



Effects of larval movement behavior and density on emergence success and adult body size in a commensal midge

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Abstract

Changes in larval density and movement behavior of a commensal midge, *Nanocladius (Plecoptera coluthus)* sp. #4, were monitored for 26 weeks in recirculating laboratory streams. Adults were captured at emergence, sexed, and weighed to assess the effect of larval density and movement behavior on emergence success and adult size. The density of midges on hosts declined with time and coincided with a springtime increase in larval movement frequency. Midges residing on hosts with high spring densities emerged significantly less than midges on hosts with low densities. Resident midge density on hosts did not influence the likelihood of successful colonization by commensals and colonizers showed no preference for initial attachment site on hosts. However, colonizing midges emerged significantly less than resident midges. Similarly, successful emergers changed tube positions significantly less often as larvae relative to non-emergers. There was no difference in adult body weight of resident midges and colonists/movers, but adult males which emerged from commensal-laden (high density) hosts were significantly smaller than males from low density hosts. These data indicate larval density and movement behavior may have strong fitness consequences for commensal midges.

Introduction

Commensalism is a form of interspecific interaction in which one species benefits while another species neither benefits nor is harmed. Among aquatic insects, the Chironomidae (non-biting midges) arguably contain the greatest number of commensal species (Tokeshi, 1993, 1995, for review). Association between midges and their host ranges from obligatory (i.e., midges require the host for life cycle completion) to facultative (i.e., hosts used but not required) and the intensity of association correlates with the degree of life cycle synchrony between commensal and host (Svensson, 1979; Jacobsen, 1995). While the occurrence, host-specificity, and emergence phenology of several commensal midge species have been documented (Steffan, 1967; Hilsenhoff, 1968; Svensson, 1980; Gotceitas & Mackay, 1980; Tokeshi, 1986; Bottorff & Knight, 1987; Tokeshi, 1995; Pennuto, 1998), we know little about intraspecific interactions of larvae on hosts. In

particular, the degree of territoriality exhibited should be influenced by tube-building space, both in terms of its availability and quality (e.g., Svensson, 1980), and this may be a function of commensal density.

Intraspecific competition for space has been documented in several groups of aquatic insects, especially among net-spinning caddisflies (Glass & Bovbjerg, 1969; Englund & Olsson, 1990; Matczak & Mackay, 1990) and blackflies (Zahar, 1951; Kim & Meritt, 1987). Within the Chironomidae, Wiley & Warren (1992) showed that larval *Cricotopus* occupying rock surfaces engaged in territory recycling more frequently than they constructed new tubes and thus restricted conspecifics from gaining access to resources. Likewise, Bottorff & Knight (1987) suggested that territoriality in midge commensals led to later instars occupying the best tube sites on their stonefly hosts. Although these works have documented intraspecific interaction effects on dispersion patterns, the fitness consequences resulting from these interac-

tions have not been investigated. For an obligate commensal midge, interactions resulting in dislodgment from the host may have important life history implications if the midge is unable to locate and reattach to another host. Similarly, if there is heterogeneity in resource availability on a host, commensals residing in resource-poor locations should do less well than conspecifics in resource-rich locations. Pennuto (1998) showed emergence success of commensal midges was reduced at high larval density and for commensals attached farthest from the thorax. In the present study, we investigate whether movement behavior or density of conspecifics has any influence on emergence success or adult body weight in a commensal chironomid midge. Obviously, midges failing to emerge will make no genetic contribution to future generations and adult size has been correlated with various fitness measures in a range of taxa (e.g., Svensson, 1979; Thornhill, 1980; Greenwood & Adams, 1987; Wallace & Anderson, 1996).

The midge, *Nanocladius (Plecopteracoluthus)* sp. #4 (Diptera: Chironomidae) appears to be an obligate commensal on the saw-combed fishfly, *Nigronia serricornis* (Megaloptera: Corydalidae). It occurs commonly on fishfly larvae in streams of southern Maine. As evidence of its obligate nature, we (1) have never sampled this species free-living, (2) have never found this species on other potential hosts, (3) have been unable to rear this species without hosts, and (4) have preliminary data from host-choice trials indicating a strong preference for *N. serricornis*.

Materials and methods

Field collections

Saw-combed fishfly hosts ($n = 25$ to 42) were collected monthly (July 1997–June 1998) from the Little River near Gorham, Maine (43°41' N, 70°29' W). A detailed description of the study site is presented in Pennuto (1997). In this river, fishflies are the largest invertebrate predator and are commonly found in riffle and snag microhabitats. They are merovoltine with a 3-yr life cycle. Fishflies were collected with kick nets (mesh = 0.5 mm), placed in buckets of river water, and returned to the lab. Each fishfly was placed between the bottom and lid of a glass petri dish, examined for midge commensals under 10x magnification on a Wild MZ-8 dissecting microscope, and host head capsule width measured with an ocular micrometer.

All fishflies were returned to the river within 5 h of capture.

The number and location (dorsal vs ventral, thorax vs abdomen, and segment number) of each midge commensal was recorded. The only midge species observed was *Nanocladius (Plecopteracoluthus)* sp. #4 (Dr Rick Jacobsen, pers. commun.). This midge is found only in lotic habitats and appears to be univoltine with a peak spring emergence. It builds an open-ended tube laterally across the body surface of its fishfly host. The midge grazes attached microbiota from near either entrance of the tube and may also graze detritus adhering to its tube (Pennuto, pers. observ.). Drs Rick Jacobsen and Ole Saether are currently preparing a description of this species. Midge prevalence on fishfly hosts (% of hosts harboring commensals), midge abundance (number of commensals per fishfly), and commensal intensity (number of midges per host fishfly) were determined for each month.

Movement observations

Forty-eight fishfly hosts harboring commensal midges were collected from the Little River during fall 1997 and maintained individually for 26 weeks in laboratory culture streams. Culture streams were small, circular tanks (12.5 cm dia.) similar to those used by Peckarsky & Cowan (1991). The 48 tanks each received water from a central 380-l, temperature-controlled reservoir. Water was recirculated to all tanks using a single centrifugal pump. Water entered each tank through a small tube creating a circular flow before exiting through a screened (1-mm mesh) overflow standpipe. All overflow water from each tank then flowed via gravity to the central reservoir before being pumped back into the tanks. Thus, midges potentially could colonize new tanks if the larvae exited with overflow water and were pumped into a new tank, but hosts were too large to exit via the overflow standpipe.

Water chemistry was maintained near ambient conditions by replacing approximately one half of the water volume per week with fresh river water. Temperature was controlled with a Frigid Units® water chiller adjusted weekly to ambient temperature. Total alkalinity (methyl orange titration), conductivity (Corning Checkmate 90), pH (Oakton pH-Tester 2), and dissolved oxygen (Winkler titration) were monitored weekly. Light conditions were maintained by ambient sunlight through a bank of windows and

supplemented with fluorescent fixtures on a timer to simulate natural conditions.

Fishflies were assessed weekly for changes in attachment location of commensals, loss of attached commensals, and occurrence of newly attached commensals (i.e., colonists). Each host was removed from its tank, placed in a small volume of stream water in a petri dish, and observed under 10× magnification using a dissecting microscope. We made two assumptions regarding movement behavior of commensals: (1) tubes occupied in consecutive weeks were occupied by the same midge and (2) midges moved the least distance necessary to reach a new position. Thus, if a host harbored the same number of commensals in consecutive weeks, but they were not in the same position, a resident must have moved to a new position. We assigned the midge that was previously located on the nearest segment to the newly occupied position as a mover. Thus, both intra- and interhost movement by commensals represents a conservative estimate of movement behavior. No commensal occurring singly on its host moved to a new position over the experiment duration, providing support for Assumption 1.

Based on these two assumptions, we defined four movement categories for midges: movers, non-movers, residents, and colonists. Movers/non-movers are labels for weekly changes in larvae distribution on the hosts whereas residents/colonists are labels for larval behavior over the experiment duration. If a host harbored the same density of commensals in consecutive weeks, but one or more occupied different locations, they were movers. Non-movers remained in the same position on consecutive weeks. Residents resided on the same host in the same location for the duration of the experiment whereas a colonist was a new arrival on a host at some point during the experiment. Thus, a midge occurring on a host with increased commensal density in consecutive weeks and occupying a position not occupied the previous week was a colonist. Ten hosts died and 10 escaped over the duration of the experiment and were replaced with newly captured fishflies harboring midge commensals. Thus, some discontinuity exists in the number of midges monitored each week.

Hosts with pupating midge larvae were isolated *in-situ* in a fly-culture tube (10 × 3.5 cm, 70-ml volume) covered with Nitex screening (63- μ m mesh) and monitored daily for commensal emergence. Adult midges were collected with an aspirator and pupal exuvia and larval skins were retrieved from the rearing vials.

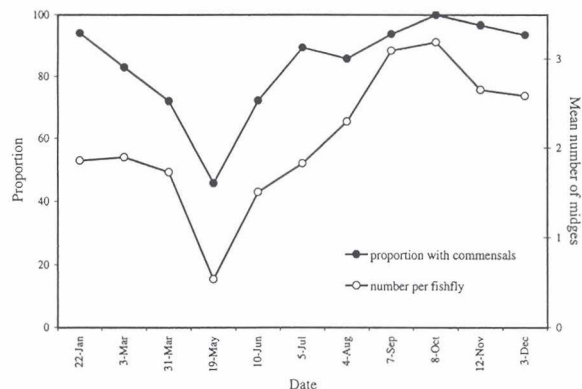


Figure 1. Seasonal changes in the proportion of hosts harboring midge commensals, commensal abundance, and commensal intensity for *Nanocladius* (*Plecopteracoluthus*) sp. #4 on its fishfly host, *Nigronia serricornis*, in the Little River, ME, 1997–1998.

Adults were sexed and weights were determined using a Cahn C-33 microbalance. Ash-free dry weights were recorded (1 h 500 °C in a Fisher 550-14 muffle furnace, APHA, 1995).

Statistical analyses

The effect of commensal movement behavior (i.e., mean number of moves per week standardized by number of weeks observed and mean number of weeks remaining in the same location) on emergence was investigated with a Student's *t*-test comparing successful and unsuccessful emergers. Colonist vs resident emergence success and springtime commensal density effects on emergence were investigated using a G-test (Sokal & Rohlf, 1981). Density and attachment site effects on new colonists were examined by chi-square. Colonists vs residents and high vs low commensal density effects on adult weight were examined using a Student's *t*-test. All analyses were performed using Statistix II (NH Analytical, Rockville, MN) with alpha levels set at 0.05.

Results

Field assessment

The proportion of fishflies harboring commensal midges remained >80% in all months except April–June when a decline occurred (Figure 1). Similarly, commensal abundance and infestation intensity remained >2 per host over much of the year, but with a marked decline in early spring (Figure 1).

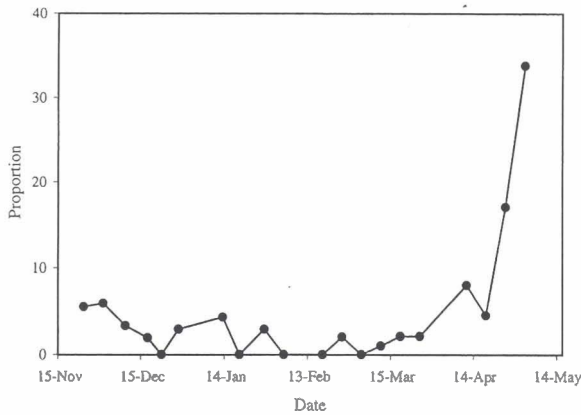


Figure 2. Weekly changes (Fall 1997 through Spring 1998) in the proportion of midge commensals moving over the body of their host in a laboratory stream.

Laboratory movement analyses

A total of 139 commensal midges were examined. Forty-two midges (30.2%) emerged successfully. However, 4 were either damaged during adult capture or escaped and were not usable for size analyses. Twenty midges (14.4%) reached the pupal stage but failed to eclose: 10 died while still attached to their host, 8 left their host successfully, but died as wrigglers in the rearing vials, and 2 were partially eaten by their host. Seventy-seven midges (55.4%) were lost from hosts and remain unaccounted. No midge larvae or pupal exuvia were located during a careful inspection of the rearing facilities. Unaccounted midges were considered non-emergers.

Midges exhibited a low, but constant rate of movement both on and between hosts throughout the observation period until 18 April. During this period, the number of movers per week ranged from 0 to 7 (Table 1) and a total of 48 movements to new locations on the same host were observed. There was a marked springtime increase in the number of midges moving to new locations (Figure 2) and this increase coincided with a decline in field densities.

The mean number of midges per host was >2 on all dates until 11 April when infestation intensity declined (Table 1). Similarly, the proportion of hosts harboring multiple midges remained high through the winter months and showed a steep decline in early April. On average, 3.9 ± 0.71 (SE) midges were lost from their host in a given week (range 0–13), though whether the loss was active or passive is unknown.

A total of 40 midges colonized new hosts (mean = 1.7 ± 0.36 ; range 0–6 per week) (Table 1). There

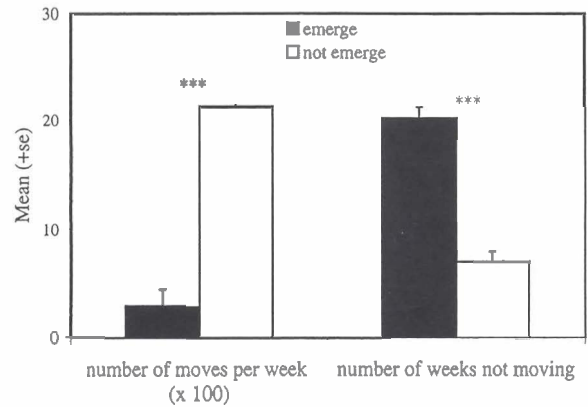


Figure 3. Proportion of midges emerging successfully as a function of movement behavior. *** = significant difference at $P < 0.001$.

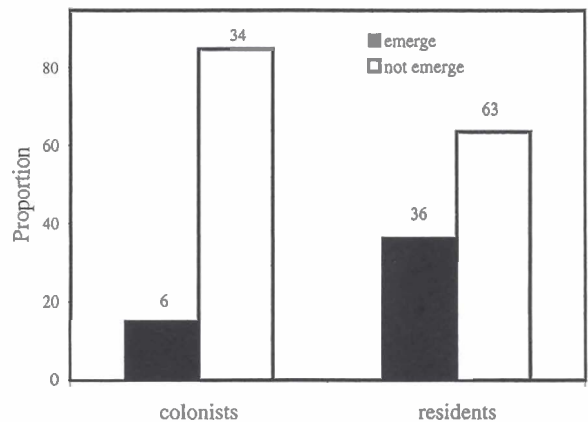


Figure 4. Proportion of colonizer and resident midges emerging successfully from laboratory streams. Numbers above bars = sample size.

was no significant difference in the tube location of colonists (i.e., the thorax vs abdomen) ($\chi^2 = 0.08$, $df = 1$, $P > 0.05$) and colonists showed no preference for hosts with low commensal density ($\chi^2 = 0.59$, $df = 2$, $P > 0.05$).

Potential fitness effects

Movement behavior of larvae had a significant effect on emergence success. Successful emigrants moved less frequently ($t = 3.45$, $df = 114$, $P < 0.001$) and remained in the same location longer before moving ($t = 9.89$, $df = 114$, $P < 0.001$) than non-emigrants (Figure 3). Resident midges emerged more frequently than colonists ($G_{adj} = 6.61$, $df = 1$, $P < 0.025$, Figure 4). In fact, 30 of 38 emigrants (~80%) were residents. Midges residing on hosts with low springtime commensal density emerged more frequently

Table 1. Summary data of commensal midge winter movements on their fishfly hosts in laboratory streams

Date	No. of hosts	No. of midges	Mean no. per host	No. midges moving	Mean no. segments moved	No. losses	No. gains
10/31	8	22	2.8 ± 1.8	0		4	1
11/2	10	27	2.7 ± 1.4	1	–	0	3
11/10	10	26	2.6 ± 1.6	3	3.0 ± 5.2	1	2
11/17	30	66	2.2 ± 1.2	3	2.0 ± 1.0	1	0
11/24	34	72	2.1 ± 1.2	4	1.0 ± 0.0	5	3
12/3	33	67	2.0 ± 1.3	4	3.3 ± 2.6	5	1
12/9	32	61	1.9 ± 1.2	2	6.0 ± 2.8	6	0
12/17	45	104	2.3 ± 1.2	2	4.3 ± 4.9	2	0
12/22	45	105	2.3 ± 1.0	0	–	2	3
12/28	45	105	2.3 ± 1.0	3	3.3 ± 2.1	1	0
1/13	44	93	2.1 ± 1.0	4	4.5 ± 1.7	13	1
1/19	48	107	2.2 ± 1.3	0	–	0	2
1/28	48	103	2.1 ± 1.2	3	1.0 ± 0.0	7	3
2/4	48	103	2.1 ± 1.2	1		0	5
2/18	48	101	2.1 ± 1.1	0	–	10	3
2/25	48	101	2.1 ± 1.0	2	1.0 ± 0.0	4	0
3/4	48	102	2.1 ± 1.0	0		1	0
3/11	48	99	2.1 ± 1.0	1	–	3	2
3/18	48	98	2.0 ± 1.0	2	5.0 ± 1.4	1	0
3/25	48	99	2.1 ± 1.1	2	2.0 ± 0.0	2	1
4/11	48	90	1.9 ± 1.0	7	1.9 ± 0.4	9	0
4/18	47	89	1.9 ± 1.1	4	3.8 ± 1.5	6	5
4/25	44	82	1.9 ± 1.0	14	2.4 ± 1.6	6	1
5/2	43	82	1.9 ± 1.0	27	1.9 ± 0.8	6	4

Means are ±S.D. No. midges moving = number of midges occurring in different locations in consecutive weeks. No. losses = number of hosts harboring fewer midges in consecutive weeks. No. gains = number of hosts harboring more midges in consecutive weeks.

than midges on hosts with high commensal density ($G_{adj} = 12.6$, $df = 3$, $P < 0.01$, Figure 5). There was no significant difference in adult weights of residents and colonists/movers ($t = 0.35$, $df = 36$, $P > 0.05$). However, males emerging from hosts with springtime densities >2 were about half as large as males emerging from hosts with densities ≤ 2 ($t = 2.78$, $df = 14$, $P = 0.015$). There was no difference in female weights at different densities ($t = 0.61$, $df = 20$, $P > 0.05$, Figure 6).

Discussion

A complex interaction exists between midge density on hosts, movement behavior, and emergence success in the studied commensal chironomids. Midges on hosts with high commensal densities (1) did not emerge as frequently, (2) moved around and were

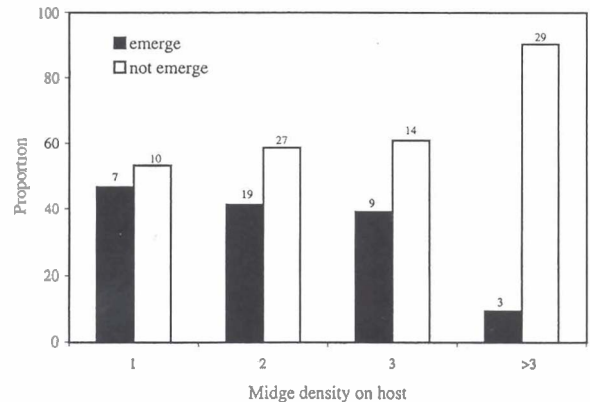


Figure 5. Proportion of midges emerging successfully based on springtime commensal density on hosts. Number above bars = sample size.

lost more, (3) resided in less desirable locations, and (4) emerged at smaller sizes (for males only) rel-

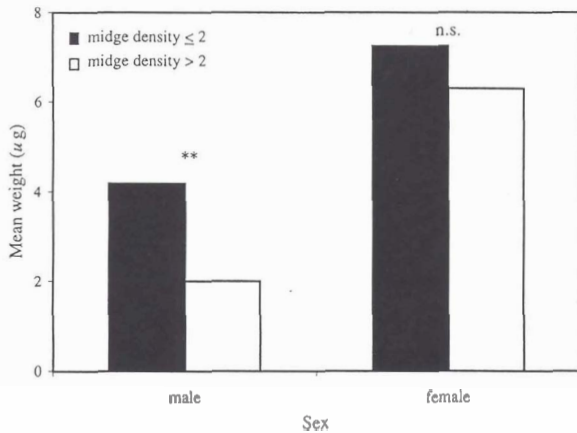


Figure 6. Ash-free dry weight (AFDW) of adult midges from hosts with low (≤ 2) and high (> 2) commensal density. ** = significant differences at $P = 0.015$. n.s. = not significant.

ative to midges on hosts with low densities. The specific mechanisms controlling these effects are unclear, but likely include seasonal changes in territorial behaviors among midge larvae on their host, resource availability, and host density.

Field data show this midge has a strong emergence peak in early May and corroborate the movement and density data from laboratory observations. In the lab, midges began to move over the host body with increasing frequency as they neared pupation and the timing was in synchrony with declining field densities on hosts. All larvae moved towards the thorax as they neared emergence. Potentially, the thorax provides a needed sclerotized surface for pupal chamber attachment (e.g., Bottorff & Knight, 1987). However, most larvae did not reach the pupal stage. The larvae moving most frequently and residing farthest away from the thorax were less likely to emerge than those remaining stationary or residing on or near the thorax. Larvae residing farther away from the thorax had to travel further to pupate, increasing their likelihood of encountering a conspecific. In our lab aggressive interactions were observed between larvae during spring and this could explain the loss of commensals as they neared pupation.

Winter movement patterns of this midge indicate greater activity than has been previously suggested for other commensals (e.g., Bottorff & Knight 1987). On average, most midges (>95%) remained in their tubes from week-to-week, but movements increased 10-fold as spring approached. Movement over the host body surface increases the possibility of dislodgment from the host, a potentially costly occurrence indicated

by the observation that larvae cannot emerge without a host (Pennuto, unpublished data). Commensals were capable of locating and attaching to new hosts throughout the winter period and forty percent of these colonizations occurred on hosts that previously lost a midge, suggesting that midges may be re-attaching to their original host. The rate of re-attachment in this laboratory stream system is probably somewhat elevated due to the enclosed nature of the laboratory stream and rates of successful re-attachment in the field might be lower. Regardless of ability to locate and re-attach to hosts, remaining attached was clearly a better strategy in terms of emergence success. Resident midges emerged more than twice as frequently as colonizers (36 vs 15%). Thus, a large proportion of colonizers had no mating opportunities.

Springtime density of conspecifics on a host played a significant role in determining the likelihood of emergence. Intraspecific interactions among insect larvae can result in lower body weights, reduced feeding opportunities, reduced emergence success, and lower fecundity in adults (e.g., Kajak, 1963; Rasmussen, 1985; Iwakuma, 1986; Peckarsky & Cowan, 1991; Wiley & Warren, 1992). In particular, Wiley & Warren (1992) demonstrated that tube-building behavior in *Cricotopus* midge larvae restricted access of conspecifics to food resources. This type of interference competition may also play a role in this commensalism during springtime movement to the thorax for pupation if resident midges prevent movers from crossing their tubes. Alternatively, commensals residing on a host with low midge density may have access to food resources of higher quality and/or quantity than commensals on a host with high midge density and thus develop and emerge more successfully.

Males emerging from hosts with high commensal densities (> 2) were significantly smaller than males emerging from hosts with low commensal densities. Most reports on insect mating systems suggest that adult body size in males is a prime determinant of reproductive success (e.g., Parker, 1970; Svensson, 1979; Thornhill, 1980; Borgia, 1982; Butler, 1984; Greenwood & Adams, 1987; Flecker et al., 1988; Peckarsky & Cowan, 1991; Wallace & Anderson, 1996). In contrast, recent works by McLachlan and colleagues (e.g., McLachlan & Cant, 1985; McLachlan & Allen, 1987; Neems et al., 1990) provide evidence that small male midges may have higher reproductive success than large males due to enhanced aerodynamic maneuverability. Similarly, males capable of emerging under high-density conditions might

represent superior competitors as larvae and this may translate into more successful adults. Whether the small size of males from high-density hosts translates into reduced mating opportunities or otherwise reduces fitness or whether small males experience greater reproductive success remains untested. There have been no published accounts of the reproductive behavior of this midge or any other species in the subgenus, preventing direct comparisons of male size and fitness. For example, we do not know if this species forms mating swarms, mates aerially, or whether there is any size difference in males gaining copulations.

Several hypotheses seem worthy of investigation if strong intraspecific interaction among larvae plays an important role in determining emergence success or adult weight (in males), and potentially fitness, in this midge commensal. Strong intraspecific interaction should lead to an increase in niche breadth (e.g., Begon et al., 1990) as conspecifics are forced to more marginal habitats. In the system studied here, interactions might force commensals further from the thorax, force abandonment of the host, or use of alternative hosts. A systematic survey of commensal populations at different host densities might provide some insight into this possibility. Similarly, removal experiments or manipulations of commensal density on hosts would allow the density-movement behavior interaction to be uncoupled and provide insights into the real risks involved with or the proximate factors leading to a decision to move. Obviously, commensals that fail to emerge will have no mating opportunities and their fitness is zero. We still need a basic understanding of mating behavior in commensal species to link larval and adult stages. Obligate commensal (or parasitic) species provide unique systems to determine how larval intraspecific interactions and adult reproductive success are linked as hosts are easily manipulated and can be viewed as discrete resource units. Future investigations merging larval and adult stages will improve our understanding of fitness consequences of intraspecific behaviors.

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