The Condor 101:246–254

FORAGING ECOLOGY AND DIET SELECTIVITY OF TREE SWALLOWS FEEDING NESTLINGS[1]

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Abstract. We studied the foraging ecology of a population of Tree Swallows (*Tachycineta bicolor*) breeding in New York State over a period of 5 years. While feeding nestlings, adult Tree Swallows tended to spend most of their time within sight of their nest box and less than 12 m above the ground. Major insect taxa captured include Diptera, Hemiptera, and Odonata, ranging in length from mainly 0–10 mm, with some individuals up to 60 mm. The sex of the parent delivering the food had no significant effect on diet composition. Selection for or against food categories was determined by comparing the proportion of insects of different types in the diet of Tree Swallows to the proportions available in the air column. Tree Swallows showed consistent selection for insects larger than 3 mm and against smaller insects, especially Diptera in the suborder Nematocera. Only minor differences in diet were observed among years, and the effects of the abundance of food available were generally small. The patterns of selectivity found in this population were consistent with those found in previous studies on this species carried out in other locations, and these patterns are likely the result of differences in the profitability or visibility of prey types.

Key words: diet selectivity, foraging, insect sampling, Tachycineta bicolor, *Tree Swallow.*

INTRODUCTION

Tree Swallows (*Tachycineta bicolor*) are aerial insectivores and members of a distinct guild which forages on insects in the air column. Swallows have proven to be valuable subjects for the study of foraging behavior and ecology because their feeding behavior is relatively easy to observe and because their prey resources are relatively easy to identify and sample accurately (Southwood 1978, Cooper and Whitmore 1990). Foraging conditions are known to influence several components of the reproductive biology of Tree Swallows (Quinney et al. 1986, Hussell and Quinney 1987, Dunn and Hannon 1992), and starvation is an important source of mortality for both adults and nestlings (Lombardo 1986, Robertson et al. 1992, McCarty 1995), making an understanding of foraging critical to understanding their ecology as a whole.

Foraging theory makes predictions about what kinds of food items an individual should include in its diet and how diet should change with changes in prey availability. We test two specific predictions common to many models of foraging theory: (1) individuals should include only the most profitable items in their diet and (2) individuals should become more selective as food becomes more abundant. Parents with older chicks face increasing foraging demands, and, given constant absolute food availability, their relative food availability might be expected to decline. We thus tested whether parents decreased the selectivity of their foraging when their chicks grew older.

As necessary background to evaluating these hypotheses, we also examined how sexual differences between parents and spatial and temporal differences among samples affected the observed pattern of foraging. Environmental conditions that influence foraging change over several different temporal and spatial scales, and the effects of most of these changes on conclusions drawn from a single short-term study are unknown. In our study, we examined foraging behavior and diet at two sites and over five seasons, and we look for differences in behavior and diet across a much larger geographic scale by comparing our results to those of previous studies conducted at several locations throughout the species' range.

METHODS

STUDY SITE

Tree Swallows breeding in nest-boxes were studied at two sites near Ithaca, New York

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[1] Received 2 March 1998. Accepted 5 January 1999.

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(42°30′N, 76°27′W). These sites are part of the Cornell University Experimental Ponds Facility; both consist of large, flat, open, grassy areas with regularly spaced man-made ponds and a large, marshy lake. The sites are surrounded by forest and abandoned farm fields. Nest-boxes were mounted on poles approximately 1.5 m above ground and equipped with conical metal predator guards. Most boxes were within 2 m of open water and were spaced ≥ 20 m apart. Unit One is a 13-ha site with 41 0.1-ha ponds and a 6-ha lake. There were 105 nest-boxes at this site, used by 55–75 pairs of breeding swallows. Unit Two, located 2 km east of Unit One, is a 20-ha site with 50 0.1-ha ponds and a 7-ha lake. Starting in 1990, 10 nest boxes were erected at Unit Two, each spaced 40 m apart. In 1991 and 1992 there were 22 boxes available, and 27 boxes were available in 1993. Breeding pairs ranged from 10 in 1990 and 1991 to 23 pairs in 1993.

INSECT SAMPLING

Suction traps are the best available method for minimizing bias in the measurement of the abundance of aerial insects (Service 1977, Southwood 1978, Muirhead-Thomson 1991). A 12.2-m Rothamsted aerial insect trap (Macaulay et al. 1988) located at Unit One was used from 1989–1993. The Rothamsted trap design has been used extensively for monitoring of insect pests (Taylor et al. 1981, Woiwood et al. 1984), in studies of insect migration and dynamics (Taylor 1986), and in previous studies of Hirundine ecology (Bryant 1973, Bryant and Turner 1982, Turner 1982b). The Rothamsted trap we used included a specially designed fan that renders it nearly immune to wind-induced variation in trapping efficiency and which is capable of capturing even large fast-flying insects (Macaulay et al. 1988, Muirhead-Thomson 1991). This feature improves its performance dramatically relative to the whirligig nets (Holroyd 1983) and drift nets (Quinney and Ankney 1985) used in other North American studies of swallow foraging.

Insect availability can vary on small spatial scales. In the vertical dimension, insect abundances decrease with increasing altitude; however, abundances at different altitudes are highly correlated over time (Taylor 1974, McCarty 1995). Differences in patterns of insect abundance at different altitudes thus should not influence our conclusions. Insect distributions are often patchy in the horizontal dimension as well. The 12.2-m Rothamsted trap is tall enough to obtain a sample that is relatively immune to small-scale horizontal patchiness (Taylor and Palmer 1972). We evaluated the importance of horizontal patchiness by collecting insects using an array of seven 1.5 and 2-m suction traps placed at distances varying from 1 m to 1 km apart. The numbers of insects caught per trap on a given day were highly correlated among all low-elevation traps, regardless of distance. The correlations between insect catches at 12.2 m and those at 1.5 and 2 m increased with distance up to nearly $r = 1.0$ (McCarty 1995), indicating that the 12.2-m samples used in this study are an integrated and representative sample of overall insect abundance.

Daily samples were collected in 70% ethanol between approximately 06:30 and 17:30 during the swallow breeding season (approximately 1 May through 25 July). Insect samples were examined under a dissecting microscope and identified to order, with the exception of Diptera, which were identified to suborders Nematocera and Brachycera. Small numbers of spiders (Aranae) were found in both the suction trap and diet samples; these have been included in the subsequent analyses in the "other taxa" category. Large numbers of thrips (Order Thysanoptera) occasionally occur in the suction trap samples, however because of the small size of thrips (usually <0.5 mm) and the fact that they were never observed in swallow diets, all analyses reported here exclude thrips. Insects were sorted into size categories of 3–5, 5–7, 7–9, 9–11, 11–13, and >13 mm in length (excluding antennae and ovipositors). Body lengths were converted to mass using conversion factors based on dry mass of insects of known length (McCarty 1995).

FORAGING SITE USE

The use of foraging sites by adult Tree Swallows feeding young was quantified using focal-nest observations in 1990, 1991, and 1992. In 1990 and 1991, the focus of the observations was the use of horizontal space by the swallows. For these observations, each breeding site was divided into several foraging habitats corresponding to ponds or upland fields, and 15- or 30-min focal observations were taken on breeding pairs. During observations, the observer waited until an adult left the nest and recorded what habitat type(s) the swallow foraged over and the time spent over each type (to the nearest minute). The observer continued to follow the focal bird until it returned to the nest or was lost from sight. If the observer lost sight of the swallow, the time at which it was last seen was recorded along with information on the sex of the forager if known and the reason the bird was lost, i.e., it left the Pond Unit or the observer was no longer sure which foraging swallow was the focal bird. In 1992, information about horizontal use of space was recorded, but observations focused on the vertical strata used by the swallows. The air column was divided into three strata (0–2 m, 2–12 m, >12 m), and observers recorded the use of each stratum to the nearest second, using laptop computers running an event recorder program. The limits of vertical strata were based on observations in 1990 and 1991 and the availability of good reference objects of known height to aid height measurements in the field. Simultaneous observations of the same birds by two or three observers confirmed that all observers were able to consistently identify the stratum a swallow was using. All pairs in the population were observed for a 30-min period on either nestling day 3, 9, or 12. As in previous years, an adult was watched as it left the nest and its use of strata recorded until it returned to the nest or was lost from sight. After the focal bird returned or was lost, information on its identity, use of foraging site, and reason for ending the observation (i.e., bird returned or was lost) were recorded. For each nest, the percentage of time spent in each vertical stratum and the percentage of time foraging at the breeding site were calculated.

DIET SAMPLING

Samples of nestling Tree Swallow diets were obtained using two methods. Adult Tree Swallows collect a bolus of many insects before returning to feed the young. Each year most adults were captured during the nestling period using nest-traps. When an adult was captured, all insects in its mouth were removed, and the nest was inspected for food items that had been dropped (Quinney and Ankney 1985, Blancher et al. 1987). In 1989 and 1990, diet samples also were obtained using an artificial nestling puppet that the adults fed (McCarty and Winkler 1991). The sex of the parent was recorded and the samples stored in 70% ethanol. All diet samples were sorted and counted using the method described for the aerial insect samples above.

ANALYSIS OF SELECTIVITY

Insects chosen by the swallows were compared to insects available in the air column on the day the sample was obtained using the method of Manly et al. (1993). If use differed from availability, selectivity for or against the resource is said to have occurred (Chesson 1978). Selectivity ratios, $\hat{w}_i$, were calculated using the following equation from Manly et al. (1993):

$$\hat{w}_i = \frac{u_{i+}}{\sum_{j=1}^{n} \pi_{ij} u_{+j}}$$

where u_{i+} is the total number of items in category i for all n samples, π_{ij} is the proportion of the total food items available when sample j was collected that were in category i, and u_{+j} is the total number of items of all categories in sample j.

The standard error of $\hat{w}_i$ was calculated according to Manly et al. (1993, eq. 4.14). The null hypothesis that $\hat{w}_i = 1$ was tested by comparing $(1 - \hat{w}_i)/\mathrm{se}(\hat{w}_i)$ to the appropriate critical value from the standard normal distribution, using a Bonferroni adjustment for multiple comparisons (Manly et al. 1993). The standardized selectivity ratio, B_i, was then calculated from Manly et al. (1993) equation 4.10, with the exception of the B_i values given in Table 5. Because the raw data on individual samples from the other studies in that table were not available, the comparisons across studies there are based on samples pooled within studies (Manly et al. 1993, eq. 4.22).

The selectivity ratio, $\hat{w}_i$, can be interpreted as a ratio of use to availability, where $\hat{w}_i = 1$ indicates that no selectivity is occurring. The standardized selectivity ratio, B_i, can be interpreted as the expected relative contribution of the food type to the predator's diet if all food types were equally abundant.

Changes in selectivity with age of the nestlings being fed, date, and insect availability were examined using multiple regression. The selectivity ratio, $\hat{w}_i$, for each sample obtained was regressed on nestling age, date, and insect abundance, and the partial regression coefficients examined for each variable.

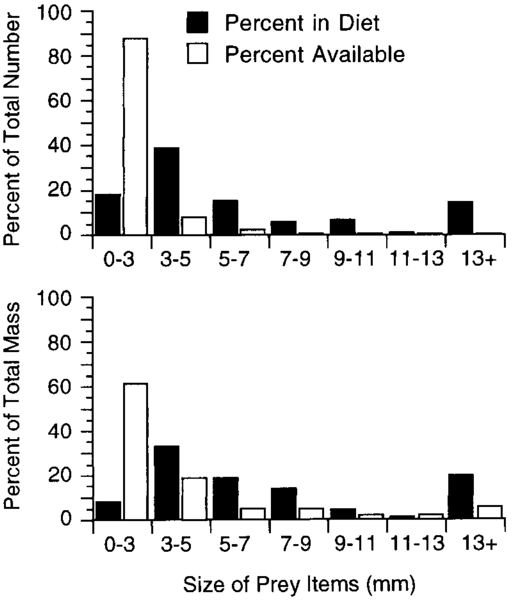

FIGURE 1. Comparison of the distribution of insect sizes found in Tree Swallow diets to the sizes of insects available in the air column. Percentages of number and mass of insects in each category are given. Based on 215 diet samples collected from 1989–1993 and pooled data on insect abundances during the nestling period for those years.

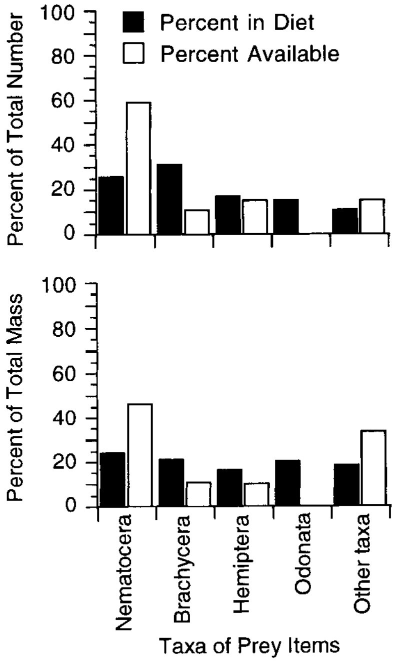

FIGURE 2. Comparison of the distribution of insect taxa found in Tree Swallow diets to the taxa of insects available in the air column. Percentages of number and mass of insects in each category are given. Based on 215 diet samples collected from 1989–1993 and pooled data on insect abundances during the nestling period for those years.

RESULTS

INSECT SAMPLING

Insect abundance did not change systematically with date during the main nestling-rearing phase in June in any of the five years analyzed (least squares regression of total number of insects captured on date, $P > 0.20$ for each year). However, there was a large amount of day-to-day variation in insect abundance, with daily catches differing by as much as two orders of magnitude (McCarty and Winkler 1999). The insect fauna consisted of a large proportion of insects less than 3 mm long (Fig. 1). Nematoceran Dipterans made up over half of the June samples, with Brachyceran Dipterans and Hemiptera (= Homoptera + Heteroptera) being next in abundance (Fig. 2). Arthropods from at least eight other orders made up the remaining insect catch (McCarty 1995).

FORAGING SITE USE

Foraging swallows generally remained near the breeding area, foraging in open areas over fields and ponds. A swallow was considered to be "on site" when it was foraging within the confines of the Pond Unit (delineated by a 2 m fence) and was "off-site" if it was observed leaving the Pond Unit. During focal nest observations, Tree Swallows spent about 12% of the foraging time off site, 40–100% of the period within view on site, and the remainder of the period lost from view but with no evidence that they had left the site (Table 1). The exception to this was ob-

TABLE 1. Comparison of the percent of foraging trips within the study area for each breeding site in each year. N is the number of observation periods (each observation period counts as one observation in the ANOVA), and *n* is the mean number of foraging trips per observation period.

Site	1990	1991	1992
Unit 1	40.2 ± 8.4	60.3 ± 10.8	78.0 ± 3.5
N (*n*)	19 (4.6)	8 (5.1)	70 (4.9)
Unit 2	97.4 ± 2.6	100.0 ± 0	95.5 ± 2.1
N (*n*)	13 (4.5)	8 (5.9)	31 (4.6)
F	30.0	13.7	6.9
P	<0.001	<0.01	<0.01

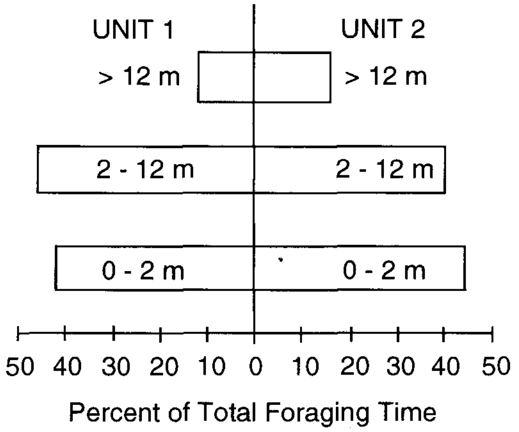

FIGURE 3. Proportion of time spent foraging at different heights by Tree Swallows feeding nestlings. Based on 72, 30-min focal nest observations at Pond Unit One and 33 focal nest observations at Unit Two.

TABLE 2. Comparisons between the composition of diet samples obtained from male and female parents. Values given are means of percents ± 1 SE. n = 107 for females and 91 for males. P-values for t-tests. None of the means are significantly different when adjusted for multiple comparisons.

Category	Male	Female	P
Size (mm)			
0–3	19.0 ± 2.7	18.7 ± 2.4	0.93
3–5	44.3 ± 3.5	34.2 ± 3.0	0.03
5–7	12.5 ± 1.8	17.8 ± 2.5	0.09
7–9	4.7 ± 1.0	6.3 ± 1.6	0.43
9+	19.5 ± 3.9	23.0 ± 3.7	0.51
Taxa			
Diptera–Nematocera	27.7 ± 3.8	26.5 ± 3.5	0.82
Diptera–Brachycera	29.8 ± 3.6	31.7 ± 3.4	0.70
Hemiptera	17.5 ± 3.2	17.9 ± 2.9	0.93
Odonata	13.0 ± 3.4	14.2 ± 3.2	0.80
Other taxa	12.1 ± 2.6	9.8 ± 2.1	0.49

served in 1990 when swallows at Unit One spent a significant amount of time off site. During this period we observed many swallows foraging over old fields approximately 100–300 m from the breeding area. There were significant differences between the two Pond Units in the percent of time spent foraging at the breeding colony, with swallows at Unit Two spending significantly more time on site than those at Unit One in all three years (Table 1). This result underestimates the differences in foraging site use, because the area defined as on-site was smaller at Unit Two than at Unit One.

Tree Swallows spent the vast majority of their time foraging between 0 and 12 m above the ground (Fig. 3). Swallows spent less than 20% of their time foraging above 12 m, significantly less than the proportion of time spent below 12 m (paired t-test, $t_{104} = 9.60$, $P < 0.001$). Proportion of time spent below 2 m and between 2 m and 12 m are not significantly different (paired t-test, $t_{104} = 0.27$, $P > 0.80$). The proportions of time spent in each stratum did not differ between sites ($F_{1,103} = 1.55$, $P > 0.20$; Fig. 3).

NESTLING DIET

A total of 215 diet samples was obtained between 1989 and 1993. These samples were obtained between 4 June and 17 July, with 86% obtained in June. Comparing the hatch days of the nests from which diet samples were taken to the hatch days of the population as a whole, more samples were obtained from later hatching nests than would be expected (hatch day for sampled nests $\bar{x}$ = 9 June, hatch day for population $\bar{x}$ = 4 June, $t_{391} = 5.4$, $P < 0.001$). Samples were taken from nestlings as young as day 2 and as old as day 16 ($\bar{x}$ = day 10). Sampling effort was concentrated, however, in the middle of this range, with 51% of samples obtained between days 8–12 inclusive, 24% from nestlings younger than day 8, and 25% from nestlings older than day 12.

Tree Swallow diets consisted of a wide range of insect sizes from at least 11 orders. Sizes ranged from insects less than 1 mm in length to large Anisopteran Odonates over 50 mm long. Insects in the 3–5 mm class made up the largest proportion of the diet by numbers and on a dry mass basis (Fig. 1). Diptera were the most frequently eaten taxa, with Hemiptera and Odonata also making up a large part of the diet (Fig. 2). None of the other orders accounted for more than 5% of the total diet by number. Diptera were the most important taxon based on dry mass (Fig. 2), although Hemiptera, Odonata, and "other taxa" could be equally important in some years.

The sex of the adult from which a sample was obtained did not have a significant influence on the size or taxonomic composition of the sample (Table 2).

SELECTIVITY FOR SIZE AND TAXA

The selectivity ratios, w_i, indicate that insects in the 0–3 mm size range are selected against (i.e.,

TABLE 3. Components used in calculating selectivity for insect taxa and sizes in Tree Swallow diets. Diet samples from 1989–1993 pooled, $n = 213$ samples. u_i = number of items in category i used, m_i = number of items of category i available, w_i ± SE = selectivity ratio ± Standard Error of w_i, and B_i = selectivity index standardized to minimum of 0, maximum of 1.0. Selection ratios, w_i, calculated from selectivity ratios for each sample (for further details see text). *next to w_i indicates a selectivity ratio significantly different from 1, using Bonferroni adjustment for multiple comparisons (overall $\alpha < 0.05$).

Category	u_i	m_i	w_i ± SE	B_i
Size (mm)				
0–3	995	56,061	0.289 ± 0.002*	0.009
3–5	1,926	7,191	6.295 ± 0.051*	0.207
5–7	704	2,540	8.290 ± 0.122*	0.272
7–9	149	314	6.023 ± 0.119*	0.198
9+	106	183	9.582 ± 0.178*	0.314
Taxa				
Nematocera	2,005	39,840	0.842 ± 0.005*	0.020
Brachycera	780	7,410	2.015 ± 0.017*	0.048
Hemiptera	728	9,158	1.348 ± 0.014*	0.032
Odonata	57	19	37.500 ± 1.167*	0.887
Other taxa	310	9,802	0.552 ± 0.006*	0.013

w_i, < 1) and that larger insects are selected for, with the probability of selectivity generally increasing with the size of the insect (Table 3). Nematocera and other taxa are avoided to some degree, whereas Odonata and Brachyceran Diptera are actively preferred. Tree Swallows also show significant selectivity for Hemiptera, but the preference is weak, with Hemiptera generally being eaten in proportions similar to their availability (Table 3).

CHANGES IN SELECTIVITY

The multiple regression analysis of selectivity ratios found relatively few changes in selectivity with insect availability, nestling age, or date (Table 4). However, selectivity for insects in the 3–5 mm range decreased with increasing overall insect abundance, and selectivity for insects larger than 9 mm increased with increasing insect abundance (Table 4).

Only for insects less than 3 mm in length did the partial regression coefficients indicate that selectivity changed significantly with chick age. Even though it appears that these small insects were incorporated more in diets of older chicks, the multiple regression explains only a small amount of the variance in selectivity of insects smaller than 3 mm ($R^2 = 0.03$, Table 4). Selection for 5–7 mm insects decreases slightly with age, but not significantly so ($P = 0.11$) The selectivity for both Brachyceran and Nematoceran Diptera shows a negative relationship with age, but again the partial regression coefficients are not significant (Table 4).

TABLE 4. Change in selectivity, w_i, with age of chicks being fed, date, and total food availability. Diet samples from 1989–1993 pooled, $n = 206$ samples. For each category of dependent variable, the overall adjusted multiple R^2 is given, as well as the standardized partial regression coefficients for age, date, and food availability. * $P < 0.05$, ** $P < 0.01$, *** $P < 0.001$.

Category	Overall R^2	Age	Date	Food available
Size (mm)				
0–3	0.03	0.17*	0.02	0.04
3–5	0.05*	0.08	−0.04	−0.20**
5–7	0.04	−0.14	−0.09	0.08
7–9	0.01	0.04	−0.05	−0.03
9+	0.22***	−0.01	0.40***	0.25**
Taxa				
Nematocera	0.05*	−0.10	−0.17*	0.01
Brachycera	0.04*	−0.14*	−0.10	0.02
Hemiptera	0.06**	0.07	0.21**	−0.04
Other taxa	0.01	0.10	0.03	0.02

Insects in the largest size group showed increasing selectivity with date of the samples (Table 4). There also were significant changes in the taxonomic composition of the diets with date, with selectivity for Nematoceran Diptera decreasing over time and selectivity for Hemiptera increasing with date.

DISCUSSION

During the breeding season, Tree Swallows rely almost entirely on aerial insects captured during prolonged cruising flights both to feed themselves and their dependent offspring. Analysis of site use indicates Tree Swallows feeding nestlings tend to forage within 100–200 m of their nest, primarily at altitudes below 12 m (Table 1, Fig. 3). Swallows breeding at our Unit One site spent significantly more time off-site than those at Unit Two, and among-year differences also exist within a site (Table 1). The breeding sites in the present study were mosaics of ponds and land, and in the course of a single foraging bout, the swallows moved freely from one habitat to another at the breeding site. This pattern of foraging behavior is similar to that reported in studies of Tree Swallow foraging from other areas (Holroyd 1983, Quinney and Ankney 1985, St.

Louis et al. 1990), and it indicates that Tree Swallows at the sites studied here are foraging in the same habitat where resource availability was measured.

NESTLING DIET

Nestlings were fed a diverse array of insect taxa and sizes (Fig. 1), but parents were highly selective in their choice of insects (Table 3). Males and females fed similar prey types to their offspring and no differences between sexes in selectivity were found (Table 2). Adults captured large numbers of relatively small insects (<3 mm), especially Nematoceran Diptera. Nematocera made up over half the items brought to the nest in each year (Fig. 2), but they comprised considerably less of the biomass delivered. The observed selectivity for insects larger than these small Nematocera (Table 3) suggests that the relative profitability or visibility of available insects is correlated with size.

The selectivity measures are based on availability as measured by the 12-m sample. However, Hemiptera become more abundant with altitude, and Nematocera become less so (McCarty 1995). Because the birds spent a large amount of time foraging below 12 m (Fig. 3), the availability of Hemiptera used in the calculation of selectivity may be over-estimated, and the availability of Nematocera may be underestimated. However, neither of these effects would alter our conclusions: Nematocera were found to be selected against based on the 12-m sample, and an underestimate of available Nematocera would only increase the degree of selectivity against Nematocera. Similarly, we found weak selectivity for Hemiptera; if their availability had been overestimated, it would simply increase the estimate of the degree to which they are selected.

CHANGES IN SELECTIVITY

Nestling Tree Swallows grow from a mass of less than 2 g at hatching to a peak of up to 24 g before fledging (Zach and Mayoh 1982, McCarty 1995). Given the change in energy demands of the brood associated with this growth, selectivity for large insects would be expected to be lower for adults feeding older nestlings than those feeding younger. Selectivity for insect size exhibited relatively few changes over the course of chick development, but the changes in size selectivity that were significant were consistent with our expectations, with selectivity for insects < 3 mm increasing with age and selectivity for intermediate-sized insects (5–7 mm) possibly decreasing with age (Table 4). Selectivity for Diptera, including both the relatively small Nematocera and the larger Brachycera, decreased slightly with nestling age. Holroyd (1983) also found little change in nestling Tree Swallow diet with chick age, as did Kožená (1980) in the Barn Swallow (*Hirundo rustica*).

Insect abundances changed dramatically from day to day (McCarty and Winkler 1999), and these changes affect swallow reproductive success (McCarty 1995). Because obtaining the necessary food is easier when food is abundant, we expected that Tree Swallow selectivities would increase with increases in insect abundance (Emlen 1966, MacArthur and Pianka 1966, Stephens 1990). Although this expectation was not met for several size classes, selectivity for the largest insects did increase with increasing insect abundance, and selectivity for insects in the 3–5 mm range also decreased (Table 4).

Quinney and Ankney (1985) also concluded that Tree Swallows showed higher selectivity for profitable prey types at sites where food was abundant. In determining the profitability of prey, however, Quinney and Ankney assumed that insects occur in patches of uniform-sized individuals, and that smaller, more abundant insects formed larger patches. Using these assumptions, small, abundant insects (2–5 mm) were considered the most profitable because they occurred in the largest patches. Our observations of Tree Swallow foraging showed no evidence of a reliance on relatively dense patches of insects while feeding nestlings. Tree Swallows feeding nestlings were observed to cover areas much larger than a single insect swarm and to return with a heterogeneous assortment of insect sizes and taxa after most foraging bouts (but see McCarty 1997 for the pre-breeding season). Therefore, we have ranked prey based on biomass alone and assumed that swallows are making choices based on individual items, not on patch quality. Using these rankings, our analysis of Quinney and Ankney's (1985) data (Table 5) suggests that selectivity for large insects (≥ 7 mm) was not higher where insects were more abundant (their Sewage site), whereas selectivity for insects ≤ 6 mm was higher where insects were more abundant.

All studies of Tree Swallows indicate that

TABLE 5. Selectivity for insect size and taxonomic categories in Tree Swallow diets from other studies. Standardized selectivity probabilities, B_i, given, based on equation 4.22 of Manly et al. (1993). Note that these equations give slightly different values for Ithaca than does equation 4.10 (Manly et al. 1993) used in Table 3. See text for details. Ithaca = Ithaca, NY, this study; Long Point = Long Point, Ontario, Holroyd 1983; Upper P = Upper Peninsula, Michigan, Pijanowski 1991; Backus = Backus Field, Port Rowan, Ontario, Quinney and Ankney 1985; Sewage = Sewage Lagoon, Port Rowan, Ontario, Quinney and Ankney 1985. Note that Backus and Sewage sites use different size categories.

Category	Ithaca	Long Point	Upper P		Backus	Sewage
Size (mm)				Size (mm)		
0–3	0.011	0.047	0.004	1–3	0.027	0.098
3–5	0.166	0.050	0.383	4–6	0.193	0.351
5–7	0.172	0.155	0.195			
7–9	0.294	0.128	0.283	7–10	0.780	0.551
9+	0.358	0.620	0.135			
Taxa						
Nematocera	0.185	0.200	0.686		0.161	0.211
Brachycera	0.386	0.175	0.183		0.629	0.215
Hemiptera	0.292	0.389	0.057		0.090	0.359
Other taxa	0.137	0.236	0.078		0.120	0.215

they feed on a distribution of food items that is skewed towards larger insects than the distribution of available insects (Table 5). This pattern is universal among studies of foraging in other species of swallows (e.g., Hespenheide 1975, Turner 1982a, 1983, Dyrcz 1984) and in insectivorous birds in general (Gibb and Betts 1963, Hespenheide 1971). This may be either because larger prey are more profitable or because they are more visible (cf. Li et al. 1985). Reports of Tree Swallow diets from studies that have not measured insect availability show a range of diet composition similar to that reported here and in Table 5 (Blancher et al. 1987, Acosta and Mugica 1990, Blancher and McNicol 1991).

The aspects of Tree Swallow foraging ecology measured here show little variability due to fluctuations in environmental conditions during the nestling period. Although the environment varies both spatially and temporally, consistent patterns in prey choice and site use were found, and Tree Swallows appear to be integrating information from a variety of scales to produce a remarkably consistent pattern of resource use during the nestling period.

ACKNOWLEDGMENTS

This research was supported by grants to JPM from Sigma Xi and the Andrew W. Mellon Student Research Fund of Cornell University, and by grants to DWW from NSF (IBN-9207231) and USDA (Hatch Grant No. 183-428). Institutional support from the Division of Biological Sciences and the Section of Ecology and Systematics vastly improved working conditions at the Cornell Experimental Ponds Facility, and we thank Peter Bruns, Nelson Hairston Jr., and Peter Marks for making that possible. Bob Johnson continues to make the Cornell Ponds Facility an enjoyable and productive place to work. We are grateful to Paul Allen, Beth Christman, Elizabeth Daut, Suzanne Kelley, Eric Klopfer, Ray Moranz, David O'Neill, Bryan Stuart, and Jeannette Zamon for their assistance in gathering insect samples, and to Shao Chen, Barrett Klein, Ray Moranz, Allison Offerman, and Erich Tilgner for assistance in processing those samples. Richard Holmes kindly loaned us the 2-m Johnson and Taylor insect traps, and Gerald Wilkinson loaned us his 1.5-m suction traps. Stephen Emlen, Nelson Hairston Jr., and L. LaReesa Wolfenbarger provided helpful comments on earlier drafts of this paper.

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