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Prey-mediated Dispersal Behavior of Carcinops pumilio
(Coleoptera: Histeridae)

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ABSTRACT Dispersal behavior of the histerid predator, Carcinops pumilio (Erichson), was examined from the standpoint of life-history parameters and nutritional background. No significant differences were found between dispersing and nondispersing populations with respect to sex ratios, mating condition, parity, ovarian development, or morphometric characters. Flight and phototactic behaviors of dispersing beetles were reversed following administration of a dipteran prey meal. Withholding prey from beetles that had previously fed on many prey induced a delayed flight response which began on day 4 after deprivation, peaked on days 5 and 6, and returned to initial levels by day 9.

KEY WORDS Carcinops pumilio, dispersal, predation

Carcinops pumilio (Erichson), is a histerid predator commonly found in commercial egg-production facilities (Legner & Olton 1970, Pfeiffer & Axtell 1980). Adult and immature beetles inhabit the surface layers of the manure and forage for dipteran and acarine prey, and thus are interesting from the standpoint of filth fly pest management (Peck & Anderson 1969, Axtell 1981). Now cosmopolitan, C. pumilio is believed to have originated in Africa (Hinton 1945), and may have lived in the nests of wild birds prior to man's domestication of fowl (Hicks 1959).

Despite the widespread distribution of this beetle in nature and the very high population densities found in poultry houses, little is known of its means of movement from one farm to another, a distance that frequently spans many kilometers. Under normal circumstances, Carcinops is repelled by strong light and rarely flies. During a study of the bionomics of fly predators in Massachusetts (Geden & Stoffolano 1987), we occasionally observed large numbers of adult beetles climbing the inside walls of poultry houses, flying about the overhead lights, and initiating flight from windows.

Such incidents of dispersal did not appear to be correlated with calendar date, but occurred at various times and to varying degrees from May to September. Times of peak dispersal coincided with long manure accumulation times (3-4 mo), when adult C. pumilio populations are most abundant and immature beetles are present in relatively low numbers (Geden 1984).

The objectives of the present study were to investigate dispersal in C. pumilio with respect to the following: physiological age (mating condition, parity, and ovarian state) of dispersers and nondispersers; sex ratios of dispersers compared with nondispersers; morphometric analysis of dispersers and nondispersers; and potential for reversal and induction of dispersal under experimental conditions.

Materials and Methods

Beetles were collected from a commercial egg-production facility with a long history of natural fly suppression in Hubbardston, Mass. For comparisons of “dispersing” and “nondispersing” C. pumilio, dispersers were defined as those beetles that were actively climbing the inside walls of poultry houses, and were collected by gently scraping individuals from the walls with a putty knife. Nondispersing beetles were collected beneath the manure surface with a moistened paintbrush.

Morphometric Analysis of Dispersers and Nondispersers. To test the possibility that dispersal was a delayed response to competition among larvae, which resulted in the production of smaller adults, morphometric measurements of dispersers and nondispersers collected in the field were made. Only females were measured, because there are slight size differences in certain characters between sexes (Geden & Stoffolano 1987). Measurements were made of 25 dispersing and nondispersing C. pumilio using an ocular micrometer under a dissecting microscope. The following characters were measured for each individual: head width across eyes (HW); maximum pronotal width (PWM); pronotal width across points at head (PWH); maximum pronotal length (PLM); right
elytral width at anterior end (EWA); maximum right elytral length (ELM); diagonal length of right elytron from inner left (anterior) to outer right (posterior) points (ELD); and the lengths of the fore, middle, and hind femora (FF, MF, HF) and tibiae (FT, MT, HT). Data were analyzed by one-way analysis of variance.

Sex Ratios and Reproductive Status of Dispersers and Nondispersers. Sex ratios of dispersers and nondispersers were determined by dissecting 200 beetles collected on each of three sample dates in 1980 and 1981. Additional female beetles were collected for determinations of mating condition, parity (oviposition position), and ovarian condition. One hundred live dispersing and nondispersing *C. pumilio* females were dissected in physiological saline for determination of parity as evidenced by the presence of follicular relics ("yellow bodies," corpora lutea) at the bases of the lateral oviducts. In addition, the spermathecae of 25 beetles from each group were examined under a compound microscope for the presence of sperm. Possible differences between dispersing and nondispersing beetles with respect to sex ratios, parity, and mating condition were analyzed by two by two \( \chi^2 \) tests of independence (Sokal & Rohlf 1981). Finally, the ovarian condition of 25 female dispersers and nondispersers was determined. *C. pumilio* has four ovarioles per ovary and develops and deposits eggs singly (Geden 1984). The condition of the two most-developed oocytes was therefore determined by dissecting specimens under a dissecting microscope and ascribing an index value ranging from 1 to 3 according to the following criteria: 1, undeveloped oocyte, no visible yolk deposition through early-developed oocyte, some yolk, length \( \leq 0.35 \text{ mm} \); 2, oocyte length 0.35–0.65 mm; 3, mature oocyte, length >0.65. Separate \( G \) tests of independence (Sokal & Rohlf 1981) were conducted on the frequency of dispersing and nondispersing beetles that fell into the described oocyte categories for the most and second most-developed oocytes.

Phototactic and Flight Initiation Responses of Dispersers and Nondispersers. Dispersing and nondispersing *C. pumilio* were first tested for phototactic response in a simple light/dark choice chamber, which consisted of a 30-cm length of clear plastic tubing (20 mm diameter) with clear plastic cups affixed to either end. Half the length of the tubing and one of the collecting cups were wrapped in black electrical tape; the other half and its cup were left clear. The light end of the chamber was oriented toward a south-facing window in a room with no artificial lighting. Tests were run within 4 h of beetle collections between 1300 and 1500 hours (EST). A replicate consisted of 50 beetles introduced into the middle of the chamber through a hole at its midpoint. For the following 5 min, beetles found in the light end of the chamber were counted and scored as photopositive.

Flight initiation was investigated by the use of take-off chambers. Each chamber consisted of a ca. 500-ml paper container with a clear plastic lid. A 30-ml plastic cup filled two-thirds full with sand, with a dental-wick bridge arching across the surface of the sand, was placed inside the chamber. The bridge was essential for monitoring flight initiation because beetles were reluctant to take off from the flat surface of the sand.

Beetles were introduced, in replicates of 20 beetles per chamber, onto the surface of the sand in the inner container. Chambers were then placed near a south-facing window in a room with no artificial lighting for a 1-h observation period. Because beetles were unable to climb the surface of the inner container, any that were found in the outer container after 1 h were scored as positive for flight initiation. Ten replicates of dispersers and nondispersers were tested in both the phototactic and flight assays. Differences between dispersers and nondispersers were analyzed by one-way analysis of variance (ANOVA).

Effects of Feeding Treatments on Dispersing *C. pumilio*. To test whether dispersal was appetitive and driven by hunger, dispersers were collected from the field, subjected to pretreatment phototactic and flight assays as described above, then held for 24 h on four different feeding treatments. These were: water only (saturated dental wick); water plus granulated sucrose; "prey-free" manure, which had been collected in the field, thoroughly dried in a microwave oven, and re-moistened to ca. 60\% water; and water plus house fly eggs and newly hatched larvae. After 24 h on these feeding treatments, beetles were assayed again for phototaxis and flight initiation. Phototaxis tests were run with 50 beetles per replicate and five replicates per treatment, and flight assays were conducted with 25 beetles per replicate and five replicates per treatment. Differences among treatments within flight and phototaxis assays were analyzed by one-way analysis of variance and Student–Newman–Keuls range test (Newman 1939).

Induction of Dispersal in Prey-deprived Beetles. The effect of prey deprivation on flight induction was also investigated. Beetles used in this study were obtained from a laboratory culture and were approximately 4 wk old at the start of the experiment. For the first 4 wk of life, beetles were maintained in CSMA house fly medium with high densities of larvae of the small dung fly, *Coprocoa hirtula* (Rondani) (Diptera: Sphaeroceridae), in a rearing room maintained at 30–31°C, 24 h light and 60–70\% RH. *C. hirtula* is a natural prey item in the diet of *C. pumilio* in the field and is more easily manipulated for beetle maintenance than is the house fly (Geden 1984). After 4 wk on this diet, beetles were transferred to containers with moistened dental wick only and assayed daily for flight initiation. Assays were conducted with 20 beetles per replicate, 15 replicates per day. Between assays, beetles were returned to the rearing room. An equal
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Table 1. Comparisons of sex ratios, parity, and ovarian condition of dispersing and nondispersing C. pumilio collected from poultry houses

<table>
<thead>
<tr>
<th>Ovarian condition, oocyte 1</th>
<th>Collection no.</th>
<th>Dispersers</th>
<th>Nondispersers</th>
</tr>
</thead>
<tbody>
<tr>
<td>No. in oocyte category 1</td>
<td></td>
<td>61</td>
<td>64</td>
</tr>
<tr>
<td>No. in oocyte category 2</td>
<td></td>
<td>39</td>
<td>36</td>
</tr>
<tr>
<td>No. in oocyte category 3</td>
<td></td>
<td>58</td>
<td>54</td>
</tr>
<tr>
<td>No. in oocyte category 4</td>
<td></td>
<td>42</td>
<td>46</td>
</tr>
<tr>
<td>No. in oocyte category 5</td>
<td></td>
<td>54</td>
<td>57</td>
</tr>
<tr>
<td>No. in oocyte category 6</td>
<td></td>
<td>46</td>
<td>43</td>
</tr>
<tr>
<td>% ?</td>
<td>1</td>
<td>94</td>
<td>98</td>
</tr>
<tr>
<td>% nulliparous</td>
<td>2</td>
<td>6</td>
<td>2</td>
</tr>
<tr>
<td>% parous</td>
<td>2</td>
<td>2</td>
<td>2</td>
</tr>
<tr>
<td>% nulliparous</td>
<td>9</td>
<td>7</td>
<td>9</td>
</tr>
<tr>
<td>% parous</td>
<td>16</td>
<td>16</td>
<td>14</td>
</tr>
<tr>
<td>% nulliparous</td>
<td></td>
<td>16</td>
<td>15</td>
</tr>
<tr>
<td>% parous</td>
<td></td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>% nulliparous</td>
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<td></td>
<td></td>
</tr>
<tr>
<td>G/q</td>
<td>0.202</td>
<td></td>
<td>P &gt; 0.05</td>
</tr>
</tbody>
</table>

Results

Morphometric Analysis of Dispersers and Nondispersers. No significant morphometric differences ($F < 3.0$ in all cases; $df = 1,48$; $P > 0.05$; ANOVA) were found between dispersing and nondispersing beetles for any of the characters that were examined (not presented in a table).

Sex Ratios and Reproductive Status of Dispersers and Nondispersers. No significant differences in sex ratios were found between dispersing and nondispersing beetles on any of the three collection dates, with a total, male-biased sex ratio of male/female 348:252 (Table 1). Similarly, no significant differences between dispersers and nondispersers were found with respect to parity or the condition of the two most-developed oocytes (Table 1). All beetles that were examined for mating status were found to have mated (not presented in a table).

Phototactic and Flight Initiation Responses of Field-collected Dispersers and Nondispersers. When field-collected dispersing and nondispersing C. pumilio were assayed for phototactic response, 47.0 dispersers (94.0%) oriented towards the light end of the chamber; in contrast, only 14.4 (28.8%) of the nondispersers were positively phototactic ($F = 789.81$; $df = 1,18$; $P < 0.001$; ANOVA). Differences were even more pronounced in flight initiation assays, where 18.1 dispersers initiated flight (90.4%) compared with 0.4 (2.2%) of the nondispersers ($F = 193.70$; $df = 1,18$; $P < 0.001$; ANOVA).

Observation of beetles in the flight chambers confirmed that those that were found in the outer containers at the end of the observation period had flown and not crawled from the inner container. Dispersing beetles displayed a characteristic behavior of crossing and recrossing the dental wick bridge before taking off. Beetles that flew struck the walls of the outer container and fell to the bottom. Nondispersing beetles, on the other hand, usually did not climb the arched wick, but burrowed into the sand at its base. Most nondispersers which did climb the wick did not display the crossing and recrossing behavior of the dispersers, except for the small percentage that flew.

During handling of these beetles collected in the field, another behavioral difference was noted. Nondispersers, when touched by the paint brush, frequently exhibited thanatosis (Hinton 1945), retracting the head and legs for as long as 1 min. Dispersers, on the other hand, did not show this behavior, but continued to move actively when contacted.

Effects of Feeding Treatments on Dispersers. Results of the tests for the effect of diet on the behavior of dispersers collected in the field are presented in Table 2. Pretreatment assays on the day of collection confirmed that beetles were in dispersal mode, with 90% showing a positive phototactic response and 92% initiating flight. Maintaining these beetles for 24 h on water and water plus sucrose had no significant effect on either dispersal-related behavior. Administration of "prey-
free" manure had a slight, but not statistically significant, effect on both behaviors. Beetles that were allowed to feed on prey showed a profound reversal in dispersal behavior, with only ca. 4% attracted to light and initiating flight.

Induction of Dispersal in Prey-deprived C. pumilio. The effect of prey deprivation on colony beetles previously fed on many prey is illustrated in Fig. 1. On the first day of starvation, virtually none of the beetles initiated flight. Flight initiation remained infrequent on the following 2 d, but on day 4, a sudden increase in flight propensity was observed, which increased further on day 5 to 67% and remained high on day 6. Flight initiation then dropped on day 7. On days 9 and 10, no flight was observed at all. No flight was observed at any time among prey-fed controls (not presented in figure).

Discussion

The majority of migrating species that have been studied migrate as postteneral adults before the development or deposition of the first egg batch (Dingle 1965, 1966, Johnson 1969, Messina 1982, Meyer 1982). In the present study, no evidence for this "oogenesis flight syndrome" was found in C. pumilio, most dispersing beetles having undergone at least one oviposition. In this species, the use of follicular relics as an indicator of age may, however, mask real age differences between the two groups. Mated, parous females may have lived as long as 8 or 380 d (Geden 1984). Further experimental work with individuals of known precise age is needed.

Administration of prey in the form of house fly eggs and larvae was found to reverse both parameters of dispersal measured in this study, phototaxis and flight initiation. Water-only and water-sucrose treatments had no significant effect on these behaviors, suggesting that if dispersal in this species is appetitive, it is not driven and maintained by water or carbohydrate deprivation.

The observation that flight could be induced by withholding the usual food source from Carcinops has several parallels with other species, although most examples of this phenomenon are from phytophagous species. Meyer (1982) has shown that the alfalfa weevil exhibits two flight periods, one of which is a postteneral, prereproductive, prediapause syndrome. A second, postdiapause period of flight may be induced by withholding fresh alfalfa from the beetles (Meyer 1982). Dingle & Arora (1973) found that female Dysdercus spp. histolyze the flight muscles and develop eggs when fed continuously after eclosion, but undergo flight if starved for several days following emergence. The bugs continue to fly and do not histolyze the flight muscles until they are presented with food. Solbreck & Pehrson (1979) found similar results with another seed bug, Neacoryphus bicructis (Say), and noted a critical balance among food density, egg production, diapause-inducing conditions, and migration.

Rankin (1978) investigated hormonal regulation of flight in Oncopeltus fasciatus (Say) and reviewed the literature available on other species. In Oncopeltus, starvation or feeding on suboptimal food items causes recently emerged females to delay reproduction and undergo long flights. Juvenile hormone (JH) was found to play a dual role in modulating reproductive and migratory efforts. Stengel (1974) found that JH plays a role in the direction, as well as the expression, of flight in the migratory cockchafer, Melolontha melolontha L. In the present study, Carcinops also showed a delayed response to starvation, with virtually no flight being noted until day 4 of deprivation. JH may play a role in the flight of this species as well, although perhaps in a different manner. Because ovarian condition appears to have no effect on flight, it is possible that high JH titers associated with feeding and subsequent ovarian development inhibit flight, this behavior being released in re-

<table>
<thead>
<tr>
<th>Pretreatment</th>
<th>% no. positively initiating flight</th>
<th>% no. initiating flight</th>
</tr>
</thead>
<tbody>
<tr>
<td>Water only</td>
<td>43.6a</td>
<td>19.3a</td>
</tr>
<tr>
<td>Water and sucrose</td>
<td>41.0a</td>
<td>19.3a</td>
</tr>
<tr>
<td>Prey-free manure</td>
<td>34.3ab</td>
<td>13.6ab</td>
</tr>
<tr>
<td>Water and prey</td>
<td>1.8b</td>
<td>1.2b</td>
</tr>
</tbody>
</table>

*Means followed by the same letter within a column are not significantly different (P > 0.05; Student-Newman-Keuls test).

Based on five replicates of 50 and 25 beetles per treatment in phototactic and flight initiation assays, respectively.

![Fig. 1. Flight initiation response of C. pumilio that were placed on water-only regimes after being maintained for 4 wk on a diet rich in dipteran prey.](image-url)
sponse to lower titers. Because males appear to disperse as readily as females, other hemolymph-borne factors associated with feeding may be involved as well.

The observed decline in flight after day 6 is more difficult to interpret. Beetles that have fed on many prey can survive on water alone for 30 d before significant mortality is observed (Geden 1984). On days 7–10, when flight declined, beetles clearly had not exhausted their nutrient reserves, but appeared to have responded to internal cues that shut off flight. A similar rise and fall in levels of flight behavior in response to starvation has been observed in the stilt bug, Jalysus spinosus (Say) (Elsey 1974), and represents one of the few investigations of this phenomenon in a generally flightless predator. Jalysus spinosus, when deprived of its usual prey (tobacco hornworm eggs), did not show significant flight activity until day 4 after deprivation. Flight continued to increase and peaked on day 7, followed by a gradual decline to the level of fed controls on day 12. In contrast to Carcinops, however, the decline in Jalysus flight appeared to be associated with decreasing fuel reserves, because mortality was much higher toward the end of the starvation period than at the beginning, and higher than the fed controls at the same time (Elsey 1974).

Before the domestication of fowl and the ensuing artificial accumulation of large and stable deposits of poultry manure, C. pumilio was presumably associated with the nests of wild birds, where it fed on dipterans and other prey. Given the temporary nature of these natural habitats, selection for prey-mediated dispersal behavior seems to have been strong. In modern, multihouse poultry-production facilities, this behavior may result in beetles leaving poultry houses where there are few prey and colonizing adjacent houses where flies are more abundant. Further work is needed to determine the distance that individual Carcinops can fly, and the factors that shut off flight and lead to foraging in new habitats.

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