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PREY SIZE SELECTION BY TREE SWALLOWS

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ABSTRACT.—Diets were determined for Tree Swallows (*Tachycineta bicolor*) that collected flying insects for nestlings and foraged at two locations, 3.25 km apart, where food abundance differed. At both locations, more than 99% of prey in the diets were 10 mm or less in length and at least 95% of the diets consisted of insects from the orders Diptera and Homoptera. Regardless of location, Tree Swallows were selective in the sizes of prey that they delivered to their young. They chose more valuable prey but did not completely reject less valuable items, and the diet was closer to the optimum at the location where food abundance was greatest. Received 9 November 1983, accepted 10 October 1984.

THE problem of food choice has received considerable attention recently (reviews by Pyke et al. 1977, Krebs 1978). According to optimal-foraging theory, efficient predators maximize their net rate of energy intake during foraging bouts by distinguishing between items of differing profitability, e.g. energy content per unit handling time (Emlen 1966, MacArthur and Pianka 1966, Schoener 1971, Charnov 1973). To achieve an optimal diet, predators should prefer the more profitable prey, ignore unprofitable prey regardless of how common they are, and be more selective when profitable prey are common (Pulliam 1974, Pearson 1974, Charnov 1976). Numerous laboratory and field studies have sought to test one or more of these predictions (e.g. Werner and Hall 1974, Emlen and Emlen 1975, Charnov 1976, Krebs et al. 1977, Davies 1977, Goss-Custard 1977, Zach 1978, Craig et al. 1979, Jaeger and Barnard 1981, Lacher et al. 1982, Sutherland 1982). Aerial insectivores such as the Hirundinidae apparently do not always forage in a manner consistent with all of these predictions. Common House-Martins (*Delichon urbica*) and Barn Swallows (*Hirundo rustica*) discriminate between prey

items primarily by size when they feed nestlings. These species prefer larger, more valuable prey items and show an increase in diet breadth with a decrease in relative rate of encounter with larger items as predicted by optimal-foraging theory (Bryant 1973, Turner 1982). Contrary to the theory, Turner (1982) found that small items of low value were included in the diet when high-ranking items were abundant and that more small items were taken when they were relatively abundant.

Using a comparative approach, we sought to determine whether Tree Swallows (*Tachycineta bicolor*) feeding nestlings discriminate between size classes of insects and, if so, whether the birds take more valuable prey and ignore the least valuable items. We also investigated whether Tree Swallows were more selective in their choice of food when high-ranking prey were more abundant. Pyke et al. (1977) emphasized that only when animals forage for an energy source such as plant nectar or different-sized items of one kind of food will the simple optimal-diet theories be predictive. The two Tree Swallow populations we studied were particularly appropriate for examining food-choice questions, because the swallows captured largely one type of food of different sizes (nematoceran flies from 1 to 10 mm in length) and one of the populations had a greater abun-

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dance of larger, more valuable size classes of these prey available to it.

METHODS

We studied two populations of Tree Swallows near Port Rowan, Ontario (42°37'N, 80°27'W) between 1979 and 1982. Backus Field and Sewage Lagoon (Port Rowan's secondary waste treatment ponds) are 3.25 km apart and have been occupied by breeding Tree Swallows since 1976 and 1977, respectively. There are about 50 pairs of Tree Swallows in each population nesting in boxes spaced at 24-m intervals in lines or grids. The only major difference between the environments used by the Tree Swallows appears to be the greater food supply at Sewage Lagoon; high insect productivity at waste treatment ponds is well documented (e.g. Swanson 1977).

Adults captured flying insects and delivered food to their offspring as a bolus of insects. We forced parents to depress a perch that extended across the box entrance in order to enter their nests. A depressed perch released a spring-loaded net covering the entrance hole and prevented the parent from leaving the box. An observer nearby then removed the food bolus from a parent's bill or throat with forceps and placed the bolus in a vial of 70% ethanol. Birds were sexed by presence of a brood patch (females) or cloacal protuberance (males), banded with standard U.S. Fish and Wildlife Service bands if not previously banded, and released. The breeding performance of yearling females differs from that of older females (De Steven 1978), and therefore we did not use boluses obtained from yearling females in the results that follow.

Flying insects were trapped in suspended nets similar to the "stationary aerial tow-nets" used by Johnson (1950). We used conical nets made from 1-mm square wire mesh screening that were 61-cm long, 30.5-cm diameter at the mouth of the net, and 2.5-cm diameter at the rear, where the cone opened into the center of a cylindrical sleeve (7.6-cm diameter × 15.2 cm). An opening at the lower rear of the sleeve allowed entry of insects into a jar of 70% ethanol. The center of the mouth of each net was 2 m above ground. We watched many birds forage near this height [Holroyd (1972) found that Tree Swallows in a population about 35 km southeast of Port Rowan spent 47% of their foraging time below heights of 4.6 m]. The nets were mounted on poles that enabled them to revolve so that the mouth of the net always faced into the wind. Insects flew or were blown into the nets and collected in the jar of ethanol. Two nets were placed among the nest boxes in each area. We estimated a maximal foraging radius of about 400 m from a given nest box at both locations, but during the nestling period most adults foraged within 250 m of their nests at both areas. The nets collected insects from shortly

after dawn until dusk on the days that food boluses were obtained. Regression equations (Hussell MS) were used to calculate hourly wind speeds at Backus Field and Sewage Lagoon in 1980 and 1981. We also calculated an index of the abundance of flying insects (mg dry weight/km wind) at each location for these years.

All insects from the net catches and boluses were identified to order except Dipterans, which were classified as either suborder Nematocera or other Diptera. All insects were measured to the nearest 1 mm. We weighed samples of insects trapped in the nets from each order or suborder and size class so that each of the years 1979–1981 was represented equally. Within years, insects were randomly chosen so that each day sampled was represented equally whenever possible. Insects were dried to constant weight using the following procedure (after Winberg 1971): samples of up to 90 individuals were transferred from 70% ethanol to number 1 Whatman filter paper and spread out as a single layer of insects for 15 min. Samples were then placed on preweighed trays and oven-dried for 3 h at 95°C. Thereafter, they were weighed on a Sartorius analytical balance to the nearest 0.1 mg, and mean dry weights were calculated (Table 1).

Tree Swallows may divide prey sizes into categories different from those described above. Therefore, we also classified prey as small, medium, or large in relation to the bill width of adult Tree Swallows, which Holroyd (1972) found to average 12.9 mm. Small prey were shorter than 25% of the average bill width (size classes 1, 2, and 3 mm); medium prey were 25–50% of the bill width (4, 5, and 6 mm); and large prey were longer than 50% of the bill width (7, 8, 9, and 10 mm).

RESULTS

Ninety-one boluses (3,318 insects) and 93 day-long net catches (4,258 insects) were obtained in June 1979–1982 during the nestling period (23 days sampled at Backus Field and 24 days at Sewage Lagoon). Brood size and age of young during the sampling period averaged 4.9 young and 9.4 days at Backus Field and 5.1 young and 8.7 days at Sewage Lagoon. The boluses showed that the birds fed on a continuous range of prey sizes of very few taxa. Seventy-four percent of the diet at Backus Field were Dipterans, most of which were Nematocerans (Table 2). Sewage Lagoon swallows captured Nematocerans almost exclusively. At both locations, at least 80% of all prey in the diet longer than 5 mm were Nematocerans. The longest insect obtained from a Tree Swallow was a 42-mm Odonatan, but

TABLE 1. Mean dry weight (mg) of insects from net catches. Numbers of insects weighed are in parentheses.

Taxon	Length (mm)	Sewage Lagoon	Backus Field
Nematocera	1	0.02 (90)	0.05 (24)
	2	0.07 (90)	0.11 (60)
	3	0.18 (90)	0.21 (60)
	4	0.25 (90)	0.28 (24)
	5	0.35 (90)	0.41 (15)
	6	0.57 (75)	0.73 (6)
	7	1.21 (75)	0.59 (12)
	8	1.49 (45)	1.10 (5)
	9	1.45 (12)	
	10	1.61 (7)	
Other Diptera	1	0.03 (6)	0.11 (7)
	2	0.11 (45)	0.25 (23)
	3	0.49 (11)	0.47 (39)
	4	0.68 (12)	0.94 (27)
	5	1.01 (8)	1.76 (12)
Homoptera	1	0.04 (25)	0.09 (42)
	2	0.11 (25)	0.18 (46)
	3		0.64 (11)
	4		1.33 (8)
Hymenoptera	2		0.28 (14)
	3		0.39 (16)
	4		1.23 (18)
	5		2.40 (3)

only 18 of 3,318 insects in the diet samples were longer than 10 mm (less than 0.7% of the insects in the diet of the birds, regardless of location). Similarly, only 2 of 4,258 insects caught in the suspended nets were longer than 10 mm. Therefore, we have excluded insects longer than 10 mm from the analyses that follow.

The insect taxa and the proportion of the taxa that were trapped by the nets were very similar to those in the diet of the Tree Swallows except other Diptera and the Homoptera at Backus Field (Table 2). In 1980 and 1981, the insect biomass index (mg/km wind) on the days that boluses were obtained was on average 8-fold greater at the Sewage Lagoon than at Backus Field. However, the absolute abundance of the two smallest size classes of insects found in the nets (1 and 2 mm) was similar between areas, but there were fewer larger prey at Backus Field.

Swallows were selective in the sizes of insects that they captured. At both locations the distribution of sizes of insects captured by the birds from the 10 size classes was significantly different from the distribution of sizes present

TABLE 2. Insect taxa in Tree Swallow diet and net catches. Percentages are based on total number of insects in all samples.

	<i>n</i>	Diptera			Other orders
		Nematocera	Other	Homoptera	
Backus Field					
Diet	43 ^a	44%	30%	21%	5%
Net	46 ^b	46%	8%	39%	7%
Sewage Lagoon					
Diet	48 ^a	90%	4%	5%	1%
Net	47 ^b	92%	4%	3%	1%

^a Number of boluses (for Backus Field, *n* = 26 females, 16 males, 1 sex unknown; for Sewage Lagoon, *n* = 25 females, 23 males).

^b Number of net catches.

in the nets (Kolmogorov-Smirnov one-sample test: *D* = 0.47 for Backus Field and 0.28 for Sewage Lagoon, *P* < 0.001 for both; Fig. 1). The two smallest size classes (1 and 2 mm) were most underrepresented in the diets of both populations in relation to their abundance in the nets. The distribution of numbers of insects captured as small, medium, or large also differed significantly from the distribution of these sizes present in the net catches ($\chi^2 = 3,559$ for Backus Field and 750 for Sewage Lagoon, *P* < 0.001 for both; Table 3).

Were the Tree Swallows selective of prey sizes in a manner consistent with optimal-foraging theory? To answer this question, we compared the expected rank order of prey-size consumption under an optimal-diet model with the rank order of occurrence of prey sizes in boluses. First, we assumed that handling time for all size classes of insects was uniform and trivial (indeed, it may be close to zero based on observations of foraging swallows). In other words, a Tree Swallow in flight does not slow down its search for food or lessen its ability to handle the next food item encountered by handling the item just encountered. We consider this reasonable because an adult Tree Swallow bill is wider than even the largest insects encountered at either location. Thus, a Tree Swallow should capture every insect encountered because some positive energy (or other value) is gained over a small interval of search time, but zero gain would result if that item were rejected. Second, we assumed that the birds foraged in a heterogeneous environment. The ae-

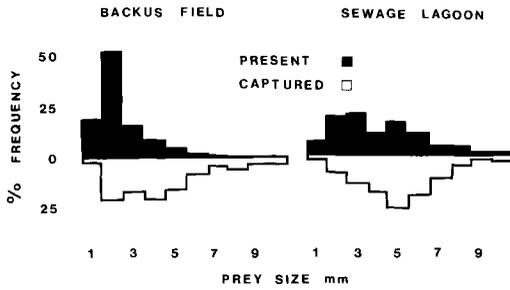


Fig. 1. Distribution of insect sizes in the net catches compared with those captured by Tree Swallows.

rial insect prey were commonly found in patches, and each patch was characterized by the abundance and size of individuals in it. We assumed that individuals in a patch were in the same size class (being largely conspecific and having emerged at about the same time) and that the more abundant size classes formed larger patches.

The optimal-foraging problem faced by the birds is their choice among patches of different profitability. The profitability of a patch, once encountered, will be proportional to its biomass per unit volume. Given the assumptions concerning patch size and provided that patches are distributed independently of distance (vertical or horizontal) from the nest, a good estimate of profitability is insect abundance \times biomass per insect. Our measure of profitability of a given prey size class is the biomass of each insect taxon/size class \times its relative abundance in the net samples. If Tree Swallows forage optimally, we predict that the insects found in a bolus, reflecting the choice of patches by a bird, should exhibit the same rank order of food sizes as the rank order of profitabilities, as estimated by the biomass of the size class \times the relative abundance in the net samples (see also Pulliam 1981). We do not predict that Tree Swallows will either always take a given prey size (or a patch of a certain prey size) or never take it, as would a model such as Charnov's (1976). Because patches vary temporally and spatially, so will optimal strategies. However, total consumption over an extended time period should follow the rank order of profitability. A secondary advantage of our predictions is that they suggest how Tree Swallows may choose between patches. The optical density of a patch

TABLE 3. Small, medium, and large prey in the diet and net catches.*

	Prey size		
	Small	Medium	Large
Backus Field			
Diet	533 (41%)	588 (45%)	183 (14%)
Net	615 (86%)	92 (13%)	7 (1%)
Sewage Lagoon			
Diet	385 (19%)	1,215 (61%)	396 (20%)
Net	1,689 (48%)	1,521 (43%)	332 (9%)

* Small, 1-3 mm; medium, 4-6 mm; large, 7-10 mm.

of insects in the visual field will be the product of the abundance and the size of the individuals in a patch (distance held constant). This coincides with our measure of profitability.

In general, value rankings were very similar to the rank order of occurrence of size classes in the diet at both locations (Fig. 2). For example, the 4 most valuable prey sizes at Backus Field (2-5 mm) were also the most common in the diet, contributing 77% of the diet. The least valuable items at Backus Field (6-9 mm) contributed less than 20% of the swallows' diet. Tree Swallows, then, preferentially foraged for more valuable prey but did not completely ignore the less valuable items. Additionally, the value of prey size classes differed between Backus Field and the Sewage Lagoon. The most valuable prey at the Sewage Lagoon was larger than the most valuable ones at Backus Field because of the greater abundance of larger prey at the Sewage Lagoon. The two most valuable sizes at Backus Field were 2 and 3 mm, but they were 5 and 6 mm at the Sewage Lagoon. Optimal-foraging theory predicts that Sewage Lagoon swallows should capture more of these larger, more valuable prey than Backus Field swallows. Our results confirm this prediction: 24% of the diet of Backus Field swallows was composed of 5- and 6-mm insects, but 44% of the diet at the Sewage Lagoon came from these size classes. Optimal-foraging theory also predicts that predators should be more selective in their choice of food when high-ranking prey are more abundant. Thus, Sewage Lagoon swallows should have been more selective than Backus Field birds, i.e. closer correspondence between observed size classes in the diet and value rankings should have occurred at the Sewage Lagoon than at Backus Field (Fig. 2).

Kendall's coefficient of rank correlation was 0.60 ($P < 0.05$) for the Sewage Lagoon diets and 0.40 ($P > 0.05$) for the Backus Field diets. The diet of Sewage Lagoon Tree Swallows was closer to the optimum than was the diet of Backus Field Tree Swallows.

DISCUSSION

Several other studies have shown that birds discriminate between prey and select foods of high value (e.g. Bryant 1973, Davies 1977, Goss-Custard 1977, Krebs et al. 1977, Zach 1978, Sutherland 1982, Turner 1982). Some of these studies showed, as we did, that the least valuable prey were not completely rejected by the birds and that selectivity is greater when high-ranking prey are more abundant (Goss-Custard 1977, Krebs et al. 1977, Turner 1982). We can offer several possibilities to explain why Tree Swallow diets did not coincide exactly with the optimal diets. We divided prey into 10 size classes, but Tree Swallows may differentiate prey otherwise. Additionally, we examined diets only in June when nestlings were fed. The types and sizes of prey available and eaten by Tree Swallows at other times of the year are not well known but may influence their prey selection when feeding nestlings. Our estimates of available prey were based on averages from day-long trapping of insects, but insect abundance can change rapidly during a given day. Handling times of Nematoceran prey up to 10 mm in length are certainly trivial but may not have been as uniform as we assumed. Greater handling times for large prey would have made the smaller items more valuable and the larger prey less valuable than assumed in our analysis. This would not greatly alter the value rankings of prey sizes at Backus Field, and the observed diet of Sewage Lagoon swallows would coincide more closely with the optimum if valuable prey were somewhat smaller than we estimated. On the other hand, the deviations from the optimum we observed may have been caused partly by sampling by the birds for available alternative prey (Smith and Sweatman 1974, Krebs and Cowie 1976, Krebs et al. 1978). As Turner (1982) points out, this type of sampling might be particularly important to hirundines because prey distribution and abundance can change rapidly. We found, as did Turner (1982), that boluses usually con-

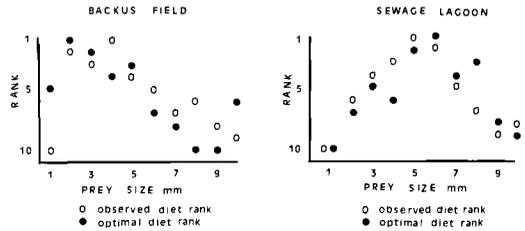


Fig. 2. Ranked values of prey sizes (1 = most valuable, 10 = least valuable) in optimal diet (closed circles) compared with rank order of occurrence in sizes (1 = most common, 10 = least common) in the observed diet (open circles) of Tree Swallows.

tained more than one prey size and taxon, suggesting that sampling by the birds may have occurred. Alternatively, we predicted that if a less valuable item was encountered while a bird foraged for a more valuable item, it should not be ignored because it can be captured quickly without reducing foraging efficiency (Turner 1982). In summary, Tree Swallows collecting food for nestlings and foraging in two areas where food abundance differed were selective in the sizes of prey they captured. Birds in both populations took more valuable prey but did not completely reject less valuable items, and the Tree Swallow diet was closer to the optimum in the area where food abundance was greatest. Thus, as predicted by optimal-foraging theory, Tree Swallows preferred more profitable prey and were more selective when profitable prey were common, but we believe that they did not ignore the less valuable prey items because their foraging efficiency was not compromised.

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