

LARVAL FEEDING BY MALE *POLISTES FUSCATUS*  
AND *POLISTES METRICUS* (HYMENOPTERA : VESPIDAE)

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SUMMARY

Male *Polistes fuscatus* fed malaxated prey to larvae, with feeding behaviors similar in major aspects to females feeding larvae. A single instance of larval feeding by a male *P. metricus* is also reported, and literature references to other observations of male social wasps feeding larvae are summarized.

RESUME

**Approvisionnement des larves par des mâles de *Polistes fuscatus*  
et de *Polistes metricus***

Nous avons observé des mâles de *Polistes fuscatus* qui donnaient aux larves des proies malaxées, avec des comportements semblables, à bien des points de vue, à ceux des femelles qui approvisionnent les larves. Nous rapportons aussi un exemple de mâle de *Polistes metricus* qui approvisionnait les larves. Enfin, nous résumons les autres observations de mâles nourrissant les larves, qui sont décrites dans la littérature.

On 1 June 1977 near Eureka, Missouri, we transferred eight *Polistes* nests from a building's eaves to observation shelters on the building's windows, moving the adult females on each nest under CO<sub>2</sub> anesthesia. Two weeks later we began periodic one hour observations at two *P. fuscatus* and one *P. metricus* colonies, recording the number of arrivals and departures by adults and the number of larval feedings and trophallactic exchanges.

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On 27 July we saw a male on nest 3 (*P. fuscatus*) take a food mass from a worker. He then malaxated (chewed) the item for about three minutes, entered and remained in a nest cell for 7-10 seconds, withdrew from the cell without the food item, and then cleaned himself like workers do after feeding larvae. About four minutes later another worker returned to the nest with a large food item, malaxated it, and fed a portion to a larva. The same male then approached this worker and appeared to take a small portion of the remaining food mass. Although the male was not facing us, his behavior indicated malaxation. He then entered a nest cell, withdrew after about 10 seconds and cleaned himself.

On 5 August at nest 4 (*P. fuscatus*) a male approached a returning forager and divided a large food mass in half with her. He malaxated the mass for more than three minutes before feeding it whole to a larva. The food mass could be seen on the larva's mouth after the male withdrew; a passing worker antennated the food, took it, and then fed three more larvae with it. Males fed larvae at this same nest on 12, 14, 16, and 17 August. Data summarizing these observations on *P. fuscatus* are presented in Table I.

In mid-August the involvement of males in food handling on nest 4 was more pronounced than the data indicate. On 16 August the adult sex ratio was approximately 1 : 1, but all but 2 or 3 males at a time were on top of the nest while all females were on the face of the nest. The few males on the nest face handled part or all of four out of five food loads returned to the nest during the observation period. The ratio of gynes to workers among the females could not be determined, and at this date gynes were assumed to be present, but even considering gyne presence and inactivity, the pronounced activity of the few males among the more numerous females was conspicuous. Despite this, females fed more larvae, because the males fed only one larva each.

The behaviors of the male *P. fuscatus* feeding larvae were identical in most respects to those of females feeding larvae. Males took food from workers by approaching them face to face, mutually stroking antennae, then dividing the item with the worker or taking it entire. Immediately after feeding larvae each male used the forelegs, alternately or simultaneously, to rub the head, antennae, scapular regions, and mid and hind legs, which were then usually used in cleaning the abdomen and wings. The approach behavior was identical to that used by both males and females soliciting trophallaxis, and the cleaning behavior was indistinguishable from isolated bouts of grooming. The *sequence* of behaviors with grooming immediately following larval feeding, is very distinctive, however, and was identical in both sexes. On one occasion a male, after cleaning, then solicited saliva from larvae. Such solicitation after feeding was occasionally also seen in females, but it was not part of the usual sequence of feeding behaviors in either sex.

Table I. — Observational data on male *Polistes fuscatus* feeding larvae. The adults were not individually marked, so it was not possible to discriminate worker from gyne females. Males varied somewhat in eye color, thus allowing individual discrimination. The nests were collected on 2 September. A question mark (?) indicates data not collected; parentheses () indicate estimated values.

Tableau I. — Résultats des observations de mâles nourrissant les larves chez *Polistes fuscatus*. Les imagos n'ayant pas été marqués, il n'a pas été possible de distinguer les ouvrières des femelles fertiles. En revanche, il a été possible de reconnaître individuellement les mâles, en raison de la couleur différente de leur yeux. Les nids ont été récoltés le 2 septembre. L'absence de résultats est indiquée par un point d'interrogation. Les parenthèses indiquent les valeurs estimées.

Date	Time of day at start (C.D.T.)	N nest cells (open/capped)	N adults on nest ( $\delta/\varphi$ )	N adults feeding larvae ( $\delta/\varphi$ )	N larvae fed (by $\delta/\varphi$ by $\varphi/\varphi$ )	Elapsed Observation Time (min)
Nest 3						
27 July	4:11 pm	80/7	3/7	1/1	2/2	33
28 July	3:47 pm	82/7	3/6	0/1	0/3	60
1 Aug.	1:15 pm	81/9	1/7	0/2	0/8	60
3 Aug.	6:30 pm	81/9	2/6	0/1	0/5	30
4 Aug.	3:20 pm	81/9	2/6	0/1	0/7	60
12 Aug.	12:05 pm	84/6	12/12	0/2	0/9	60
16 Aug.	11:45 am	?	10/10	1/1	1/4	15
2 Sept.	—	90/0	13/8	—	—	—
Nest 4						
1 Aug.	12:10 pm	(160)/38	5/18	0/8	0/41	60
3 Aug.	5:24 pm	182/37	3/11	0/1	0/1	60
4 Aug.	2:15 pm	(185)/38	7/14	0/1	0/4	60
5 Aug.	3:40 pm	189/33	4/13	1/2	1/5	60
12 Aug.	10:55 am	(199)/23	10/15	1/3	1/6	60
14 Aug.	4:11 pm	?	9+/10+	3/4	4/8+	45
16 Aug.	10:10 am	?	12/12	4*/5	3/12	95
17 Aug.	12:45 pm	(220)/8	12/14	1/6	4/16	60
25 Aug.	? pm	?	12/12	1**/2	0/6	60
2 Sept.	—	234/0	10/11	—	—	—

\* one  $\delta$  surrendered entire food item to a  $\varphi$

\*\* dropped food after unsuccessful apparent feeding attempts

On several occasions *P. fuscatus* males approached females which had food items, apparently intending to solicit that food item, and the females either rebuffed the males or turned and moved away from them. On other occasions females with food items approached males as if to offer to share or surrender the food item, and the males turned away with apparent disinterest. Once a male surrendered an entire food item to a female who then fed larvae with it. All these behaviors were also seen in females.

At least three features distinguish the males' behavior in *P. fuscatus* from that of females: males were never seen to forage for prey; most

feedings by males involved only a single larva ; and males spent a longer time malaxating. Length of time spent malaxating was not measured accurately for either sex, but for females the time was noted to almost always be less than three minutes ; once the malaxation time was as brief as 15 seconds. In males, malaxation time was noted to be regularly three minutes or longer, and we recorded instances of prolonged malaxation lasting 6, 9 and 52 minutes.

On 20 July the six females then on nest 6 (*P. metricus*) destroyed parts of their nest and brood. (Late season brood destruction is apparently common in many *Polistes*, [DELEURANCE, 1952]. This mid season destruction seems more unusual, though G.J. Gamboa [personal communication] reports it as a regular response to parasitoid infestation in *P. metricus* in eastern Kansas.) One female took part of a pupa, malaxated it, and divided it with several other females and two males. Some of the females and one male fed the pupal fragments to small larvae. ENTEMAN (1902) reported an unnamed *Polistes* similarly taking portions of dead larvae and malaxating them. One male then took a larval fragment and "carried it over the nest in the same searching manner as the female, and finally fed it to a larva."

Single instances of a male feeding a larva are reported for *Polistes gallicus* (HELDMANN, 1936), *P. dubius* (STEINER, 1932), *P. snelleni* (YAMANE, 1969) and *P. fuscatus* (WEST EBERHARD, 1969). JEANNE (1972) saw several males feed larvae in *Mischocyttarus drewseni*, and M. Litte (personal communication) found that males of *M. labiatus* and *M. flavitarsus* occasionally feed larvae. The behavior is also reported for vespine wasps, including *Vespula lewisii* (T. SHIDA, cited in YAMANE, 1969, q.v.). ISHAY and IKAN (1968) incorrectly cite ISHAY (1964) as reporting the behavior in *Vespa orientalis*, however, J. ISHAY (personal communication) says the behavior does occur in *V. orientalis*, though very infrequently. R.D. AKRE (personal communication) has seen males of *Vespula* species feed larvae, though always in situations involving questionable circumstances. ROUBAUD (1916) saw males of *Belonogaster junceus* regularly taking and malaxating food items, but he did not say whether the items were then fed to larvae. Male feeding of liquid food to larvae is recorded for *P. dubius* (WEYRAUCH, 1928).

JEANNE (1972) suggests that larval feeding in male *M. drewseni* is associated with extracting liquid nourishment from food during malaxation, as indicated by a comparatively long malaxation time. He also suggests that larval feeding by male *M. drewseni* may only have functioned to discard a food pellet after taking nourishment, since sometimes males simply dropped food items after malaxation. JEANNE's first suggestion is based on an observation paralleled by our own : male *P. fuscatus* as well as *M. drewseni* malaxate for longer periods than do females. Corroborating observations for Jeanne's second suggestion are provided by RABB (1950), who saw several

males *P. metricus* malaxate solid food items and ingest some of them and drop the others without feeding larvae. We saw one food item dropped by a male *P. fuscatus*, but only after repeated apparent attempts to feed larvae. We feel that Jeanne's suggestions could be accurate, but studies quantifying the actual nourishment extracted, if any, by males during malaxation have not been done. Furthermore, the extent to which females might similarly extract nourishment during malaxation has not been documented. EVANS and WEST EBERHARD (1970) note that the provision morsel grows visibly smaller during malaxation, and Rau and Rau (1918, p. 281) report self nourishment and subsequent discarding of a food item in a female *P. carolina* (reported as *P. rubiginosus*, but see BOHART and MENKE, 1974).

In early July, 1979, males of *Polistes exclamans* were also seen to provision larvae. The nest was in an observation shelter at the same field site as 1977. Three observers, working independently, each saw one of several unmarked males take a provision load from a returning forager and then malaxate that provision. Following malaxation two of the males gave the provision to a single larva; one of the males dropped the provision after malaxation. In one instance the malaxation was noted to be much longer in duration than is typical for females.

#### References

- BOHART R.M., MENKE A.S., 1974. — Names of some North American vespoid wasps. *J. Kans. Ent. Soc.*, 47, 459-469.
- DELEURANCE E.P., 1952. — Etude du cycle biologique du couvain chez *Polistes*. Les phases « couvain normal » et « couvain abortif ». *Behaviour*, 4, 104-115.
- ENTEMAN M.M., 1902. — Some observations on the behavior of the social wasps. *Pop. Sci. Monthly*, 61, 339-351.
- EVANS H.E., WEST EBERHARD M.J., 1970. — The Wasps. *Univ. Michigan Press.*, edit., Ann Arbor Mi VI + 265 p.
- HELDMANN G., 1936. — Über die Entwicklung der polygynen Wabe von *Polistes gallica* L. *Arb. Phys. Angew. Ent. Berlin-Dahlem*, 3, 257-259.
- ISHAY J., 1964. — Observations sur la biologie de la Guêpe Orientale *Vespa orientalis* F. *Ins. Soc.*, 11, 193-206.
- ISHAY J., IKAN R., 1968. — Gluconeogenesis in the Oriental Hornet *Vespa orientalis* F. *Ecology*, 49, 169-171.
- JEANNE R.L., 1972. — Social Biology of the Neotropical wasp *Mischocyttarus drewseni*. *Bull. Mus. Comp. Zool. (Harvard Univ.)*, 144, 63-150.
- RABB R.L., 1950. — A contribution to the ecology of *Polistes* in North Carolina. *M.Sc. thesis*, N.C. State Univ. Raleigh.
- RAU P., RAU N., 1918. — Wasp Studies Afield. *Princeton Univ. Press*, edit., Princeton, XII + 372 p.
- ROUBAUD E., 1916. — Recherches biologiques sur les guêpes solitaires et sociales d'Afrique. La genèse de la vie sociale et l'évolution de l'instinct maternel chez les *Vespidés*. *Ann. Sci. Nat. Zool.*, 10<sup>e</sup> Ser., 1, 1-160.
- STEINER A., 1932. — Die Arbeitsteilung der Feldwespe *Polistes dubia* K. *Z. Vergl. Physiologie*, 17, 101-152.
- WEST EBERHARD M.J., 1969. — The social biology of polistine wasps. *Misc. Pub. Mus. Zool. (Univ. Michigan)*, 140, 1-101.
- WEYRAUCH W., 1928. — Beitrag zur Biologie von *Polistes*. *Biol. Zbl.*, 48, 407-427.
- YAMANE S., 1969. — Preliminary observations on the life history of two polistine wasps, *Polistes snelleni* and *P. biglumis* in Sapparo, Northern Japan. *J. Fac. Sci. Hokkaido Univ.*, Ser. VI, *Zool.*, 17, 78-105.