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ADULT NOURISHMENT DURING LARVAL PROVISIONING IN A PRIMITIVELY EUSOCIAL WASP, *POLISTES METRICUS* SAY

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SUMMARY

In the laboratory, female *Polistes metricus* on recently collected nests malaxated larval provisions containing radioactive fructose. Recovery of radioactivity from the adults showed that they extracted substantial liquid or semisolid material from the provision morsel during malaxation. The extracted material was held in the crop, and it could be regurgitated. Adults allowed to regurgitate to larvae exhibited significantly less radioactivity than wasps isolated before regurgitation could occur. Midguts and wing muscles from provisioning adults show a pattern of radioactivity assimilation, with peaked activity at two hours following malaxation. These results confirm a previously observed pattern of larval provisioning and, for the first time, demonstrate adult nourishment to be concomitant with the provisioning behavior.

RESUME

Alimentation de l'adulte au cours de l'approvisionnement des larves chez une guêpe primitivement eusociale, Polistes metricus **Say**

Au laboratoire, la femelle de *Polistes metricus* sur des nids récemment récoltés malaxent des provisions destinées aux larves, contenant du fructose radio-actif. Le fait que de la radio-activité se retrouve chez les adultes montre qu'ils extraient une part substantielle de liquide ou de matériel semi-solide au cours de la malaxation de ces provisions. Ce matériel extrait se retrouve au niveau du gésier et peut être régurgité. Les adultes ayant la possibilité de régurgiter aux larves manifestent une radio-activité significativement inférieure aux guêpes mises en isolement avant de pouvoir régurgiter. L'intestin moyen et les muscles alaires des approvisionneuses montrent un patron d'assimilation radio-active, avec un pic d'activité deux heures après la malaxation. Ces résultats confirment un patron d'approvisionnement des larves précédemment observé et, pour la première fois, démontrent une alimentation de l'adulte en relation avec le comportement d'approvisionnement.

INTRODUCTION

Social wasps of the family Vespidae are well known to malaxate prey before provisioning their larvae. That is, a female wasp takes an insect or insect fragment and chews or squeezes it with her mandibles, usually while rotating it with her forelegs, before feeding the resultant pulpy mass directly to larvæ. Malaxation of prey (not larval provisions) occurs infrequently but in apparently a wide variety of social and non-social wasps (EVANS and EBERHARD, 1970). For example, LIN (1978) reports « hypermalaxation » (HUBER, 1961, *in* LIN, 1978) in the digger wasp *Diodontus franclemonti* (Sphecidæ). During periods of very hot weather the adult *D. franclemonti* malaxated and then discarded a series of aphids, probably as a source of water and perhaps of nourishment. EVANS and EBERHARD (1970) note that, in general, feeding on prey by adult wasps probably occurs under conditions of scarcity of nectar or honeydew ; they also note, though, that some species may require proteinaçeous food as adults.

Species that would appear to require proteinaceous nourishment as adults are those that are long-lived and, in particular, that have a prolonged period of reproductive activity. Queens of eusocial Vespidæ are conspicuous in these regards. Though it has been suggested that adult wasps may nourish themselves as they malaxate prey, little attention has been paid to the possibility that adults may nourish themselves by malaxation of larval provisions. JEANNE (1972) suggested that male *Mischocyttarus drewseni* (Vespidæ) that malaxated larval provisions are « more selfish than worker-like » in that their malaxation seems primarily directed toward self nourishment. HUNT and NOONAN (1979) presented data on malaxation of larval provisions by males of three *Polistes* species that indicated support for JEANNE'S suggestion ; they also noted the absence of data to document nourishment of adult females during malaxation of larval provisions. The following study was therefore designed to investigate the potential for self-nourishment during malaxation of larval provisions by female *Polistes* wasps.

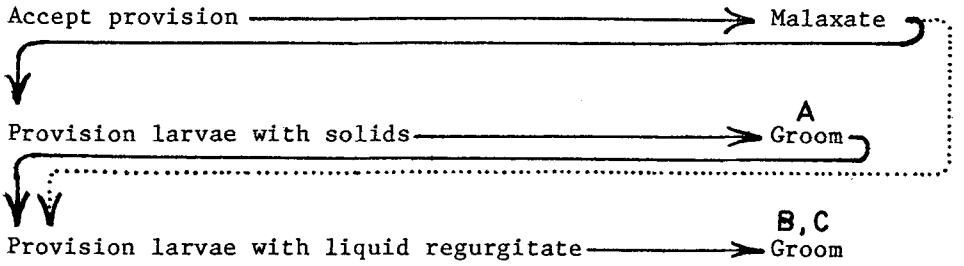
METHODS

Colonies of *Polistes metricus* Say (Vespidae) were collected near St. Louis, Missouri. Collections were made near sunset or sunrise to make it more likely that most adults of the colony were on the nest. The nest was then attached to the ceiling of an aluminum screen mosquito rearing cage (30 cm on a side), and the adults were introduced into the cage. Most colonies were collected in the evening and used in experiments the following morning.

Live lepidopteran larvae (Cabbage Butterfly, *Pieris rapae*, and Cabbage Looper, *Trichoplusia ni*) were collected in a local garden. In the laboratory a small (< 1 cm) whole lepidopteran larva or a fragment of a larger larva was then used as a provision morsel. The morsel was injected, using a microliter syringle with 1 µl 5 % ethanol

containing 1 μCi ^{14}C fructose (obtained from ICN Corp.). The injected morsel was taken from the tip of the syringe onto the point of a teasing needle and offered to a wasp that was on the face of its nest. Slow, careful presentation made it possible to move the morsel to the wasp without alarming her. If the morsel could be brought into contact with the wasp's mouthparts, she usually took the morsel and began to malaxate it. The wasps typically malaxated the morsel for one to a few minutes before feeding it to larvae.

Typical provisioning behavior in these wasps involved a specific sequence of provisioning and grooming behaviors (*fig. 1*) :



The letters A and B indicate points in this sequence where wasps were removed from the nest and isolated as follows : A = Group I (run in 1978), B = Group II (run in 1979). In a third group of wasps (Group III), assayed in 1982, the provision morsel was taken from the adult wasp at the completion of malaxation but before any larvae had received solid provision. These wasps were then closely observed until one or more larvae had been visited (for possible provisioning with liquid regurgitate) and the adult then groomed herself ; during this grooming, then, she was removed from the nest and isolated. The dotted arrow and letter C in the flow diagram illustrate this sequence.

The isolated wasps were held in 500 ml plastic containers for varied time periods (see Results). Following that, the Group I and Group II wasps were chilled briefly in a refrigerator and then transferred to a test tube immersed in an acetone/dry ice bath that froze the wasp completely in less than 30 sec. The frozen wasp was quickly divided, using a razor blade, into four parts :

1) head,
2) thorax (including propodeum with appendages,
3) anterior gaster (abdominal segments II-IV),
4) posterior gaster (abdominal segments V-X).

Each of these four parts was placed into separate test tubes containing 1 ml 5 % ethanol and crushed using a glass stirring rod. The test tubes were then centrifuged for 5 minutes at 10,000 *g*, and the supernatant was decanted into a scintillation vial for counting. The Group III wasps were asphyxiated using ethyl acetate. The legs and wings were then clipped off ; the wasp was pinned to a wax pan, and the midgut and wing muscles were removed. The midgut was tied off from the intact crop before removal, and the esophagus was exposed before removing the wing muscle. The excised tissues were transferred to separate test tubes, macerated in 1.0 ml NCS tissue solubilizer (obtained from Amersham/Searle), and counted, as were the the Group I and II samples, using 5 ml Bray's solution and a Packard Tri-Carb liquid scintillation spectrometer. Recorded counts per minute (CPM) were converted for reporting as disinte-

grations per minute (DPM) using an experimentally established quenching factor of 60 %.

Once the experimental wasps had been isolated, all other adult wasps on each nest were promptly collected and discarded. Larvae were removed individually from the nest, weighed, and placed into test tubes containing 1 ml 5 % ethanol. The larvae were macerated with stirring rods, centrifuged for 5 min. at 10,000 *g*, and the supernatant was decanted for scintillation counting. Appropriate controls for background counts were run for all sample procedures.

RESULTS

Figure 2 presents the distribution among the four sampled body regions of radioactivity for the Group I wasps, which were isolated immediately

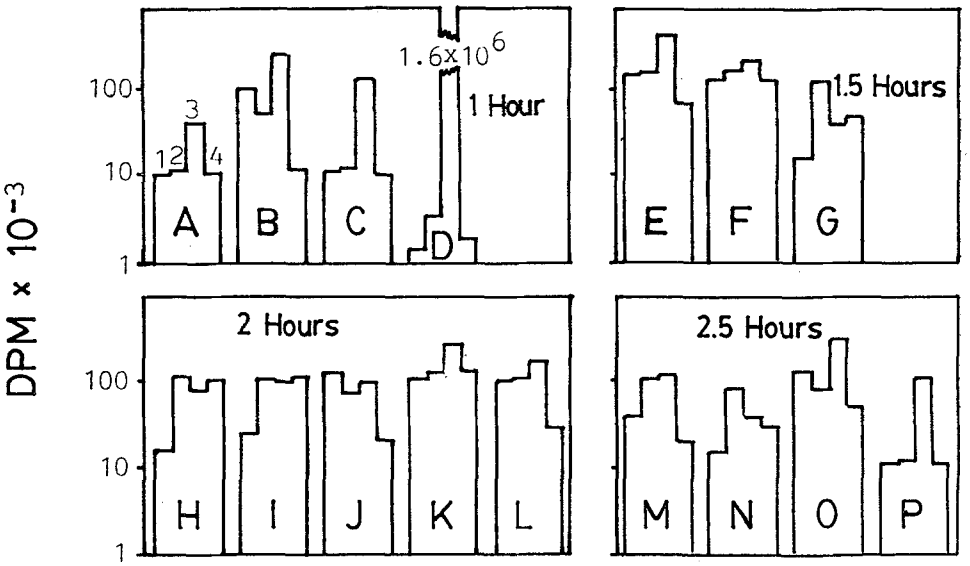


Fig. 2. — Distribution of recovered label activity, as disintegrations per minute (DPM), from Group I wasps. Each histogram corresponds to a single adult female wasps as identified in table 1. The four bars of each histogram correspond to the four body regions numbered in the text and in this figure on histogram A. The times that the adult wasps were held in isolation are shown for each of four subgroups.

Fig. 2. — Répartition de la radio-activité récupérée, en désintégration par minute (DPM), pour les guêpes du groupe I. Chaque histogramme correspond à une seule femelle adulte comme il est montré dans le tableau I. Les quatre barres de chaque histogramme correspondent aux quatre régions du corps décrites dans le texte et dans cette figure sur l'histogramme A. Les durées pendant lesquelles les guêpes adultes sont isolées sont montrées pour chacun des quatre sous-groupes.

following larval provisioning. Activity was found in all body sections of all wasps. Distribution of the label among the four sampled body regions includes several notable features. Eleven of 16 wasps (A-F, K-M, O, and P) show highest activity in the anterior gaster region, which contains the crop. Three wasps (B, J, and O) visibly regurgitated during freezing, and these wasps show substantial activity in the head region. Two of the time period sub-groups (1 hr and 2.5 hr) show significantly non-random patterning of activity among the four body regions (FRIEDMAN two-way analysis of variance, χ^2_r = 7.1 and 8.8 ; both $p < .0001$ (SIEGEL, 1956). The pattern of label distribution is random at 1.5 hr (χ^2_r = 3.3 ; $.4 < p < .5$) and at 2 hr (χ^2_r = 1.1 ; $.8 < p < .9$). Recovered DPM from Group II wasps *(fig. 3)*, which were isolated for 1 hr following cell visits (mean time between first and second groomings = 5.7 min. ; range = 1.5 to 11.5 min), was distributed nonrandomly among the four body regions (χ^2_r = 151.7 ; $p < .0001$) ; six of 8 wasps have highest recovered activity in one of the gaster regions.

Group I and Group II wasps differ significantly in % DPM recovered from the adults (*table I* ; Mann-Whitney U = 10.5, $p < .002$ [SIEGEL, 1956]), with lower recovery from Group II wasps, which had been permitted to regurgitate crop contents to larvæ.

Table I summarizes the % DPM recovered data from Groups I and II. No significant difference exists between groups in % DPM recovered from

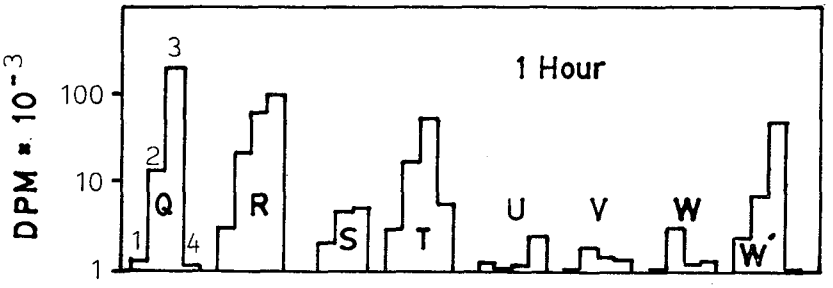


Fig. 3. — Distribution of recovered label activity, as disintegrations per minute (DPM), from Group II wasps. Each histogram corresponds to a single adult female wasp as identified in table 1. The four bars of each histogram correspond to the four body regions numbered in the text and in this figure on histogram Q. All Group II wasps were held in isolation for one hour.

Fig. 3. — Distribution de la radio-activité récupérée, en désintégrations par minute (DPM), pour les guêpes du groupe II. Chaque histogramme correspond à une seule femelle adulte, comme il est montré dans le tableau I. Les quatre barres de chaque histogramme correspondent aux quatre régions du corps décrites dans le texte et dans cette figure sur l'histogramme Q. Toutes les guêpes du groupe II ont été maintenues en isolement pendant une heure.

Table I. — Recovery of radioactive label activity from adults and larvae of *Polistes metricus* on experimental nests.. Data are presented as % of label injected into the provision morsel and measured as disintegrations per minute (DPM). The provision morsel was either a small, whole lepidopteran larva (*w*) or fragment of a larger lepidopteran larva (*f*). The experimental adults are identified by letters (A, B, ..., W') that correspond to the letters shown in Figures 1 and 2. When more than one wasp was present on a nest no attempt was made to discriminate queens from workers. Group I wasps were assayed on the dates shown in 1978; Group II dates are for 1979.

Tableau I. — Niveau de radio-activité retrouvé chez les adultes et les larves de *Polistes metricus* sur des nids expérimentaux. Les données sont présentées en pourcentage du niveau injecté dans le morceau de nourriture et mesurées en désintégrations par minute (DPM). Le morceau de nourriture était soit une petite larve de lépidoptère entière (W), soit un fragment de larve plus grande (f). Les adultes expérimentaux sont identifiés par des lettres (A, B, ... W') qui correspondent à celles qui figurent dans les figures 1 et 2. Quand plus d'une guêpe était présente sur un nid, nous n'avons pas recherché à discriminer les reines des ouvrières. Les guêpes du groupe I ont été expérimentées aux dates montrées en 1978; les dates du groupe II correspondent à 1979.

Nest	Date	Experimental Adultes	Total # Adults on Nest	Provision Morsel	% DPM Recovered		
					Adults	Larvae	Nest Total *
Group I							
1	21 Jul	A,B	4	f,f	5.9, 33.4	5.5	25.2
2	25 Jul	E	3	w	45.3	14.5	59.8
3	26 Jul	H	2	w	17.9	4.5	22.5
4	26 Jul	I	6	w	23.4	21.8	45.3
5	28 Jul	C	2	f	14.0	20.8	34.8
6	28 Jul	J.L	3	w,w	19.8, 27.9	10.4	34.3
7	28 Jul	F,G	5	f,f	40.0, 14.1	8.0	35.1
8	1 Aug	D	4	w	77.4	9.5	86.9
9	1 Aug	K	3	f	49.8	15.9	65.8
10	4 Aug	M,N	3	?,?+	16.5, 10.4	41.3	54.7
11	4 Aug	O	4	?	40.5	37.8	78.3
12	4 Aug	P	5	?	8.0	45.3	53.4
Group II							
13	27 Jun	Q	1	f	23.4	7.8	31.2
14	27 Jun	R	1	f	12.4	13.5	25.9
15	27 Jun	S	1	w	0.9	19.9	20.7
16	3 Jul	T	1	?	6.0	54.2	60.2
17	10 Jul	U	5	f	0.2	37.9	38.1
18	11 Jul	V	5	f	0.3	28.1	28.4
19	11 Jul	W,W'	5	f	0.4, 3.9	33.7	36.0

* Total DPM recovery is less than 100 % due to experimental procedure. Background counts were high, especially for large larvae, and excretion by isolated adults was uncontrolled for. Also, equal initial counts in all provision morsels were assumed but not demonstrated.

\+ ? Signifies unrecorded data.

larvæ (Mann-Whitney U = 22 ; n.s.) ; no significant difference in % DPM recovered is attributable to the provision morsel being either a whole larva or a fragment (Mann-Whitney U = 20 ; n.s.). No significant between-group difference exists in total % DPM recovered from adults and larvæ combined (Mann-Whitney U = 18 ; n.s.). Among the Group II wasps, which were isolated following visits to larvæ in which regurgitation might have occured, six adults (S-W') retained very little label activity, but two (Q, R) retained substantial amounts of label activity. The wet weight distributions of all larvæ did not differ between Groups I and II (χ^2 = 4.57 ; n.s.).

Though the Group II wasps were permitted an opportunity to regurgitate crop contents to larvæ, larvæ receiving regurgitate could not be distinguished from larvæ receiving provision morsel. In Group II, therefore, the morsel was taken from the adult female before provisioning ; she was then observed until she visited one or more larvæ and then groomed herself ; timed isolation was then begun. In 3 of 12 nests no radioactivity was recovered from any larvæ ; in 4 nests, 1 larva showed label activity ; in 5 nests, 2 larvæ showed label activity.

The random distribution among body regions of label activity in Group I adult wasps at 1.5 hr and 2 hr suggests assimilation, but the data are not conclusive. Therefore, midgut and wing muscle tissues were excised from Group III wasps at varied times following isolation. The pattern of label activity is shown for the assayed tissues of Group III wasps in *figure 4.*

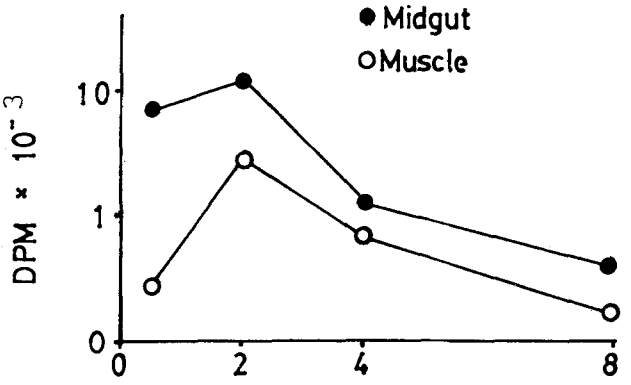


Fig. 4. — Recovery of label activity, as disintegrations per minute (DPM), from isolated midguts and thorasic muscle of Group III wasps, which were run in 1982. Isolation times are shown on the abscissa. Each point on the figure is an average for three experimental wasps.

Fig. 4. — Récupération de radio-activité, en désintégrations par minute (DPM), d'intestins moyens isolés et de muscle thoracique de guêpes du groupe III, qui ont été étudiées en 1982. Les durées d'isolement sont montrées en abscisses. Chaque point sur la figure est une moyenne de trois guêpes expérimentales.

A similar pattern is seen in both tissues : low activity shortly after isolation ; peaked activity at 2 hrs of isolation ; and physiological decay of label activity at 4 hr and 8 hr.

DISCUSSION

A pattern is apparent in the data for the adult wasps. A female extracts liquid and/or semisolids from the provision morsel during malaxation. The extracted material is held in the crop, which is located in the anterior portion of the gaster. The crop contents can be regurgitated, and regurgitation for the purpose of feeding larvæ normally follows shortly after the provisioning of larvæ with solids. This pattern was observed in *Polistes fadwigæ* by YOSHIKAWA (1962). JEANNE (1972) used colored dyes to document the same pattern in *Mischocyttarus drewseni*. The present data thus confirm these earlier reports. These data show, in addition, that the majority of the crop contents may be regurgitated, or a substantial portion may be retained. Furthermore, a portion of the crop contents is rapidly assimilated and distributed to other body regions of the adult wasps ; label activity in midgut and wing muscle peaks at 2 hr then diminishes in a physiological decay curve.

At the present time it is not possible to determine the quantity of adult nourishment that might be garnered under natural conditions by the pathway documented here. Neither is it possible at present to determine the relative importance to provioning adults of this mode of nourishment versus larva-adult trophallaxis. Larva-adult trophallaxis, however, is viewed as having evolved as a derivative behavior of malaxation of larval provisions (HUNT, BAKER and BAKER, 1982), and so adult nourishment via malaxation of larval provisions is presumed to have appeared first in the evolutionary history of eusocial Vespidæ.

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