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SPACING BEHAVIOUR BY LARVAL *ISCHNURA CERVULA* SELYS: EFFECTS OF HUNGER, PREVIOUS INTERACTIONS, AND FAMILIARITY WITH AN AREA (ZYGOPTERA: COENAGRIONIDAE)

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Larval *I. cervula* are aggressive towards conspecifics and exclude them from areas of food concentration. The effects of hunger, previous interactions, and familiarity with an area on dominance of larvae were determined. Dominance was defined as the ability of one animal to supplant another. At low levels of hunger (starved for 3 or 6 days) dominance of hungry animals was not significantly different from that of well-fed animals. At higher hunger levels (starved for 9 or 12 days) hungry animals were less dominant. Animals previously matched with a large animal tended to be less dominant than animals previously matched with a smaller animal. Dominance of animals moved from familiar areas to unfamiliar areas was not significantly different from dominance of animals allowed to remain in familiar areas. Thus, differences in hunger and outcome of previous interactions will help maintain the exclusion while familiarity with an area will have no effect.

INTRODUCTION

Larvae of some species of dragonflies are aggressive (ROSS, 1971; MACHADO, 1977; ROWE, 1980; BAKER, 1981) and can exclude conspecifics from areas of food concentration (BAKER, 1980). This spacing behaviour may affect variation in larval growth rates and act to regulate the number of larvae that emerge as adults (MACAN, 1977). Spacing may also affect the impact of larval predation on prey population (ROSS, 1971; THOMPSON, 1978; BAKER, 1980).

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Most of the work on larval spacing behaviour has been done in the laboratory and there is an obvious need for studies on spacing behaviour under field conditions. However, before useful field tests can be formulated, more information is needed on factors affecting spacing behaviour. My previous experiments on use of feeding areas (BAKER, 1980) were run only for 10 days, and in those experiments some animals that had remained at feeding areas for several days were displaced by other animals. If displacement of animals at feeding sites is frequent, and if differences in diet must be maintained for long periods to cause differences in growth rate, then short term exclusion of animals may have little or no effect on variation in growth rates. The basic problem is whether exclusion is maintained over long enough periods to affect larval growth.

Because spacing behaviour of odonate larvae is apparently based on aggressive interactions with dominant animals controlling feeding areas (BAKER, 1981), one approach to the determination of persistence of spacing behaviour is to elucidate factors affecting dominance. WILSON (1975) notes that few attempts have been made to determine what factors affect dominance status of individuals. This paucity of information is curious since social dominance is often considered an important factor in population dynamics (BROWN, 1975). An understanding of factors affecting the degree and persistence of dominance may be crucial to understanding the effects of dominance on population dynamics.

Experiments in this paper were designed to test if larvae of *Ischnura cervula* exclude conspecifics from areas of food concentration and to test the effects of hunger, previous interactions, and familiarity with an area, on dominance of larval *I. cervula*. I operationally define dominance as the supplanting of one animal by another; therefore, an animal is considered dominant over another if it forces the other animal to retreat.

GENERAL METHODS

Larval *Ischnura cervula* were collected with a dip net from the aquatic vegetation of a pond at Pitt Meadows, B.C. The pond is described by CANNINGS & DOERKSEN (1979).

In the laboratory, larvae were kept individually in 160 ml styrofoam cups, half filled with dechlorinated water. Animals were kept at approximately 18°C and at a natural photoperiod; they were fed one or two *Tubifex* worms every other day.

EXPERIMENTS

EXPERIMENT 1: EFFECTS OF FOOD AND NUMBER OF LARVAE ON USE OF SPACE

Methods I tested if larval *I. cervula* exclude conspecifics from areas of food concentration by first testing if solitary larvae remain near areas of food concentration; I then compared the amount of time solitary larvae spent at a feeding area to the amount of time several larvae spent at a feeding area. I used white plastic pails (20 cm in diameter by 14 cm high) each containing a lattice of 2.0 mm dowels. Lattices consisted of a square frame of dowels (10 cm by 10 cm) supported at the four corners by vertical dowels 7.5 cm high. Corners were formed by pushing the ends of the dowels into a small cork. The base of one upright dowel rested in a plastic vial (2.0 cm by 2.5 cm in diameter). The vial was used to hold food (*Tubifex*); the dowel leading into the vial will be referred to as the feeding area. Pails were filled with dechlorinated water.

There were three experimental conditions: (1) one larva/pail, no food; (2) one larva/pail, food; (3) four larvae/pail, food. In the pails with food there were more worms offered in the vial per day than the larvae could possibly eat in a single day. Each condition was replicated in eight pails. Larvae in pails with four individuals were uniquely marked by clipping tips of the caudal lamellae two days before the experiment. Animals were starved one day before the experiment. Animals had head widths of 2.2 - 2.6 mm. In each tank with four individuals the animals were selected to be the same size; greatest difference in head widths of animals in a pail was 0.20 mm.

At 1000 hrs of the first day of the experiment, larvae were added to pails by lifting them out of the cups in a large bore pipette and releasing them at the water surface in the centre of the pail. Position of each larva was recorded five times a day for ten days at two hour intervals starting at 0900 hrs. Only three observations were made on the first day, starting at 1200 hrs. Positions of larvae were recorded as which section of dowel they were on. Positions of animals not on dowels were recorded according to which quarter of the pail they were in. Quarters were defined by positions of the four upright dowels.

Table I
Frequency of observations of individual larvae on feeding areas. (Each larva was observed 48 times; larvae are ranked according to frequency)

Pail No.	Rank			
	1	*2*	*3*	*4*
1	41	1	0	0
2	39	16	0	0
3	38	10	3	0
4	45	13	13	2
5	41	6	2	0
6	30	13	5	0
7	48	6	1	0
8	23	14	1	0

Results — Solitary animals in pails with no food were on the feeding areas in 13.8% of the observations. Solitary animals in pails with food were on the feeding areas in 72.1% of the observations. A Mann-Whitney test indicated a significant difference ($P<0.01$) between the two groups. Larvae of *I. cervula* remain near areas of food concentration.

For the two groups with food present, the number of times an individual was seen on the feeding area, relative to the number of larvae present, was significantly higher ($P<0.01$) in the single larva group (72.1%) than in the four larvae group (26.7%). In pails with four individuals, some individuals were almost always seen on the feeding area while others were never observed on the feeding area (Tab. I). Some individuals excluded others from the feeding areas.

EXPERIMENT 2: EFFECTS OF HUNGER ON DOMINANCE

Methods — I tested effects of hunger on dominance of larval *I. cervula* by starving animals for different periods and comparing their ability to supplant a well-fed larva. I used four different periods of starvation. Larvae (housed individually in cups) were starved 3, 6, 9, or 12 days before being tested. Animals were fed ad lib the day before the starvation period began. Each starved animal was paired with an animal that had been fed ad lib while the other animal starved. Animals ranged in head width from 1.72 mm to 3.40 mm but animals in each pair were selected to be the same size; no pair differed in head width by more than 0.12 mm.

Paired animals were observed in arenas. Arenas were plastic petri dishes 8.8 cm in diameter and 1.9 cm deep. A perch made of 2.0 mm dowel 2.5 cm long was attached horizontally to the bottom with silicone; also, the bottom of the dish was roughened with sand paper to provide a grip for the larvae. Dishes were filled with dechlorinated water. A trial consisted of lifting a hungry animal and a well-fed animal from their cups and placing them in the arena. I randomized the order in which animals were introduced into arenas. After placing animals in the arena I recorded all interactions for 3 h. Interactions were defined as for *Coenagrion resolutum* (BAKER, 1981); larvae were considered to interact if one larva exhibited Swim, Crawl Sideways, Run Away, or Turn Away when it was within 2 cm of another animal. The animal that moved away lost the interaction while the one that did not move, or moved toward the other animal, won the interaction. Winners were defined as (1) the individual to win the first interaction and (2) the individual to win the most interactions during the observation period.

Because arenas were small, and because larvae moved slowly, I could observe up to 24 pairs at a time. Dishes were arranged on a table with strips of paper around them to prevent animals from seeing into adjacent dishes.

Results — Animals fed ad lib and animals starved for 3 or 6 days were not significantly different in their dominance ($P>0.05$, sign test, for both first interactions and total interactions) (Tab. II). However, animals starved for 9 or 12 days were less dominant than animals fed ad lib ($P<0.01$ for first interactions and $P<0.05$ for total interactions).

Table II

Frequency of wins and losses among starved animals matched with well-fed animals. ("First" column indicates frequency of wins and losses based on first interaction only; "Total" column indicates frequency based on all interactions during the 3 h period)

Starvation period (days)	First		Total		
	wins	losses	wins	losses	ties
3	20	24	19	24	1
6	20	19	17	19	3
9	12	27	13	25	1
12	10	26	9	23	4

EXPERIMENT 3: EFFECTS OF PREVIOUS INTERACTIONS ON DOMINANCE

Methods — I tested effects of previous interactions on dominance by pairing animals that had previously been dominated by a larger conspecific with animals that had previously dominated a smaller conspecific. Animals were divided into 3 size classes; large, head width 2.56 — 3.60 mm; medium, head width 1.92 — 2.52 mm; and small, head width 1.36 — 1.76 mm. The experimental treatment involved pairing small larvae with medium sized larvae and medium sized larvae with large larvae. Difference in head width of each pair ranged from 0.32 — 1.20 mm. I used the same neutral arenas used in Experiment 2. Animals in these pairs were allowed to interact for 2 days; larvae were starved during this period. To test if the larger animal in each pair dominated the smaller animal, I observed 18 pairs for 6 h (3 h each day) and determined which animal won the majority of interactions in each pair. I purposely observed those pairs with the smallest differences in head widths (0.32 — 0.80 mm). In all 18 pairs (7 medium versus small, 11 medium versus large) I observed during the treatment period, the larger animal in each pair was the total winner. Therefore, differences in size of larvae were enough to ensure smaller animals were dominated by larger animals.

After the treatment period I paired medium sized animals from the group originally paired with large animals with medium sized animals from the group treated with small animals. In each pair of medium sized animals the difference in head width was 0.12 mm or less. A trial was similar to that in Experiment 2. Larvae were lifted from their treatment arenas and placed in identical but unused arenas.

Results — When all interactions were used to determine an overall winner for each pair of medium sized animals, there was an insignificant trend towards the animal previously treated with a smaller animal winning more interactions than animals previously treated with larger animals (Tab. III). Animals previously paired with smaller animals were dominant over animals previously paired with larger animals when winners were determined from the first interaction ($P<0.05$, sign test).

Table III
Frequency of wins and losses among animals previously allowed to dominate smaller animals matched with animals previously dominated by larger animals. ("First" row indicates frequency of wins and losses based on first interaction only; "Total" row indicates frequency based on all interactions during the 3 h period)

	Wins	Losses	Ties
First	39	22	—
Total	35	23	3

EXPERIMENT 4: EFFECTS OF FAMILIARITY WITH AN AREA ON DOMINANCE

Methods — I tested effects of familiarity of an area on dominance by introducing naive "intruder" larvae into arenas previously occupied by experienced "original" larvae. I used two different experimental arrangements. In the first arrangement I used equal numbers of two types of arenas. I purposely made the two arenas different so that intruders would recognize that they were moved to new surroundings. One type of arena was identical to those described above except dishes were placed on bright yellow paper rather than white. The other type of arena was made of a similar dish but the perch was made of 3.00 mm dowel. Also, the wider dowels were wrapped with black thread. Arenas with wider perches were placed on green paper. Enchytraeid worms were added to the arenas with the green paper and *Tubifex* worms were added to the arenas on yellow paper. Thus the two arenas differed in type of food, background colour, and diameter, texture, and colour of the perch.

A single larva was added to each arena and kept there for five days. On the sixth day I removed half of the larvae from the green arenas and half of the larvae from the yellow arenas and placed them in the remaining arenas of the opposite colour. Larvae were paired according to size, and no pair differed by more than 0.12 mm in head width. Animals moved to a new type of arena were labelled "intruders"; animals not moved were labelled "originals". Trials were run as in Experiments 2 and 3.

The second type of experimental arrangement in this section was similar to the first except intruder larvae were kept for five days in styrofoam cups and fed enchytraeid worms. No perch was provided but larvae could cling to the walls of the cup. Originals were kept for 5 days in clear 40 ml plastic vials supplied with a 5 cm perch, 2.0 mm in diameter. The perch was placed diagonally in the vial so it rested on the floor of the vial against the vial wall and extended to near the top of the vial on the opposite side. The floor of the vial was covered with window screening to provide traction. Original animals were fed *Tubifex*.

Results — Intruders were winners as frequently as originals based on the total of the interactions (18 versus 19 and 1 pair tied) and on the first interaction only (18 versus 20) in the first experiment. Even in the second experiment with even more diverse arenas, intruders and originals won similar numbers of interactions (11 versus 11 for total data, 2 pairs tied; and 13 versus 11 for first interaction only). Familiarity with an area does not affect dominance of larvae.

DISCUSSION

Behavioural interactions between larvae of *Ischnura cervula* were similar to those of *Coenagrion resolutum* (BAKER, 1981). Also, similar to *C. resolutum* (BAKER, 1980), some larvae of *I. cervula* exclude conspecifics from areas of food concentration.

Experiment 2 suggests that increased hunger does not increase an animal's chance of supplanting another individual; rather, very hungry animals are less dominant than well fed animals. ROSS (1971) found that large hungry larvae of *Anax junius* were more likely to stalk and strike at smaller conspecifics than were large well-fed larvae. Also, HOPPENHEIT (1964a, *in* CURIO, 1975) reported that hungry larvae of *Aeshna cyanea* attacked large objects that well-fed larvae retreated from. While starved larvae of *I. cervula* were not dominant to well-fed larvae, starved larvae approached and struck at *Tubifex* sooner than well-fed larvae. Also, starved larvae attacked large worms that well-fed larvae avoided. Thus, hunger does increase feeding aggression in larval *I. cervula* but does not increase dominance over well-fed larvae of a similar size. In relation to this finding, MACHADO (1977) reported that "overfeeding" larvae of *Roppaneura beckeri* did not affect the "rate of displacement when two larvae were put together." Also, ROWE (1980) found that larvae of *Xanthocnemis zealandica* were aggressive to conspecifics but ignored or avoided Trichoptera or Ephemeroptera that were of a similar size to *X. zealandica*. These results suggest aggressive interactions between larvae are not simply attempts at predation.

The observed relationship between dominance and previous experience is similar to the findings of ALEXANDER (1961) for field crickets and EWING & EWING (1973) for cockroaches. Both Alexander and Ewing & Ewing could lower the dominance status of an animal by treating it with a more aggressive animal. When treated animals were rematched with animals they had previously dominated they usually became subordinate. However, Alexander found effects of previous domination were short lived and, when rematched, previously dominant animals could reassert their dominance in a matter of minutes. This result is similar to mine in that the influence of previous experience was shown only in the first interactions. Previous domination should tend to maintain the persistence of exclusion but may be of little importance since the effect is weak.

Experiment 4 suggest that familiarity with a feeding area does not increase an animal's chance of winning interactions. Animals removed from familiar areas and placed in a novel area occupied by an experienced animal were as likely to win interactions as were experienced animals. Therefore, familiarity with an area will have no effect on the persistence of the exclusion. That an individual's dominance is not site specific supports my previous suggestion that aggression shown by animals does not represent territorial defense (BAKER, 1981).

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