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AQUATIC COMMUNITY CHARACTERISTICS INFLUENCE THE FORAGING PATTERNS OF TREE SWALLOWS[1]

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Abstract: During periods of inclement spring weather, Tree Swallows (*Tachycineta bicolor*) were observed foraging close to the surface of a series of experimentally manipulated ponds. Censuses of foraging swallows during these periods indicated that the use of ponds for foraging was positively affected by earlier additions of nutrients and the removal of fish from the ponds. Collections of emerging insects from these ponds indicated that nutrient additions and the removal of fish greatly increased the numbers of insects emerging from those ponds. The ability of Tree Swallows to exploit local concentrations of food may be critical to their ability to return to the breeding grounds before aerial insects are reliably available.

Key words: Tree Swallow, Tachycineta bicolor, *foraging, experimental pond communities, trophic cascade.*

Tree Swallows (*Tachycineta bicolor*) are aerial insectivores that rely heavily for their food on adult stages of insects with aquatic larvae. However, individuals typically arrive on their breeding grounds in northern North America before weather conditions ensure a constant supply of aerial insects (Robertson et al. 1992, McCarty 1995). Tree Swallows have several traits that help them to survive periods of low food availability (Weatherhead et al. 1985, Stutchbury and Robertson 1990). Unlike other swallows, Tree Swallows are able to subsist for long periods of time on fruit, especially bay-berries (*Myrica* spp.), when insects are not available (Chapman 1955, Turner and Rose 1989, Place and Stiles 1992). Tree Swallows also may increase their ability to survive stressful periods by adjusting their foraging to exploit localized food sources such as emerging aquatic insects (Dence 1946, Cohen and Dymerski 1986). The ability to exploit such local concentrations of available insects undoubtedly influences the ability of Tree Swallows to return to their breeding area early in the season. In this paper, I report observations of locally concentrated foraging activity by Tree Swallows associated with both the biotic and abiotic characteristics of the aquatic communities over which they forage. This information is significant because it shows that Tree Swallows are able to perceive and exploit small patches of abundant food and because it demonstrates an influence of aquatic community dynamics on the ecology of a terrestrial bird.

METHODS

This study was conducted at the Cornell University Experimental Ponds Facility Unit Two, located northeast of Ithaca, New York (42°30′N, 76°27′W), during April and early May 1992. This site consists of 50, 0.1-ha artificial ponds and a 5-ha reservoir (see Hall et al. 1970 for a detailed description of the site). In 1992, 15 pairs of Tree Swallows bred at the site, and an additional 78 pairs of Tree Swallows bred at a second site, Ponds Unit One, located 2 km away. Early in the breeding season, large numbers of migrant swallows and breeding Tree Swallows from this second site forage at Ponds Unit Two.

At the time of this study, 16 of the 50 ponds were part of an experiment manipulating nutrients and animal communities. Ponds were manipulated in a 2 × 2 factorial design with four ponds per treatment combination (Morin et al. 1991, Hairston and Howarth, unpubl. data). Manipulations consisted of high phosphorus (HP) or low phosphorus (LP) additions, combined with either fish present (+F) or fish absent (−F), to create the four treatments of: HP + F; LP + F; HP − F; LP − F (Morin et al. 1991, Hairston and Howarth, unpubl. data). Ponds were fertilized with P in the form of H_3PO_4 twice weekly during the summer of 1991, with HP ponds receiving P at a rate of $0.56\ g \cdot m^{-3} \cdot year^{-1}$ and LP ponds receiving $0.056\ g \cdot m^{-3} \cdot year^{-1}$. Fish-present ponds

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TABLE 1. Insect emergence from experimental ponds. Mean numbers of insects per pond per day (±SE) are given for each treatment. Emergence is significantly influenced by pond treatment, with ponds with high levels of nutrient additions and no fish (HN − F) being significantly higher than all other treatments ($F_{3,24}$ = 5.47, P = 0.005). HN = high levels of nutrients added, LN = low levels of nutrients added, +F = fish present in the ponds, −F = fish absent from ponds, n = the number of samples from each treatment type.

Treatment	Insects/trap	n
HN − F	423 ± 159	6
LN − F	92 ± 28	8
HN + F	83 ± 14	11
LN + F	33 ± 15	3

had populations of fathead minnows (*Pimephales promelas*), whereas fish-absent ponds had no fish present. Minnows initially were added to the ponds in the fall of 1990 at densities of approximately 10 g · m^{-3} for the +F ponds, while −F ponds contained less than 0.001 g · m^{-3} (Hairston and Howarth, unpubl. data). In 1990, I measured production of insects from these ponds using floating emergence traps (Morgan et al. 1963). Ponds had received either high levels of nutrient additions (HN; 12.1 g · m^{-3} · $year^{-1}$ of NH_4NO_3 plus 0.56 g · m^{-3} · $year^{-1}$ of H_3PO_4) or low levels of nutrient additions (LN; 0.56 g · m^{-3} · $year^{-1}$ of H_3PO_4) paired with fish present (+F) and fish absent (−F) to form four treatment groups (Table 1).

During the breeding season, Tree Swallows usually forage widely around the breeding site and show no preference for individual ponds (pers. observ.). They spend the majority of their time foraging at altitudes greater than 2 m (McCarty 1995), and usually do not exhibit group foraging described for other species of swallows (Emlen 1952, Emlen and Demong 1975, Brown 1988). However, during cold, wet weather common in the pre-breeding season (late March to early May), I regularly observed swallows at Pond Unit Two congregating over particular ponds, dipping and catching insects at or near the surface of the water. Between 17 April and 4 May 1992 I visited this site on six of these wet, cold days and censused the number of swallows foraging over each pond at the facility. For each census I circled the grounds of the Ponds Unit two times, stopping at each pond twice and counting the number of swallows foraging within 2 m of the surface of the pond. The mean of the two counts was used as the level of foraging activity for that pond on that census day. Over 80% of foraging activity was observed over the 16 ponds in the experimental group. Only seven of the remaining 34 ponds experienced any foraging activity, and of these, two fishless ponds accounted for over 70% of the swallow activity observed away from the 16 experimental ponds. For all subsequent analyses I have focused on only the 16 ponds in the experimental group, because they accounted for most of the foraging activity observed and because accurate information about the nutrients and fish community were available for these ponds. Census means for each pond were summed and the effects of the pond treatments on foraging activity was analyzed using ANOVA.

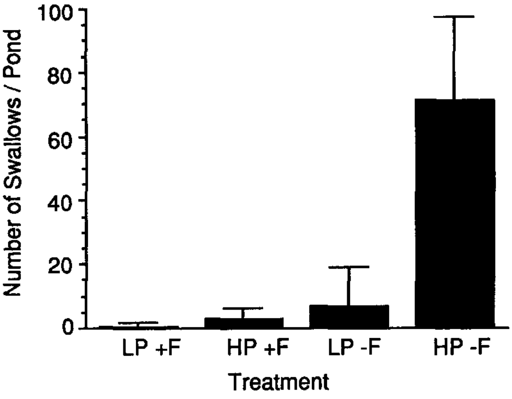

FIGURE 1. Tree Swallow foraging activity over ponds. Each treatment consists of four ponds and represents a different combination of nutrients and the presence or absence of fish. Solid bars represent the mean level of foraging activity for the four ponds in a treatment with all observation days combined; error bars are the standard deviation of the mean. ANOVA shows that foraging over ponds with high levels of phosphorus additions and no fish (HP − F) is significantly higher than over other ponds; differences between other treatments are not significant (Fisher PLSD). HP = high phosphorus levels, LP = low phosphorus levels, +F = fish present in the ponds, −F = fish absent.

RESULTS AND DISCUSSION

The emergence data indicate that both nutrient additions and the absence of fish tended to increase insect production (Table 1). A survey of insect larvae in the ponds during 1992 indicated that the nutrient treatments from 1991 produced the same pattern of high insect abundance associated with absence of fish and additions of nutrients (McCarty, unpubl. data).

There was a significant effect of pond treatment on foraging activity ($F_{3,12}$ = 20.8 $P < 0.001$, Fig. 1); activity over HP − F ponds was significantly higher than over any of the other treatments (Fisher's PLSD $P < 0.05$). There was a significant effect on foraging activity of Nutrients ($P < 0.001$) and Fish ($P < 0.001$), as well as a significant interaction between the two factors ($P = 0.001$).

These results indicate that foraging of Tree Swallows is influenced by both biotic and abiotic characteristics of the aquatic community. Previous work has shown that both the foraging ecology (St. Louis et al. 1990, Blancher and McNicol 1991) and the reproductive success (Blancher and McNicol 1988, St. Louis and Barlow 1993) of Tree Swallows is affected by the pH of the water they forage over. My results show that, not only do the abiotic properties of ponds influence foraging, but the biotic community in the ponds also affects foraging. It is clear that the swallows are responding to differences in insect emergence, but the mechanism causing the increased insect emergence has not been studied. Although addition of nutrients increases insect production as expected, the presence of fish also increases primary production (Morin et al 1991) but has a negative effect on insect production (Table 1). Therefore, fish must be having a direct, negative effect on insect production. Fathead minnows feed on small insect larvae (Becker 1983), and it is likely that they, like other small predatory freshwater fish, are reducing insect abundance through predation (Hambright et al. 1986, Diehl 1993). Other features of the ponds with fish, such as low macrophyte density, also may contribute to the decline in insect abundance.

The effect of the pond community on the foraging of Tree Swallows may have significant effects on the survival and reproduction of swallows. Tree Swallows are the first swallow species to return to central New York in the spring (Bent 1942, Sheppard 1977). As aerial insectivores, they are at great risk of starvation from periods of cold and wet weather at this time, and high levels of adult mortality occur in the spring (Weatherhead et al. 1985, Lombardo 1986, Littrell 1992). In addition to possible direct effects on survival, the ability to exploit localized food resources during periods of low overall food abundance may have an effect on the timing of breeding, possibly through effects on nutritional condition (but see Winkler and Allen 1996). The swallows at Ponds Unit Two bred significantly earlier than did Tree Swallows breeding at sites less than 5 km away where the behaviors described here are not observed, even though overall food availability was similar (McCarty 1995). Whether this difference is due in part to the availability of food during inclement weather remains to be shown.

These results show that both biotic and abiotic characteristics of aquatic communities influence the foraging behavior of Tree Swallows. This effect seems especially significant given that the aquatic and terrestrial communities are often viewed as distinct systems, and treated as such in ecological research. The influence of properties of the aquatic community on insectivorous birds in this and other studies suggests that analyses of communities and food-webs delimited by the air-water boundary may be ignoring important interactions between these systems.

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THE MATING STRATEGIES OF EASTERN SCREECH-OWLS: A GENETIC ANALYSIS[1]

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Abstract: We used genetic analysis to examine the mating strategies of male and female Eastern Screech-Owls (*Otus asio*) in central Kentucky. DNA fingerprinting revealed no evidence of extra-pair fertilizations in 23 broods (80 nestlings). Such results suggest that pursuit of extra-pair copulations by male and female screech-owls may be costly. One possible cost for females is the risk of losing the nest site. Alternatively, pursuit of extra-pair matings by females might be energetically expensive, thereby conflicting with egg production. Male screech-owls provide food for their mate (and young) during much of the breeding season and such feeding probably affects reproductive success. Males pursuing EPCs might have less time for foraging and, as a result, reduced reproductive success.

Key words: extra-pair fertilizations, extra-pair copulations, Eastern Screech-Owls, Otus asio, *DNA fingerprinting.*

Recent studies have provided abundant evidence that extra-pair copulations (EPCs) and fertilizations (EPFs) are important components of avian mating systems (reviewed by Birkhead and Møller 1992, Westneat and Webster 1994). However, these studies also reveal that the extent of extra-pair activity varies within populations and among species. Many factors may contribute to such variation. For example, opportunities for EPCs might vary with density (Birkhead and Møller 1992), the degree of breeding synchrony (Birkhead and Biggins 1987, Westneat et al. 1990, Stutchbury and Morton 1995), and features of the habitat (i.e., visually occluded habitats might make mate guarding more difficult; Sherman and Morton 1988). EPCs also might be more common in migratory species than in resident species (Westneat et al. 1990).

Adequately testing these and other hypotheses requires data from a large number of populations and species. Although such data are appearing at an increasing rate, most studies focus on passerines. The objective of the present study was to investigate the mating system of a non-passerine, the Eastern Screech-Owl (*Otus asio*). Specifically, we used genetic analysis (DNA fingerprinting) to examine the

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