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CARNIVORY IN ADULT FEMALE EUMENID WASPS (HYMENOPTERA:
VESPIDAE: EUMENINAE) AND ITS EFFECT ON EGG PRODUCTIONCharles F. Chilcutt^{1,2}, and David P. Cowan¹

ABSTRACT

Seventy captive adult female wasps of the eumenid genera *Ancistrocerus* and *Euodynerus* were observed to feed on multiple prey items. It was shown experimentally that *E. foraminatus* females that fed on prey had significantly larger egg volumes than adult wasps deprived of prey.

Most wasp larvae feed on arthropod prey provided for them by their parents (Spradbery 1973), but the basic food of adult wasps is presumed to be carbohydrates obtained from the nectar of flowers or honeydew of homopterous insects (Evans 1966a, 1966b; Spradbery 1973; Iwata 1976). Frequent observations of adult predatory wasps eating sugary solutions has led to the assumption by many researchers, that wasps acquire enough protein as larvae so that as adults they do not need high protein food (Hunt 1991). Nectar contains but a limited amount of protein (Hunt et al. 1982) and the amount of pollen consumed by predatory vespids is too low to be important for nourishment (Hunt et al. 1991).

Feeding by adult wasps on prey has been observed many times and Evans (1966b) divided these behaviors into 3 categories: (1) imbibing blood from the sting puncture; (2) malaxating prey, defined here as chewing prey then feeding on blood from the wound before provisioning it for the young; and (3) malaxating prey specifically for adults and not using it as provisions, referred to as hypermalaxation. Our observations are similar to hypermalaxation, but we observed entire prey being consumed including flesh, along with instances of hypermalaxation.

Many families of parasitoid wasps are known to feed from puncture wounds (Askew 1971). Those families of wasps known to malaxate their prey include the parasitoid Bethyilidae (Finlayson 1950) and the predators, Pompilidae (Evans and West-Eberhard 1970), Sphecidae (Leclercq 1959), and the solitary Vespidae (Eumeninae) (Malyshev 1968). Hypermalaxation has been described in the bethylids (Finlayson 1950), tiphiids (Burdick and Wasbauer 1959), pompilids (Evans and Yoshimoto 1962), sphecids (Lin 1978), and eumenids (Rau 1945).

Three main hypotheses have been proposed to explain why adult wasps feed on prey: (1) a source of fluids (Lin 1978) especially during flower (nectar) scarcity (Evans and West-Eberhard 1970); (2) to quiet struggling prey (i.e. Spradbery 1973); and (3) it has no function, but is a displacement activity

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exhibited by confused wasps unable to nest (Huber 1961). A fourth possibility, that female predatory wasps require proteinacious prey for egg development (Spradbery 1973) has not been tested. Evans (1966a) stated that many sphecid wasps feed on prey only under special conditions, but there is little evidence that it occurs regularly. Hunt (1991) reiterated this generally accepted opinion by stating that reports of prey-feeding by adult wasps is "fragmented and largely anecdotal", and continues "that nectar, nectar-like liquids, and body fluids of prey or carrion are the typical, and nearly exclusive, sources of adult nourishment". Several workers have argued that adult wasps are not morphologically adapted to eating solid food. Imms (1957) suggested that the mandibles of adult wasps were adapted for nest building rather than for a trophic function, Spradbery (1973) believed that adult wasps are restricted to a liquid diet by the narrowing of the esophagus in the cervical region, and Hunt (1991) emphasized the distensible crop and restrictive proventriculus. Because the prey of solitary wasps is usually widely scattered, frequent observations of predatory events in nature are unlikely and we believe that carnivory in predatory wasps has been overlooked as a source of protein for ovarian development. In this study we report on adult female carnivory in captive eumenid wasps and its relationship with egg development.

MATERIALS AND METHODS

A total of 71 adult female wasps of the eumenid genera *Ancistrocerus* and *Euodynerus* were observed nesting in captivity from 1989 to 1991. While nesting, all of these adult females were observed feeding on multiple prey items. To study the effects of adult female carnivory on ovarian development, 20 females of *Euodynerus foraminatus* (Saussure) were maintained in one gallon jars (two wasps per jar). Each was provided with water and a honey solution (to replace the nectar they would normally obtain at flowers). All females were mated to control for possible effects on egg maturation found in other insect species (De Wilde 1964).

One group of 10 females was given spruce budworm (*Choristoneura fumiferana* Clemens) caterpillars and observed the first day to ensure that each consumed the prey. Following this, they were provided with an abundance of prey (more than they could eat). A second group of 10 females was not given caterpillars. Starting 3 days after the first caterpillars were provided, one wasp from each group was dissected daily for 10 days. The length and diameter of the 2 largest eggs (one terminal oocyte from each of the paired ovaries) were measured using a dissecting microscope and ocular micrometer. Oocyte volume was approximated by multiplying the length by the square of the diameter ($V=Ld^2$). Significance for all statistical tests was set at $p \leq 0.05$. During dissection, the crop and ventriculus of each wasp was also dissected and examined for content. The head widths (an indicator of size in wasps) of the 20 *E. foraminatus* were measured using a dissecting microscope and ocular micrometer.

RESULTS

The average total egg volume (the 2 largest eggs) for the group given prey (0.809 mm^3) was significantly greater than for the group denied prey (0.330 mm^3) ($t=3.75, p < 0.001$). The average largest egg volume for the experimental group (0.520 mm^3) was significantly greater than for the control (0.255 mm^3) ($t=3.32, p < 0.005$). The average smallest egg volume for the experimental

group (0.289 mm^3) was significantly greater than for the control (0.075 mm^3) ($t=3.45$, $p < 0.005$). The average head width of the group fed on prey (3.28 mm) and the group denied prey (3.25 mm) were not significantly different ($t=0.268$, $p > 0.1$). This was important, because Larrson (1990) and O'Neill (1985) found strong correlations between head size and egg size in sphecid wasps.

All wasps fed on the sugar solutions provided, but none showed any interest in the cups containing pollen. The crops of dissected wasps were found to be distended with sugar solution. When we dissected wasp ventriculi, we found no fragments of prey, although the ventriculi did take on the darker color of prey tissues after wasp feeding.

We estimate that individual wasps ate from 6 to 18 caterpillars after being given access to prey. Due to difficulties of observation, it seems likely that the high end of the range is closest to the actual number of prey eaten. There was a distinct period before nesting began, when the wasps each ate approximately 4 caterpillars. After nesting and provisioning began, however, all females were observed eating prey at various times which we could not correlate with any phase of the nesting cycle. When wasps were deprived of prey (twice, each time for one week) nest cavities were partitioned and closed with mud, but no eggs were found. Because eumenids oviposit before provisioning, cells with only eggs might be expected if the presence of prey were not needed to stimulate ovarian development (through feeding).

Prey captured and fed upon by adult females were not always stung first. Individuals of *E. foraminatus* were more likely to chew through the prey's cervical area to kill it, and then devour the rest of the prey without a struggle. Feeding always began on the last abdominal segment and lasted from 2 to 15 min. Larger caterpillars were often only partly eaten and discarded, while smaller prey were devoured leaving only the head capsule. While eating prey, a wasp holds the caterpillar by the abdomen with her forelegs and curls her abdomen under the prey in a position similar to stinging. This position made it difficult to discern whether wasps were just holding prey or stinging it. Smaller prey were less likely to be stung because of difficulties involved in locating the normal sting region and the ease of subduing a small victim by biting it.

DISCUSSION

Our observations of prey-feeding by adult eumenids contradict the view that adult wasps feed to acquire fluids on dry days (Lin 1978). Our wasps were always provided with an ample supply of water, yet still fed on prey. The idea that adult feeding behavior is a response to flower nectar scarcity (Evans and West-Eberhard 1970) is contradicted by our observations of distended crops (filled with sugar solution) found in females dissected during the period we observed prey-feeding. This indicates that the absence of nectar is not what stimulates prey-feeding. Nor was there any indication that eating prey was a displacement activity exhibited by wasps in response to novel or confusing situations. Rather, it is a normal necessary activity associated with egg development. Our results are in line with numerous studies of parasitoid Hymenoptera that require maturation feeding on hosts (prey) for full egg development (DeWilde 1964). Flanders (1942) explained that in many species of Hymenoptera larval nutrition is insufficient for egg development to proceed in the adult without further feeding, adding that these adult females habitually feed on the body fluids of their hosts prior to oviposition. Our measurements of eggs for wasps which did not feed on prey (some eggs almost as large as those of prey-fed wasps) indicate that vitellogenesis begins in eumenid females in the

absence of prey or protein sources other than those acquired as larvae. Prey-feeding is essential to maturation of more than one egg (wasps not fed prey as adults had only one developing egg) and possibly even for maturation of the first egg. This condition is similar to that described by Flanders (1935) for the Pteromalidae and found in several dipteran species (Clements 1963).

Until now research on the effects of prey-feeding on ovarian development had not been carried out for solitary predatory wasps. The many reports of prey-feeding (on the body fluids) by adult female Sphecidae (Evans 1966a), eumenids (Iwata 1953), and pompilids (Rau 1945) have not been correlated with ovarian development. It is likely that these many anecdotal reports of predatory solitary wasps feeding on prey are involved with egg maturation. It also seems likely that more intensive studies of predatory behavior will reveal prey feeding to be a regular part of female activities and not something brought on by adverse conditions (i.e. lack of water).

Total mastication of prey as we observed for eumenids has been observed for social species. Rau (1945) described workers of *Polistes* spp. thoroughly pulping caterpillar prey in their jaws so that it could be swallowed. Chapman (1963) found *Vespula pennsylvanica* (Saussure) feeding on swarming reproductive ants. Wasps were observed "dozens of times" capturing ants and landing to chew their prey, while no prey was seen to be carried back to the nest. Examinations of the ventriculi of 20 wasps failed to reveal any ant fragments, implying that only body fluids were ingested. Unlike the soft, thinly sclerotized lepidopterans fed on by eumenids, the heavily sclerotized ant cuticle would be difficult to digest. This, along with the need for adult wasps (with a narrowed esophagus) to finely chew their food, probably is related to why no fragments were found. Chapman (1963) described the wasps biting off the heads of their ant prey and "preferring" to feed on the abdomen rather than the thorax, behaviors we described earlier for *E. foraminatus*. This behavior has also been described by Ross (1983) for *Vespula* spp. which assume the same posture we described for solitary vespids feeding on prey, enclosing "the struggling prey with the ventral surface of the gaster, the legs, and the mouthparts". Gillaspay (1979) gave descriptions of *Polistes* spp. returning to the nest with no apparent load with dissected crops containing a "thin gruel of protein food with recognizable insect parts".

Among vespids, the transition from solitary to social life has also involved the transition from feeding larvae intact prey items to feeding young completely masticated prey meat. Our results indicate that the complete chewing of prey was likely well established among the solitary ancestors (as a preadaptation) of the living social species.

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