults were trapped in their nestboxes, sexed by the presence of a brood patch or cloacal protuberance, banded with U.S. Fish and Wildlife Service bands if not previously banded, and color-marked individually with magic marker on the throat, abdomen, and under-tail coverts. I did not collect data from first-year females because very few of them nested, and one-year-old females appear to differ from older ones in several reproductive variables (De Steven, Ibis 120:516–523, 1978). Most observations were made with an 8 mm movie camera that took single frame exposures each time a bird entered and left a nestbox. Observers with binoculars or telescopes watched additional boxes. Tree Swallows captured flying insects and delivered numerous items to their young in boluses of food. We trapped some adults inside their nestboxes and collected samples of food boluses before they were fed to the nestlings to determine meal sizes. I assumed that a meal was delivered each time a parent entered its nestbox.

Results.—We observed 10 pairs of swallows for 335 h in June 1984. During this period, 6590 meals were delivered to nestlings, of which 51% were provided by males (Table 1). On average, each brood received a meal every 3 min during daylight h (nestlings were not fed at night). Male and female deliveries did not vary greatly when nestlings were 5–10 days old (males: 49–55%, females: 45–51%). Generally, males removed fecal sacs more frequently than females, but there was more variation in fecal sac removal than in feeding (Table 1). Males and females delivered meals to their young that were similar in size (about 28 mg dry, N = 12 males and 12 females). This was close to the mean value of 24 mg (N = 48) observed in other years (Quinney, unpubl. data).

When a mate died, the remaining parent successfully raised nestlings alone. Two females and one male died during handling when their nestlings were between 4 and 9 days old. Sixteen of the 17 nestlings raised by a single parent fledged, but the remaining nestling that had been raised by a male died at 24 days. Nestlings in a brood of three young raised by a female grew as well as those raised by both parents in broods of the same size (Table 2) and better than broods of three raised by two parents in a population 3.25 km distant (Backus Field) where food was much less abundant than at Sewage Lagoon (Quinney and Ankney, Auk 102:245–250, 1985). The female that raised three young delivered an average of 234 meals daily to her brood during the week when the nestlings were 6–12 days old. Broods of three of the same age raised by both parents at Sewage Lagoon received an average of 272 meals daily. Nestlings in larger broods raised by a single parent did not grow as rapidly as those raised by two parents at either location (Table 2). There were no 7-nestling broods at Backus Field, where all of the nestlings died (presumably from starvation) in two broods of smaller size (Table 2). No broods failed completely at Sewage Lagoon.

TABLE 1

FOOD DELIVERIES AND FECAL SAC REMOVAL BY MALE AND FEMALE TREE SWALLOWS

Nestbox	Brood size	Brood age (days)	Hours observed	Number of food deliveries (%)			Number of fecal sacs removed (%)		
				Male	Female	Total	Male	Female	Total
5	6	6–12	90	1223 (51)	1169 (49)	2392	264 (58)	189 (42)	453
20	6	2–3	34	223 (53)	199 (47)	422			
39	6	5–7	31	435 (58)	315 (42)	750	89 (77)	26 (23)	115
44A[a]	4	4–12	118	877 (47)	995 (53)	1872	149 (60)	97 (40)	246
45	4	6–9	52	572 (54)	490 (46)	1062	69 (38)	114 (62)	183
6A,[b] 34B, 43, 44, 52	4–7	2–14	10	41 (45)	51 (55)	92			
All	4–7	2–14	335	3371 (51)	3219 (49)	6590	571 (57)	426 (43)	997

[a] Earlier, this male fathered a brood in a box nearby. Data presented here were collected after the nestlings in his first brood had fledged.
[b] Data from these 5 nestboxes are combined because each was observed only briefly.

TABLE 2
LENGTH OF NINTH PRIMARY (MM) OF 16-DAY-OLD TREE SWALLOWS

Location	Nestlings raised by	Brood size		
		3	6	7
Sewage Lagoon	male and female	51.2 (3)[a]	49.2 (15)	48.8 (6)
	female only	52.3 (1)		40.7 (1)
	male only			35.3 (1)
Backus Field	male and female	45.1 (7)[b]	49.0 (4)[b]	

[a] (Number of broods.)
[b] Excludes measurements from one brood where all nestlings died, apparently from starvation.

Delivery rates indicate that, on average, broods of 6 young, 4–16 days old raised by both parents, received about 2300 mg wet weight of insects per h. Weatherhead (Condor 86:187–191, 1984) estimated that the mean maximum weight of a fecal sac voided by a nestling 4–16 days old was about 390 mg. Therefore, parents at Sewage Lagoon removed about 1300 mg of fecal sacs hourly, or about 57% of the wet weight of insects delivered to their young.

Discussion.—Broods of six young received an average of about 250 meals per day through the 20-day nestling period. Each parent provided meals of the same size and in equal proportions to their nestlings. The equitable allocation of food provisioning duties by the sexes is consistent with the hypothesis that male assistance in brood-rearing is substantial in monogamous species raising altricial offspring. I cannot explain why males generally removed a disproportionate number of fecal sacs (57%) or why the number of fecal sacs removed by each sex was more variable than the number of food deliveries. Perhaps age and experience are important in this regard. Sample sizes were small, but my results indicate that although both parents were not required to raise nestling Tree Swallows when food was abundant (see also Gowaty, Am. Nat. 121:149–157, 1983), the growth of nestlings in large broods raised by single parents was inferior to that of nestlings raised by both parents (see also Weatherhead, Auk 96:391–401, 1979). Furthermore, I do not know whether the survival of single parents was affected by their increased workload. Emancipation of male Tree Swallows would facilitate polygynous matings. An important test would compare the behavior of assisted and unassisted females, and the growth and survival of their nestlings in both marginal and good food habitats.

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Extrapair copulations in the Tree Swallow.—Observations of extrapair copulations and male mate guarding are varied in the Hirundinidae. Beecher and Beecher (Science 205: 1282–1285, 1979) reported that male Bank Swallows (*Riparia riparia*) guarded their mates