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SHORT COMMUNICATION

Food choice of the Neotropical harvestman *Erginulus clavotibialis* (Opiliones: Laniatores: Cosmetidae)

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Abstract. Relatively little is known about the food habits of neotropical harvestmen. We used *Erginulus clavotibialis* (Pickard-Cambridge 1905), a locally abundant species of cosmetid harvestman in Belize, in a food choice experiment. Individuals were presented with fresh fruit (pineapple) and live invertebrate prey (termites) in an experimental chamber. This species showed a strong preference for fruit, as 72% of individuals ate it first and 67% spent the most time in the fruit-containing portion of the experimental chamber. Five *E. clavotibialis* (13%) consumed termites, confirming this species' ability to capture and consume live invertebrate prey. Adult males located food more quickly than nymphs. Harvestmen feeding on fruit were also significantly more active than non-feeding individuals or those preying upon termites first. Opportunistic frugivory may be important to *E. clavotibialis* during times when fruit is available (e.g., wet season). We hypothesize that this species exhibits a generalist diet in the field.

Keywords: Diet, feeding preference, frugivory, omnivory

Tropical forests have very high biodiversity in a variety of taxa, including terrestrial plants, vertebrates and especially arthropods (Wilson 1992; Myers et al. 2000). Many of these arthropod species have not been formally described (Erwin 1982; Ødegaard 2000), and little is known about the natural history of most species. There are few ecological studies of the harvestman fauna that occurs in the forested habitats of Central America (Proud et al. 2012; Wade et al. 2011). Not surprisingly, then, there is a general lack of detailed information regarding the diet and foraging behavior of these harvestmen (Acosta & Machado 2007).

Harvestmen are typically assumed to be omnivores, consuming live and dead invertebrates, fungi and plant material (i.e., Edgar 1971; Acosta & Machado 2007); with anecdotal observations of large gonyleptids feeding on small frogs (Castanho & Pinto da Rocha 2005) and nestling birds (Benson & Chartier 2010). Several studies have recently revealed that harvestmen are more active predators than previously assumed (i.e., Gnaspini 1996; Halaj & Cady 2000). A few studies have shown evidence of frugivory by harvestmen under laboratory conditions (Capocasale & Bruno-Trezza 1964; Gnaspini 1996) or in the field (Halaj & Cady 2000; Machado & Pizo 2000). However, it remains unclear how common frugivory is among harvestmen or whether fruits are preferred over live invertebrate prey.

The distribution of the harvestman *Erginulus clavotibialis* (Pickard-Cambridge 1905) includes areas in eastern Mexico, Belize and Guatemala, where individuals are relatively abundant in forested habitats (Goodnight & Goodnight 1977). Goodnight & Goodnight (1976) provide descriptions of aspects of the natural history of *E. clavotibialis*, with a primary focus on reproduction and development. This cosmetid species forages nocturnally and is presumed to be omnivorous (Goodnight & Goodnight 1976), but this assertion has not been empirically tested. During our previous field collections, we observed three adult *E. clavotibialis* feeding on a stalk of sugarcane during the evening of 4 January 2012 at the Clarissa Falls Forest reserve (17.1160°N, 89.1198°W). We did not observe any other instances of feeding, but *E. clavotibialis* was often found under the bark of rotting logs or in palm frond sheaths containing termites. We conducted an experimental study of food preference of *E. clavotibialis* using termite prey as a proxy for live invertebrates and pineapple as a proxy for fruit. This allowed us to quantify food choice and feeding habits in an experimental arena and to assess behavioral differences in harvestmen feeding on the different food types.

We collected 39 individuals (22 adult females, 10 adult males and 7 nymphs) by hand from leaf litter, tree buttresses, logs and other debris on 19 July 2012 at the Clarissa Falls resort, Cayo District, Belize (17.1116°N, 89.1272°W). Harvestmen were placed at random into one of three communal housing chambers (2.25L rectangular polypropylene boxes: $14 \times 25 \times 7.25$ cm) lined with leaf litter and bark and kept moist, such that water condensed on the chamber walls. They were not fed for three days between field collection and the feeding experiment, and no mortality was observed between the time of collection and the end of the experiment. At the conclusion of the experiment, all specimens were preserved in 70% ethanol. Voucher specimens were deposited in the collections of the American Museum of Natural History, New York.

For the food choice experiment, each harvestman was placed in the center of experimental chambers identical to the holding chambers, but empty except for 3 small dishes (5.5 cm in diameter), located in the left, right and center thirds of the chamber. The center dish was placed upside down to hold the harvestman prior to testing. One of the side dishes held several small pieces of pineapple ($\sim$15 g) and the other held 10–12 live termites (worker caste of *Reticulotermes sp.*). After a 5 min. acclimation period, the center dish was removed and the harvestman was allowed to move around the chamber and feed for 30 min. Harvestmen could move across the chamber in $<$ 10 sec; thus, actively foraging individuals could easily contact and perceive the different food items in the chamber. The trials were conducted after dusk (1900–2400 h) in a darkened room, and harvestmen were observed under red light to minimize disturbance (Hoenen & Gnaspini 1999). In between trials, we removed the harvestmen and the food dishes, replaced food that had been consumed, cleaned the chamber with a paper towel soaked in a 50% isopropyl alcohol solution, allowed chambers to air dry, and randomly reassigned the food dishes among chambers. Each harvestman was tested only once and was then transferred to a separate chamber to hold harvestmen that had completed the experiment.

Seven feeding trials were conducted simultaneously, with two observers each recording data. We recorded the time when a harvestman moved to a different portion of the chamber and when the harvestman fed on one of the food items. We then calculated the proportion of time spent in each section and determined which section each harvestman spent the most time in (preferred area). We also recorded the time until each individual fed upon the first food item and counted the number of termites consumed during each trial. Finally, we tallied the number of times each harvestman moved from one section of the chamber to another, using the total number of

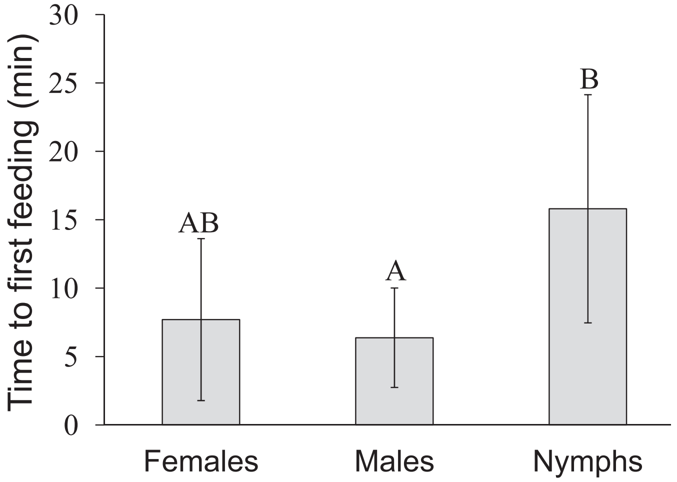

Figure 1.—Comparison of the time to the first feeding for females, males and nymphs. Bars are means, whiskers are SE. Different capital letters indicate significant difference based on the Tukey post hoc test.

sections "visited" as a measure of the frequency of movement. For most comparisons (i.e., food selection, preferred area), we pooled the data, because we did not expect differences in diet between the sexes or between nymphs and adults. However, the males of this species possess a heavily armed leg IV and nymphs are substantially smaller than adults. Thus we hypothesized that movement may vary between males, females and nymphs and compared the number of sections visited and the time to first feeding separately for males, females and nymphs.

Data on feeding preferences and preferred area of the chamber were pooled and analyzed using a G-test for goodness of fit with William's correction (Sokal & Rohlf 1994). The null hypothesis was that there would be no difference in food choice (1:1 ratio between food types) or preferred area (pineapple, termite and control sections would be preferred by an equal number of harvestmen), with the alternative hypothesis that one food type and/or section would be preferred. For females, males and nymphs, we compared the time until the first food item was fed upon and the number of sections visited, using ANOVA with Tukey's post hoc test ($\alpha = 0.05$), because these data met the assumptions of normal distributions and equality of variance. Finally, we compared the number of sections visited by harvestmen that first fed on termites or did not feed with the number of sections visited by harvestmen that first fed on pineapple using a nonparametric Mann-Whitney U test, because the variance was not equal between these groups.

Most harvestmen (28 out of 33 that ate during the experiment) fed upon pineapple first ($G_1 = 17.41$, $P < 0.0001$). Among the five individuals that ate termites first, two later consumed pineapple, and two others consumed additional termites (2–4 total) during the trial. Harvestmen spent ~50% of the time in the pineapple section and ~25% of the time in each of the other sections. The pineapple section was preferred by 26 harvestmen (26 spent the greatest proportion of time there), whereas 8 preferred the termite section and 5 preferred the control section ($G_2 = 18.72$, $P = 0.0001$). Females, males and nymphs did not differ significantly in the number of areas visited ($F_{2,36}$=1.66, $P = 0.20$), but did differ significantly in the time to first feeding ($F_{2,30} = 3.53$, $P = 0.042$), with males feeding significantly faster than nymphs ($P = 0.049$, Tukey's post hoc test; Fig. 1). Harvestmen feeding on pineapple became significantly more active (mean of 10.64 sections visited) than those not feeding on pineapple (average of 3.45 sections visited; $U = 65.5$, $z = 2.75$, $P = 0.006$). We typically observed this increased activity only after the harvestmen finished eating pineapple.

After feeding on pineapple, nearly every individual raised both of the second pair of legs to an almost vertical position and would slowly move them from side to side, often for several minutes at a time. The significance of this behavior was not clear; however, Goodnight & Goodnight (1976) also reported a similar leg-waving behavior in this species, but assumed that it could enhance prey encounter or capture rates. Because many chemosensory organs are located on the second pair of legs, it is possible that this behavior serves some sort of sensory function, but this warrants further study. Likewise, harvestmen have been observed to be attracted to chemical cues released by conspecifics rubbing their bodies on surfaces (Willemart & Hebets 2012). We did not observe this type of scent marking during our experiment, and several aspects of our experimental design (cleaning chambers with ethanol, running several chambers simultaneously, replacing food that had been partly consumed, random reassignment of feeding dishes among experimental chambers) were designed to minimize any potential chemical cues from previous individuals. It is also possible that harvestmen were seeking a food high in water content, and preferred pineapple for this reason. However, *E. clavotibialis* were maintained in a high humidity environment prior to the experiment, and termite body fluids also contain substantial water. Thus, it is more likely that harvestmen were responding to the presence of an aromatic food high in carbohydrates. Other investigators have observed that harvestmen prefer highly aromatic food items (Santos & Gnaspini 2002); thus, future studies could examine the degree to which aroma impacts feeding preferences in the laboratory or field.

In our experiment, *E. clavotibialis* showed a significant preference for fruit in captivity, but also fed upon live invertebrate prey. Frugivory by harvestmen has also been observed under laboratory conditions in other species (Capocasale & Bruno-Trezza 1964; Gnaspini 1996). However, harvestmen diets in the laboratory and field sometimes vary substantially (i.e., Edgar 1971; Gnaspini 1996; Santos & Gnaspini 2002), and thus the implications of these findings for diet in the field warrant further investigation. Likely, the incidence of frugivory will depend on the degree to which fruit sources are available in the field; many tropical forests have abundant sources of seasonably available fruits (Jordano 2000; Machado & Pizo 2000). Different harvestmen species likely vary greatly in their utilization of fruits, but little is currently known about the diets of most tropical harvestmen species (Acosta & Machado 2007). Machado & Pizo (2000) documented frugivory in the field by the gonyleptid *Neosadocus variabilis* (Mello-Leitão 1935), but not by other species occurring at that site in southeastern Brazil. Halaj & Cady (2000) found that sclerosomatid harvestmen (primarily *Leiobunum* spp. Koch 1839) frequently consumed blackberries (up to 25% of the diet) in Ohio, USA, even though invertebrates were more important overall in the diet.

Compared to invertebrate prey, fruits are typically higher in carbohydrates and lower in protein, but this can vary substantially among fruits (Machado & Pizo 2000). Machado & Pizo (2000) observed that the harvestman *N. variabilis* fed on fruits across a wide range of lipid (5.2–70.8%), carbohydrate (16.5–85.5%) and protein (4.6–10.3%) contents, with a marked preference for larger fruits that could not be carried off easily by ants. They suggested that lipid-rich fruits might substitute for a typical diet of insects, and future studies could examine whether harvestmen prefer fruits rich in carbohydrates or lipids and the degree to which frugivory is realized in the field. We hypothesize that *E. clavotibialis* exhibits a generalist diet in the field, utilizing facultative frugivory whenever fruits are abundant.

Some investigators have used stable isotope analysis (Koenig et al. 2011) or polymerase chain reaction (PCR) analysis (Lundgren et al. 2009) to quantify the diets of harvestmen. Stable isotopes of C, N and S are most frequently used for food web analyses to integrate feeding history over time and identify the carbon source and realized trophic level of consumers (Peterson & Fry 1987). Koenig et al. (2011) used N isotope analysis to document differences in trophic level for the harvestmen *Mitopus morio* (Fabricius 1779). That species showed enrichment in ^{15}N at only one of the sites, indicating that it could function as an intermediate predator or as a top invertebrate carnivore. Lundgren et al. (2009) used PCR analysis on prey DNA extracted from the gut tract of the harvestman *Phalangium opilio* (Linnaeus 1758) to document consumption of the agricultural pest *Diabrotica virgifera*. Future studies could utilize these types of analytical techniques to quantify more fully the diets of harvestmen in the field.

Despite the assumption that harvestmen are generalist omnivores, little is currently known about the diet of most species (Acosta & Macahdo 2007). Recent studies have provided new insights into the relative importance of carnivory (Gnaspini 1996; Halaj & Cady 2000; Koenig et al. 2011) and frugivory (Gnaspini 1996; Halaj & Cady 2000; Machado & Pizo 2000) in the diets of harvestmen. Facultative frugivory and diet flexibility may enable harvestmen to capitalize on seasonally variable food items when they are abundant. A challenge for future studies will be to identify how flexible the diets of various harvestmen are and the degree to which the conventional broad-based generalizations apply.

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