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PHORETIC ASSOCIATION BETWEEN THE DAUERJUVENILES OF *RHABDITIS STAMMERI* (RHABDITIDAE) AND LIFE HISTORY STAGES OF THE BURYING BEETLE *NICROPHORUS VESPILLOIDES* (COLEOPTERA: SILPHIDAE)

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Rhabditis stammeri is a carrion-dwelling nematode specifically associated with the burying beetle *Nicrophorus vespilloides*. The dauerjuveniles of the nematode utilize the beetle for transport to the carrion. Both imagines and larvae of the beetles are infested. This can be understood in the context of the complex brood care behaviour of *Nicrophorus*. In the beetle larvae, the dauerjuveniles use the gut for transportation to the pupal chamber. After pupation the dauerjuveniles are found in the pupal chamber at protected places such as the exuviae of the larvae or underneath the hindwing-anlagen of the pupae. Upon eclosion the dauerjuveniles migrate to the genitalia and gut of the young imagines. *Rhabditis stammeri* is also transmitted by imagines via copulation.

Keywords: phoresy, carrion, *Nicrophorus*, dauerjuveniles, Nematoda, *Rhabditis*

Rhabditis stammeri Völk, 1950 is a nematode that lives exclusively on carrion. Its dauerjuveniles are commonly found on *Nicrophorus* and rarely on other beetles in the same habitat (Völk, 1950). Völk, who described *R. stammeri*, overlooked the fact that there were two different sibling species involved. *R. vespillonis* (von Linstow, 1878) (Sudhaus & Richter in prep.) on *N. vespillo* and *R. stammeri* Völk, 1950 on *N. vespilloides, N. investigator* and *N. humator*. The present study elucidates the life history of *R. stammeri* with particular attention to the association between the nematode and the larvae of *Nicrophorus*.

Rhabditis stammeri is well adapted for living on carrion, but as soon as a piece of carrion is used up it is unable to actively locate the next dead animal. Many nematodes of biochores have this problem and most utilize insects as carriers to the next biochore. Sachs (1950) described such relationships for nematodes of cow pats, Körner (1954) for nematodes that live in decaying wood, and Völk (1950) for nematodes of carrion (for a summary see Sudhaus, 1976). Usually there is no specific relationship between the insect and nematode. Terrestrial nematodes have a life stage that is especially preadapted for phoresy. It is the third juvenile stage that is protected against environmental stress by the usually unshed cuticle of the second juvenile stage. Only the third juvenile stage is found on the carriers. All other stages remain on the carrion.

In adult *Nicrophorus* beetles *Rhabditis stammeri* is only found in the genitalia and the hind-gut. On the carrion the dauerjuveniles display a typical creeping and waving behaviour ("Kriechwinken"; Sachs, 1950). Both the preference for certain organs as well as this waving behaviour indicate that the nematodes have special adaptations for utilizing burying beetles (*Nicrophorus*) as carriers.

The burying beetles of the genus *Nicrophorus* are well known for their elaborate brood care (e.g. Pukowski, 1933; Milne & Milne, 1976). Males and females bury small carrion and actively feed the larvae. After a few days the male and later the female and its offspring leave the carrion (Schwarz & Müller, 1992). The larvae pupate some distance from the carrion in the pupal chamber. Here the young adults hatch after a few weeks. Before the adult beetles or their larvae leave the carrion the nematode has to associate with its carrier.

The purpose of this study was to elucidate if, how, and to what extent dauerjuveniles use the adults and larvae of *Nicrophorus* as carriers after these particular stages have left the carrion. In addition, the behaviour of the dauerjuveniles was studied in the pupal chamber and it was assessed whether dauerjuveniles are transmitted during copulation of adult beetles.

MATERIALS AND METHODS

Pairs or single females of *N. vespilloides* without nematodes were kept at 21° C in plastic boxes (9.5×9.5×6.5 cm) half filled with moist peat. Small pieces of cattle lung (20-35g) were used as carrion. Twelve hours after adding the carrion to the boxes three quarters of them were buried and provisioned with eggs. At the same time 300 μl of a suspension of dauerjuveniles of *R. stammeri* from a laboratory culture were added; a suspension was used in order to achieve a comparable nematode infestation of the different boxes. The dauerjuveniles from the suspension developed into adults on the carrion and the behaviour of their offspring was studied.

The quantitative statements of this study are based on a comparison of the different numbers of dauerjuveniles that were found at the four different points in time: first on the larvae after leaving the carrion, second immediately after pupating, third 6-7 days after pupating and fourth after leaving the pupal chamber. Since it is impossible to follow the count of dauerjuveniles of the same individual beetle larva, groups of five siblings were compared. A total of 20 larvae each from 10 females were studied. This means that 200 beetle specimens were dissected.

The beetle larvae left the carrion after 6-7 days. Five larvae from each box were collected and put into a box filled with dry peat. This was intended to desiccate all dauerjuveniles that were still attached to the integument of the larvae and which had not yet achieved protection. Afterwards the larvae were killed and the number of dauerjuveniles they carried was counted. The remaining 15 beetle larvae from each box were transferred into new boxes filled with moist peat. The offspring of one female were kept together. The larvae pupated in these boxes. In each box five pupae and exuviae were dissected immediately after pupating and a further five pupae and exuviae in each box 6-7 days later. The remaining five insects completed their development. After leaving the pupal chamber the beetles were also dissected and the dauerjuveniles were counted.

Additionally, the infestation of the beetle larvae after leaving the carrion was compared to the one of the imagines. For technical reasons only six boxes were evaluated. Only some of them were identical to the ones used in the other part of the study. The larvae and imagines were treated as described above.

In order to study the transfer of dauerjuveniles during copulation, ten imagines of one sex that were infested with dauerjuveniles were added to ten individuals of the opposite sex that were free of dauerjuveniles in ten trials. This experiment was carried out in large Petri dishes (9 cm diam) containing a small water-filled Petri dish (3.5 cm diam) to provide the necessary moisture. After 18-20 h the beetles were killed, the genitalia dissected, and the dauerjuveniles counted.

RESULTS

The adult beetles that left the carrion were infested with dauerjuveniles of *R. stammeri*. The nematodes were found in the ectodermal part of the gut (hind-gut) and the genitalia. Males and females carried a similar number of dauer-juveniles (χ^2-test, $p > 0.05$). Four of the six females but only two of the six males carried more dauerjuveniles in their gut than in their genitalia (Table I).

Only the hind-guts of the beetle larvae were infested with dauerjuveniles. The nematodes were found at an enlargement located immediately behind the

TABLE I

Numbers of Rhabditis stammeri *dauerjuveniles on adults of* Nicrophorus vespilloides *beetles after leaving the carrion*

Box	No. dauerjuveniles in adult beetles						No. dauerjuveniles in gut of larvae
	Females			Males			
	Genitalia	Gut	Total	Genitalia	Gut	Total	
A	657	1825	2482	402	651	1053	135*
B	701	1078	1779	2130	1331	3462	40
C	517	257	774	302	815	1117	71
D	93	271	364	150	74	224	6
E	157	25	182	130	59	189	25
F	569	712	1281	420	95	515	30
Total:	2694	4168	6862	3534	3026	6560	

* Mean number of 5 larvae per box (see text)

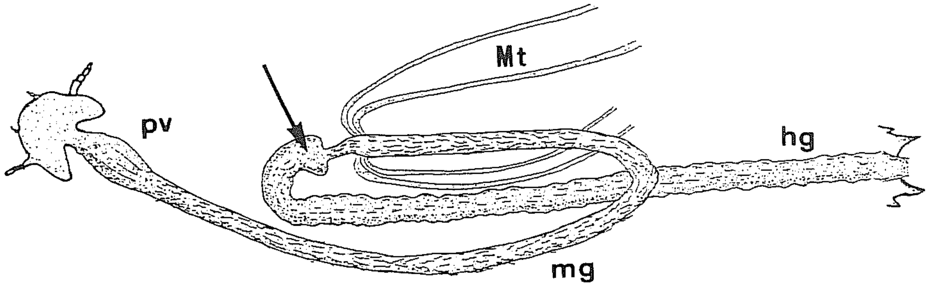

Fig. 1. Alimentary canal of *Nicrophorus vespilloides* larva: pv: proventriculus; mg: midgut; hg: hindgut; Mt: Malpighian tubules. The position of the Malpighian tubules indicates the border between hind- and midgut. The arrow points to the area of the largest concentration of dauerjuveniles.

transition point between middle and hind-gut (Fig. 1). No dauerjuveniles were found on the integument or in the intersegmental folds. After leaving the carrion, adult beetles always carried a higher number of dauerjuveniles than the larvae that were investigated. The number of dauerjuveniles on the carrion, and therefore on the insects, differed widely among the boxes although initially a similar number were added to each (Table II).

Immediately after the beetles had pupated the dauerjuveniles were found only in the exuviae. They were located in the middle of the exuvia in the cuticle of the enlargement of the hind-gut that is moulted. Rarely, a few dauerjuveniles were found outside the exuviae. The pupae were always free of dauerjuveniles. There were as many dauerjuveniles in the exuviae as in the gut of the last larval instar (Wilcoxon test, $T=17$, $p>0.05$; Table II).

Six to seven days after pupating fewer dauerjuveniles were found in the exuviae than immediately after pupating. However, now 21 in 50 pupae were infested (Table III) and carried a significant number of nematodes underneath the hindwing-anlagen. In all, a total of 29% of all dauerjuveniles were found on all pupae. The number of dauerjuveniles on pupae and in exuviae together was not significantly smaller than the number found immediately after pupating (Wilcoxon test, $T=19$, $p>0.05$; Table II).

After leaving the pupal chamber dauerjuveniles of *R. stammeri* were found in the genitalia and hind-gut of the beetles. But the number of nematodes was now considerably smaller than the number after pupating or 6-7 days later. Compared to the number of dauerjuveniles in the gut of the beetle larvae leaving the carrion, a significantly smaller number of nematodes were successful in climbing onto the freshly eclosed beetles (about 45%, Wilcoxon test, $T=1$, $p<0.01$). However, the variance among the different boxes was considerable (7-75%; Table II).

During copulation dauerjuveniles were transmitted in both directions, from males to females and *vice versa*. Only in one case were nematodes not passed on.

TABLE II

Comparison of the number of R. stammeri *dauerjuveniles at four points in time in the life cycle of* N. vespilloides *beetles*

Box	Time 1* (n=5) Sibling Number						Time 2 (n=5) Sibling Number						Time 3 (n=5) Sibling Number						Time 4 (n=4-5) Sibling Number					
	1	2	3	4	5	total	6	7	8	9	10	total	11	12	13	14	15	total	16	17	18	19	20	total
1	194	62	92	163	162	673	222	139	121	0	142	624	143	79	3	134	34	393	93	72	109	110	121	505
2	30	37	63	34	38	202	41	34	35	82	38	230	38	45	23	38	8	152	25	31	2	5		63
3	71	71	29	101	82	354	125	71	132	86	94	508	139	291	26	13	153	622	76	132	29	54	115	406
4	88	124	112	221	128	673	118	56	130	103	133	540	100	77	87	61	49	374	45	30	5	195	9	284
5	87	84	36	58	55	320	98	65	51	86	58	358	86	68	23	80	121	378	66	22	1	68	59	216
6	201	253	285	201	212	1152	180	97	166	258	162	863	45	65	122	164	126	522	79	112	97	53	71	412
7	17	47	30	30	22	146	51	60	45	50	29	235	17	28	14	37	19	115	3	12	10	10	5	40
8	160	252	130	118	144	804	170	87	46	62	90	455	45	282	136	105	133	701	14	127	93	104	119	457
9	272	82	106	75	190	725	19	122	27	157	166	491	64	105	15	235	126	545	3	9	6	11		29
10	75	56	83	19	138	371	53	85	81	115	33	367	134	44	24	66	84	352	0	17	3	2		22
Total						5420						4671						4154						2434
Box 1-10			n=50						n=50						n=50						n=47			
Median			86						86						67						31			
Quartiles (25-75%)			55-160						51-130						34-126						59-93			
Range			17-285						0-258						3-291						0-195			

* Time 1: after leaving the carrion in the hind-gut of the beetle larvae; Time 2: in the exuviae of the siblings after pupation; Time 3: in the exuviae and the pupae 6-7 days after pupation; Time 4: on the young adults after leaving the pupal chamber.

TABLE III

Numbers of R. stammeri *dauerjuveniles on the exuviae and pupae of* N. vespilloides *6-7 days after pupation*

Box	Exuviae Sibling Number 11	12	13	14	15	Total	Pupae Sibling Number 11	12	13	14	15	Total
1	143	79	2	134	1	359	0	0	1	0	33	34
2	38	45	23	38	5	149	0	0	0	0	3	3
3	139	172	0	13	81	405	0	119	26	0	72	217
4	99	37	87	52	0	275	1	40	0	9	49	99
5	86	68	0	80	121	355	0	0	23	0	0	23
6	21	6	122	135	126	410	24	59	0	29	0	112
7	17	28	14	37	19	115	0	0	0	0	0	0
8	45	3	59	99	82	288	0	279	77	6	51	413
9	64	80	4	25	119	292	0	25	11	210	7	253
10	134	3	24	66	84	311	0	41	0	0	0	41
					Total:	2959					Total:	1195

TABLE IV

Transmission of R. stammeri *dauerjuveniles by copulation of* N. vespilloides *beetles*

Number of dauerjuveniles: Infested males to females* Males	Females	% transmission	Infested females to males+ Females	Males	% transmission
62	35	36	24	1	4
34	45	57	44	5	10
42	17	29	56	4	7
7	18	72	36	11	23
38	35	48	27	11	29
9	29	76	42	0	0
76	17	18	25	17	41
27	27	50	13	6	32
0	18	100	25	9	27
35	36	51	38	11	22
330	277	x=54	330	75	x=20
		s=24			s=13

* Number remaining in infested male carriers, number transmitted to unifested females
+ Number remaining in infested female carriers, number transmitted to uninfested males

The number of dauerjuveniles transmitted from males to females was significantly larger than the number moving from females to males (χ^2-test, $p<0.01$; Table IV).

DISCUSSION

The dauerjuveniles have two ways of leaving the breeding substrate. They can either climb onto the adults or they can infest the immature beetles.

It appears that the nematodes actively search for the hind-gut and genitalia of adult beetles as well as the hind-gut of the larvae. For example, the dauerjuveniles form mass aggregations on the genital segment. The same phenomenon was observed when a few drops of anal liquid from the adult beetles is added to a mass culture of the nematodes; They immediately form large clusters on and around the drops. In addition they start to wave (Richter, 1991). Creeping wavers such as *R. stammeri* appear to combine active search for the carrier with unspecific place waving ("Platzwinken"; Sachs, 1950). During the waving the dauerjuveniles accidentally come into contact with adult and immature beetles, climb onto their carriers, and move towards favoured body parts. The smaller number of dauerjuveniles on beetle larvae can potentially be explained by the lesser attraction of their anal juice. However, the differences may also be explained by the greater mobility of adult beetles on the carrion, which increases their chances of coming into contact with a larger number of dauerjuveniles.

With regard to the behaviour of the dauerjuveniles that leave the carrion with the imagines, it is noted that they are found in protected places such as the genitalia and the hind-gut (Richter, 1991). If the beetles breed again in the same year, the dauerjuveniles can colonize another carrion. Otherwise, it is possible that they hibernate in the imagines (pers. observation). However, it is unknown whether beetles that produced offspring in one season and then hibernated are capable of breeding again in the next year. Infesting such old beetles may be an evolutionary dead-end for the nematodes.

Alternatively, dauerjuveniles that left the carrion with the imagines can potentially be transmitted from one carrier to another during copulation. It is unclear whether transmission during copulation is achieved through active movement of the nematodes. The fact that there is not only transmission from males to females but also from females to males, against the direction of sperm transfer, suggests that this is achieved through active movement. Even if it were passive, it would be advantageous for the nematodes. The transfer allows the infestation of beetles that previously carried few or no dauerjuveniles. Also, it potentially allows the nematodes to leave old beetles or males that fail to win fights over carrion but are still in a position to copulate with a successful female (Dressel & Müller, 1988). However, it has not been demonstrated beyond doubt that the transfer during copulation is adaptive.

Poinar (1971) describes the transmission of *Rhabditis adenobia* during copulation of their hosts, rhinoceros beetles (*Oryctes monoceros*). Transmission by copulation is also known in *Diplogaster coprophilus* which occurs on flies of the family Sepsidae (Kiontke, 1989). Here, the situation is slightly more complicated. Only the females of these flies inject the nematodes during oviposition into fresh cow pats, which are the preferred habitat for *D. coprophilus*. Transmission during copulation of the flies is the only way for associated nematodes that picked males as carriers to arrive at the new substrate.

An alternative strategy for leaving the carrion is in the gut of the larvae. Moving into the gut of the larval beetles is of considerable advantage for *R. stammeri*. The dauerjuveniles are protected against desiccation and the dauerjuveniles cannot slip off when the beetle larvae burrow in the soil. No other part of the body would be similarly well suited. The accumulation of the dauerjuveniles in the sac that is located between mid- and hind-gut is most easily explained by an active penetration of the gut through the anus. The narrow passage from the hind-gut to the mid-gut prevents the dauerjuveniles from infesting that part of the gut. However, it cannot be ruled out that they also or exclusively reach the hind-gut through passive ingestion through the mouth of the beetle larvae. But then it remains unclear how they avoid being defecated.

For nematodes associated with *N. investigator*, the infestation of the beetle larvae is of special importance. In this species, only the larvae overwinter. The adult beetles do not survive the winter. For *R. stammeri* this means that its only way of getting through the winter is by being associated with the larvae.

Even after pupating, it remains advantageous for the dauerjuveniles to stay within the exuvia. It protects the nematodes against desiccation and enemies. The predacious deutonymphs of the mite *Poecilochirus carabi* actively move around and take up food in the pupal chamber (Schwarz, pers. comm.). These mites are also associated with *Nicrophorus* (Müller & Schwarz, 1990; Schwarz & Müller, 1992). There would be a definite risk of being preyed upon if the dauerjuveniles stayed there. It is important to note that the lysis of the internal organs of the pupating larvae pose no threat to the nematodes because they are protected by the cuticle of the hind-gut. In other words, there is no need for them to leave the beetle larvae before they pupate. The only other similarly protected place is underneath the hindwing-anlagen of the pupae. It appears that the nematodes actively search for this place when the decay of exuviae reaches a certain point. Some dauerjuveniles stay within the exuviae until the beetle ecloses.

After eclosion, it is essential for the dauerjuveniles to infest the beetles, since they offer the only means of transportation to the next piece of carrion. The initial conditions for getting onto the beetles differ depending on where the dauerjuveniles are located. The dauerjuveniles that stayed within the exuviae of the larvae now have to leave it. The ones that were protected underneath the hindwing-anlagen of the pupae have to climb directly onto the beetle during eclosion or after eclosion from the exuvia of the pupa. During coloration the beetles stay within the pupal chamber for three days. Consequently there is ample time for the nematodes to climb onto the insect. The number of dauerjuveniles that succeed in infesting the beetles varied considerably from box to box, presumably due to varying microclimatic conditions within the pupal chambers. Other experiments showed that after the beetles left the pupal chamber, there were no nematodes found in either the exuviae of the larvae or the pupae. Dauerjuveniles that did not manage to climb onto the beetle were apparently left (dead?) in the pupal chamber.

Burying beetles use small carrion for breeding purposes only. They are also to be found on large carrion which they use exclusively for feeding purposes (Reed, 1958; Payne & King, 1969). Here, *R. stammeri* also develop and probably use other species of beetles as carriers in order to leave the substrate. Thus, utilizing adult carriers is probably the ancestral part of the association between *Nicrophorus* and *R. stammeri*. The association was closer on small carrion because it is always used by only one species of *Nicrophorus*. It was here that the nematodes also evolved the ability to utilize beetle larvae as carriers. From this point on two different generations of beetles have been used simultaneously.

Relationships between species of nematodes and other beetles, as well as other types of insect, have been frequently reported (for a summary see Poinar, 1975). There are examples for exclusively phoretic as well as obligately parasitic nematodes. There are also numerous examples of other species having a somewhat intermediate life cycle, i.e. they are facultatively parasitic (Sudhaus, 1976; Poinar, 1983). The invasion of the gut of adult and rarely immature beetles is more common in these species (e.g. Körner, 1954; Rühm, 1956) than in phoretic nematodes. It is, for example, known from a few *Parasitorhabditis* species that utilize wood-boring beetles, usually Scolytidae (Rühm, 1956). The non-waving dauerjuveniles of *Parasitorhabditis autographi* move into the guts of the beetle larvae (*Dryocoetes autographus*) and manage to get onto the adult beetles via a behaviour that has not been studied in detail (Rühm, 1956).

A similarly close association is known between a non-parasitic nematode, *Goffartia heteroceri*, with a beetle in the genus *Heterocerus* (Hirschmann, 1952). The dauerjuveniles infest beetle larvae that are about to pupate and climb onto the beetles as soon as they eclose. The active search for pupae of the insect carrier is also known from *Rhabditis dubia* (Kühne, 1988) and *Diplogaster coprophilus* (Kiontke, 1989). *R. dubia* is able to locate the puparia of cow pat psychodids; *D. coprophilus* actively searches for puparia of *Sepsis* and climbs onto the imagines as soon as they hatch. Again, the ability to search for puparia probably evolved some time after the association between nematode and adult fly.

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ZUSAMMENFASSUNG

Eine phoretische Beziehung zwischen den Dauerjuvenilen von Rhabditis stammeri (*Rhabditidae*) *und verschiedenen Stadien im Lebenszyklus des Totengräberkäfers* Nicrophorus vespilloides (*Coleoptera: Silphidae*)

Rhabditis stammeri ist ein aasbesiedelnder Nematode mit einer spezifischen phoretischen Bindung an den Totengräberkäfer *Nicrophorus vespilloides*. Diese Bindung ist im Zusammenhang mit dem komplexen Brutpflegeverhalten der Käfer zu sehen. Die Dauerlarven von *R. stammeri* nutzen nicht

nur die Imagines, sondern auch die Käferlarven, um zu einem neuen Aas zu gelangen. Bei den Imagines suchen sie die Genitalien und den Darm auf, bei den Käferlarven den Darm. Nach der Verpuppung der Käferlarven in der Puppenwiege befinden sich die Dauerlarven geschützt in der Exuvie der Käferlarve oder unter den Hinterflügelanlagen der Puppe. Nach dem Schlupf des Jungkäfers wandern die Dauerlarven in dessen Genitalien bzw. Darm. *R. stammeri*-Dauerlarven können auch während der Kopulation der Käferimagines von einen Träger auf einen anderen übertragen werden.

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