Northwest Science Notes

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An Assessment of Nestling Diet Composition in the Violet-green Swallow (*Tachycineta thalassina*)

Abstract

Aerial insectivores have undergone marked population declines in recent decades, including members of the Hirundinidae (swallows), which have long served as sentinels of environmental change. In contrast to other swallow species that breed in North America, we have a poor understanding of most aspects of the basic ecology and life history of the violet-green swallow (*Tachycineta thalassina*), a widespread species found throughout the Pacific Northwest. In this study, we investigated the diet composition of violet-green swallow nestlings to document the consumption of food resources by offspring during adult feeding visits. We identified arthropods from 13 taxonomic orders in feeding boluses and found that representation of taxonomic groups was highly uneven and dominated by Diptera and Hemiptera. Although swallows did provision some large prey, the great majority (i.e., 92.6% of 1047) of food items were < 5 mm in length. Feeding boluses collected from the congeneric tree swallow (*T. bicolor*) at the same study area and during the same time period revealed similar patterns of size and taxonomic representation of diet composition of violet-green nestlings, raising questions as to how these species partition critical resources in areas of sympatry.

Keywords: nestling diet, offspring provisioning, swallows, *Tachycineta bicolor*, *Tachycineta thalassina*

Introduction

North American avifauna classified as aerial insectivores have undergone widespread population declines in the last two decades, with species in this group experiencing more declines than any other group of passerine birds (Bohning-Gaese et al. 1993, Nebel et al. 2010). Included in this foraging guild are the swallows (family Hirundinidae), medium-sized birds that occur in a wide range of habitats and exhibit variation in several aspects of their breeding ecology (Turner 1989). Swallows are aerial insectivores that feed almost exclusively on flying invertebrates which themselves are strongly influenced by environmental conditions, so they serve as useful indicators of ecosystem health. For example, previous studies have used swallows to measure levels of environmental contaminants (McCarty 2002), to establish links between nuclear radiation and morphological abnormalities (Møller et al. 2007), to assess how intensification of agricultural practices is linked to changes in population structure (Baeta et al. 2012), and to quantify how the timing of breeding in wild populations has been altered by anthropogenic-induced climate change (Dunn and Winkler 1999).

Despite serving as environmental sentinels and playing important roles in natural ecosystems (Şekercioglu et al. 2004), there is significant variation in our understanding of basic ecology among the North American swallow species. For example, the tree swallow (*Tachycineta bicolor*) is one of the best-studied North American passerine species and has an extensive body of literature describing its ecology, behavior, and general biology

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(Jones 2003, Winkler et al. 2011). In contrast, our knowledge of the closely related violet-green swallow (*T. thalassina*) is markedly limited even though the range of this species covers much of western North America where it often breeds in sympatry with the congeneric tree swallow. Indeed, we still lack fundamental information regarding the breeding biology, social behavior, population regulation, and feeding ecology of the violet-green swallow, including the composition of food items fed to offspring during their development (Brown et al. 2011). In this study, we investigated the diet composition of food boluses provisioned to offspring by adult violet-green swallows to expand our knowledge of foraging ecology of this poorly-understood species. We quantified the size and taxonomic composition of food items collected from adults feeding offspring during the first half of the nestling period and assessed the extent to which food items obtained by male and female violet-green swallows differed. Finally, because our study sites supported breeding tree swallows we also contrasted offspring diet composition between these two closely-related species to provide insight into how they may partition food resources during the breeding season.

Methods

We investigated parental feeding of violet-green and tree swallow nestlings in a box-nesting population in the vicinity of Corvallis, Oregon (44°35’N, 123°15’W) during the 2011 breeding season. Our study population consisted of three study sites that were all located within 3 km of each other and functioned as a single population, with both species breeding at each site and a subset of individuals switching between sites to breed in successive years (Rivers, unpublished data). Although violet-green and tree swallows both arrive on study sites in late spring, tree swallows typically begin laying eggs approximately two weeks before violet-green swallows (first tree swallow egg laid during 2010-2013 breeding seasons was between 5 and 15 May, whereas this date was between 20 and 24 May for violet-green swallow). At each study site, we sampled diets of nestlings at the peak of the nestling period; violet-green swallows were sampled during 27 June to 11 July whereas tree swallows were sampled during 13 June to 10 July. Adults of both species were captured during the first half of the nestling stage (i.e., violet-green swallow: 3 to 13 days old; tree swallow: 3 to 9 days old); we did not attempt to capture adults after nestling day 13 because disturbance of the nest after this age can cause young to fledge prematurely.

We used traps to capture adults arriving at the nest with food between 0700 and 1200 h local time. In most cases, we used a “flap trap” placed inside a nest box which had a trap door that was tripped by an adult as it entered into the nest box to feed young. Additionally, we used a “wig-wag” trap that consisted of a piece of wood permanently mounted on the box that was remotely sprung by an observer after an adult entered the nest box. After setting a nest trap, we waited nearby (ca. 20-25 m from the nest) until an adult was trapped in the box and then moved as fast as possible to extricate the bird from the box, typically within 15 s after an individual was captured. Using this approach, we found that swallows often held food boluses in their mouth because their efforts were apparently focused on escape after becoming trapped. Each adult was sampled once to avoid potential issues arising from pseudoreplication. In a minority of instances (i.e., 6 of 33 nests) our sampling included collection of boluses from both male and female members attending a nest. However, we have no reason to believe that the food boluses delivered by individuals from the same nest box were non-independent because our observations of foraging individuals indicate they obtain prey away from their nest sites in areas where they mix with other *Tachycineta* swallows from the local breeding population. Shortly after capture (i.e., 1 to 3 min), we used fine forceps to remove boluses directly from the mouth and placed the contents into a 1.7 mL centrifuge tube containing a 70% alcohol solution. During a limited number of captures (approximately <5 %), a small number of invertebrates contained within the bolus escaped capture during collection. The individual prey that escaped appeared to be in similar proportions to the rest of the boluses (i.e., the most common species in a bolus also most commonly escaped) so these losses did not appear to introduce bias in our diet samples.

After field work had concluded, one of us (GN) used a dissecting microscope to characterize bolus composition relative to (1) the length and (2) the taxonomic affiliation of food items. If the taxonomic affiliation of a food item was difficult to characterize because of its condition or life stage, we classified it as "unidentified." We classified food items into either small (i.e. ≤ 5 mm) or large (i.e. > 5 mm) sizes based on total length excluding antennae, as most boluses contained prey that naturally fit into these categories. We classified food items taxonomically to order following previous studies of nestling diet in *Tachycineta* swallows (e.g., McCarty and Winkler 1999). To quantify the taxonomic composition of food boluses, we first calculated the percentage of individuals in each food bolus by order, and then calculated an average percentage for each order per bolus over the entire sample. We also examined sex-specific variation in diet composition for violet-green swallows, although this was not possible for tree swallows because of sample size constraints. All statistical calculations were conducted using SAS v.9.3 software. Given the observational nature of our study, we limited our analyses to descriptive statistics and therefore report means and 95% confidence intervals.

Results

We collected food boluses from adult swallows during 39 independent nestling feeding events (violet-green swallow: n = 33, tree swallow: n = 6) that represented 1243 total food items that could be classified to 15 distinct taxonomic groups (Table 1). Although 35% of the boluses assessed in this study contained at least one large food item, the great majority of diet items were small for both the violet-green (92.6% of 1047 food items) and tree swallow (97.7% of 257 food items). Violet-green swallow boluses contained food items identified to 13 orders whereas tree swallow boluses contained food items that were identified to 12 orders. Three orders were represented solely in the violet-green swallow boluses and two orders were unique to tree swallow boluses, although none of these orders were abundant relative to other taxa (Table 1). The representation of taxonomic groups was highly uneven and dominated by Diptera

TABLE 1. Mean (with 95% confidence intervals) taxonomic composition of boluses and total number of individuals collected from violet-green and tree swallows during 39 independent nestling provisioning events (n=1243 total food items). Food items that were difficult to characterize because of its condition or life stage were classified as "unidentified."

	Violet-green Swallow			Tree Swallow		
Order	Mean Percent	95% CI	Number of Items	Mean Percent	95% CI	Number of Items
Hemiptera	47.7	37.5-57.9	424	26.8	-1.6-55.1	53
Diptera	45.2	34.5-55.8	390	44.6	19.6-69.6	140
Hymenoptera	13.5	-1.2-28.2	36	5.9	1.7-10.0	6
Unidentified	12.8	5.8-19.9	52	12.0	-0.1-24.1	22
Araneae	9.9	6.2-13.5	53	9.3	-5.4-24.1	16
Odonata	6.7	---	1	---	---	0
Ephemeroptera	6.2	2.2-10.2	7	7.5	---	3
Coleoptera	4.1	0.5-7.7	4	9.6	-14.2-33.3	5
Plecoptera	4.0	-31.3-39.2	7	7.7	---	1
Psocoptera	3.0	-5.0-10.9	3	2.5	---	1
Isoptera	2.4	-1.5-6.3	3	13.2	-118.1-144.5	5
Dermaptera	1.8	-2.4-6.0	3	8.1	-85.1-101.2	3
Lepidoptera	1.3	-0.4-3.1	2	---	---	0
Mecoptera	1.1	---	1	---	---	0
Neuroptera	---	---	0	2.5	---	1
Trichoptera	---	---	0	7.7	---	1

and Hemiptera in both swallow species, totaling 87% and 75% of the total food items identified in boluses of the violet-green swallow and tree swallow, respectively. Although the representation of Diptera was very similar in the two species, the representation of Hemiptera was markedly higher in the violet-green swallow (Table 1). The mean number of food items per bolus was less for the violet-green swallow (29.9 items per bolus [95% CI: 20.4-39.3]) than the tree swallow (42.8 items per bolus [95% CI: -8.1-93.7]).

Boluses obtained from female violet-green swallows (n = 22) contained food items in four orders not observed in boluses collected from male violet-green swallows (i.e., Coleoptera, Dermaptera, Mecoptera, Odonata), but these orders comprised a small part of the food items obtained from females. The mean number of items per bolus did not differ between sexes in the violet-green swallow (male: 30.3 items [95% CI: 12.7, 47.9], female: 29.7 items [95% CI: 17.5, 41.9]), and the taxonomic composition of food items found in feeding boluses of males and females were generally similar.

Discussion

The great majority of food items obtained from feeding boluses of adult violet-green swallows captured in the nest were small (< 5 mm) Diptera and Hemiptera and, to a lesser extent, small Hymenoptera and Araneae. These findings are consistent with the only previous report of nestling diet known to us that qualitatively reported feeding adults provided violet-green swallow young with "gnats and flies" (Edson 1943). Our results also compliment the most comprehensive data on diet of adult violet-green swallows that found that Hemiptera and Diptera were the two most abundant food items recorded from stomach contents of adults (Beal 1918) and suggest that adults feed their offspring food items that are similar to those they consume. Our study also revealed limited differences between the food items fed to violet-green and tree swallow nestlings on our site; both species fed their offspring small (< 5 mm) prey that were dominated by species within Diptera and Hemiptera. Because we sampled food boluses being delivered to offspring in the two species during the same time period and at the same offspring developmental stage, this suggests that food resources overlapped markedly between the two species. The results from tree swallows in our study supports previous work that found tree swallows frequently feed young with Hemiptera and Diptera prey (Quinney and Ankney 1985, McCarty and Winkler 1999). One notable difference between our study and that of McCarty and Winkler (1999) is that adults in the latter study fed their offspring with aquatic-based invertebrates, whereas large water bodies were absent from our study sites and offspring were therefore fed almost exclusively with terrestrial-based food items.

One surprising result from our investigation is that many boluses collected from swallows contained members of the Araneae (spiders). North American *Tachycineta* swallows concentrate their feeding on prey that are located in the air column during the breeding season (Brown et al. 2011, Winkler et al. 2011), suggesting that the spiders found in food boluses were captured during the process of ballooning, an important means of colonization by spiders (Suter 1999). It is worth noting, however, that *Tachycineta* swallows have been observed foraging on the ground for prey (Erskine 1984, Hobson and Sealy 1987) and for items containing calcium in some areas (Blancher and McNicol 1991, Dawson and Bidwell 2005). Although ground foraging has been observed occasionally in our study area (Rivers, personal observation), the relatively high proportion of diet items represented by Araneae (9-10%) suggests that at least some spider prey were obtained by foraging adults while in the air column.

The violet-green and tree swallow occur sympatrically throughout much of western North America, and a recent review of the violet-green swallow suggested this species is similar to the tree swallow in many aspects of its ecology and life history (Brown et al. 2011, Winkler et al. 2011; but see Beasley 1996 for a notable exception regarding mating strategies). Our study supports this notion because it found limited divergence in the size and taxonomic composition of food items between the two species in an area of sympatry. Given such similarities in foraging ecology and diet composition, how are these ecologically similar and congeneric species able to partition resources in a way that allows for coexistence during the breeding season?

Explanations for the partitioning of food resources among closely-related species have traditionally focused on competitive interactions that leads to a divergence in the type of food items selected, the microhabitat in which foraging occurs, or both (MacArthur 1958, Schoener 1965). However, we found limited divergence in diet provisioned to offspring in the two species, and additional foraging observations from our study site indicate that violet-green and tree swallows forage together in similar habitats and are not segregated within the air column (Rivers and Newberry, personal observations). These two species therefore do not appear to diverge in food item type or foraging habitats as would be expected if they experienced strong competition for food resources. Instead, it appears as though food resources are abundant enough that that it allows both species to coexist during the breeding period, a finding that has been shown to be true of other species of passerine birds that specialize on flying insects (e.g., Beaver and Baldwin 1975, Frakes and Johnson 1982, Blancher and Robertson 1984). If food resources are not limiting for *Tachycineta* swallows, coexistence may be mediated by other critical resources needed for breeding, such as nest sites (Martin and Martin 2001). *Tachycineta* swallows cannot excavate cavities in substrates and therefore these nest sites are valuable resources over which individuals compete (Newton 1994, Rosvall 2008). Our study population typically has a surplus of nest sites, as evidenced by some nest boxes that go unused each season (Rivers unpublished data), so this breeding population may not currently experience competition for nesting sites. However, the earlier initiation of breeding by the tree swallow at our site may represent a mechanism by which it competes with the violet-green swallow when cavity nest sites are limited. Nevertheless, this study suggests that food resources in our study population are currently plentiful enough that they allow both species to forage in the same microhabitats and use the same type of food items to feed their offspring, and calls for additional study that helps clarify the degree to which other factors constrain coexistence of these two closely related species in areas of sympatry.

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