Chapter 11

Behavioral Aspects of Female Guarding and Inter-male Conflict in the Colorado Potato Beetle

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Sexual selection theory predicts that male insects will adopt various reproductive strategies in order to maximize their genetic contribution to future generations. According to this concept of parental investment, the sex contributing the least will more often be polygamous (Trivers 1972). Polygamy among male insects is common, although male mating strategies may be further complicated by body size (McCauley and Wade 1978, Alcock 1979, Borgia 1980, Brown 1980) and by territorial behavior which ensures access to possible mates (Alcock 1979, Wellington and Fitzpatrick 1981). Female sperm utilization strategies are similarly diverse (Walker 1980) and may influence male fitness through sperm storage, sperm competition and sperm precedence (Schlager 1960, Ladd 1966, Bartlett et al. 1968, McCauley and Reilly 1984).

Inter-male combat, as involved in obtaining a mate or a territory, or in guarding a female, varies greatly, and is well represented in several insect orders: Odonata (Alcock 1982), Diptera (Parker 1978, Borgia 1980), Lepidoptera (Davies 1978, Austad et al. 1979) and, Hymenoptera (Alcock 1979, 1982). Among Coleoptera, intensive combat between males has been reported in Chauliognathus pennsylvanicus (McCauley and Wade 1978), and in Popillia japonica (Lloyd 1979), and in the coccinellid, Leptothea galbula (Richards 1980). In the Colorado potato beetle (CPB), Leptinotarsa decemlineata Say, males show aggressive behavior toward other males and even toward females (Thibout 1982).

In 1980, I noticed the occurrence of inter-male fighting and post-copulatory female guarding in male Colorado potato beetles.

In the following discussion, the phenomenon is decribed in detail for the first time.

MATERIALS AND METHODS

Observations and experiments were conducted on both laboratory-reared and natural populations of the CPB. The laboratory population was reared on greenhouse-grown potato (mostly var. Desire) at 24-28° C, under illumination of approx. 3,000 lux and a 20L:4D photoperiod. A natural population in the vicinity of the Institute of Plant Protection was used for field experiments. The locality is situated in northwest Hungary, near Budapest, at an elevation of 310 m above sea level.

Potato plants were treated with a Bordeaux-mixture ($CaSO_4$: $Cu(OH)_2$:$3Ca(OH)_2$ complex), which partially protected the foliage from CPB damage (Jermy 1958, Szentesi 1981) and from fungal pathogens. Laboratory observations and experiments were performed at 23-24° C, 18L:6D, and 60-70% RH, on 6+ days old, sexually mature males and females (Thibout 1982).

Mating behavior - CPB males and females were confined to 2 liter glass jars with potato shoots. At 3 to 5 days, male and female beetles were placed together in the jars and the duration and intervals of mating behavior were recorded. Similar data from field observations were collected.

Female guarding and inter-male combat - Naturally occurring and laboratory derived instances of post-copulatory female guarding and inter-male conflicts were observed and recorded. The length, outcome and characteristic behavioral events of fights, and the approximate body size of combatting males were recorded.

Male displacement of another male in the process of guarding a female was observed in the laboratory and in the field. Either equal numbers or surplus males were placed into 4 liter jars or in large walk-in cages positioned over potato plants. Two to 3 females and ample potato foliage for feeding, egg-laying and spatial distribution were placed into the jars. Males and females were marked and their body weights recorded. Displacement of one male on a female by another male and fighting among males were recorded.

Dispersion and distribution of adults - The number and distribution of beetles were recorded for a 54 m x 7 m potato field. Both sexes were marked with numbered tags (Opalith-

Zeichenplättchen, Rimb-Mitlechtern, FRG) so that the dispersion of individual beetles or pairs could be recorded over time. The body weight of adults was measured (± 1 mg). Altogether, 84 males and 70 females were marked. Marked beetles were observed within 2 to 7 days after the most recent marking and up to 18 days after the first marking. Distribution of males, females and pairs relative to their positions on plants and/or the ground, and the type of activity in which they were engaged, were recorded.

RESULTS

Mating behavior - Six to 7 day old males and receptive females readily formed copulating pairs. Visual stimuli appeared to be important in conspecific recognition. Such "distant" orientation, however, does not seem to be sex specific. Males often oriented to and mounted other males, but soon abandoned them. It is likely that a contact sex pheromone produced by the female is involved in sex recognition (Levinson et al. 1979, Jermy, pers. comm.). A male touched a female's elytra with his antennae and subsequently drummed the elytral surface with his maxillary palps, seemingly providing immediate sex recognition. After the male identified the beetle as a female, he mounted her dorsally and oriented so that both sexes were facing anterior. He then grasped the female with all his legs and soon attempted intromission with his aedeagus. This is a pre-copulatory phase, as it does not necessarily end in copula. Mating, as measured from intromission until withdrawal of the aedeagus, lasted an average of 7 min (s.d. = ± 3 min) (n = 50) at 23-24°. The male was usually quiet during mating, except the antennae trembled during the early phase. Most females were either motionless or fed on foliage; however, some walked while in copula. Females that were not receptive to mating pulled the posterior part of their abdomen under the elytra, impeding intromission. After mating was completed, the male usually remained in a resting position on the female's back.

Female guarding and inter-male combat - In potato fields, pairs of CPB were frequently found on the foliage. However, thorough observations revealed that the male was usually only holding and riding the female, and mating was rarely observed in the field. If someone approached such a pair, or another CPB male was transferred to the pair, the resident (R) male either turned its back towards the approaching object, or suddenly moved toward it. It was possible to get the male to elicit this response several times from different directions. This "turning-shielding" reaction must have been elicited by visual cues, as

the response occurred from 0.5-1 m if a person was the "activator", while this response only occurred from 2-5 cm if another beetle approached. If the intruding (I) male attempted to mount the female, the R-male quickly moved opposite the direction of the intruder and attempted to dislodge the I-male. In a high proportion of observations (16 of 42), the contest was over within 5-7 seconds, ending with sudden, aggressive movements and/or tossing by the R-male. If the I-male resisted, the conflict escalated, and the R-male bent his head toward the back of the female in a jerking motion, and then quickly lifted it. The mandibles opened and closed rhythmically, and if any appendages of the I-male were seized, the R-male continued to push and pull the intruder until the I-male somehow managed to escape. The jerking motion of the R-male continued after the I-male was dislodged. If resistance or aggression by an I-male was strong, both engaged in serious fighting, during which the female was abandoned, and the tossing, jerking, pushing and pulling between R- and I-males continued on the foliage or on the ground if the combatants fell off the plant. The fighting was often so fierce that R-males moved the whole body of I-males, and mutilated the appendages of the I-male.

Table 1. Characteristics of inter-male conflict of the Colorado potato beetle observed in the field, Institute for Plant Protection, Budapest.

	1980	1983
No. of conflicts observed	93	40
Experimentally induced	84 %	60 %
Naturally occurring	16 %	40 %
Resident male won	89.2 %	90 %
Intruder male won	8.6 %	10 %
Length of combat (mean ± S.D.)	27.3 sec (±38.9)	26.4 sec (±65.7)
R-male defecated	53.7 %	52.5 %
I-male defecated	4.3 %	7.5 %
Body size relationships (visual estimation)		
R ♂ >♂ I		37.5 %
R ♂>>♂ I		2.5 %
R ♂ =♂ I		37.5 %
R ♂ <♂ I		17.5 %
R ♂<<♂ I		2.5 %

It was very characteristic of an R-male to discharge a whitish-green, feces-like drop during the fight, while an I-male never or rarely did. However, there was no apparent effect of this feces-like drop on I-males. Some features and data from field observations of intermale fighting are presented in Table 1. Fighting between two males could take considerable time, a maximum of 8 min. In the majority of cases, the R-male won and the I-male retreated. There was no difference noted between fights induced artificially (i.e., placing a male near a pair) or fights that occurred naturally.

Table 2. Number of instances when individual Colorado potato beetle males were found to possess a female, Plant Protection Institute, Budapest.

Number of males and females in cages			
Laboratory		Field	
2 ♂: 2 ♀	5 ♂: 2 ♀	3 ♂: 3 ♀	9 ♂: 3 ♀
14	10	10	5
27	3	8	3
	14	18	5
	4		6
	47		11
			5
			7
			8
			4
No. of observations		No. of observations	
77	79	36	36

A great deal of variability existed in the ability of a male to mount and guard a female for an extended period (Table 2). A sex ratio skewed toward males intensified the competition for a

female. Generally, no male preference in mounting by individual females was noted, although a few outstanding cases of preference did exist. No correlation was found between male body weight and success in mounting a female. Interestingly, the male found most frequently with females when in a group with excess males had a relatively low body weight, and exhibited extreme aggressiveness.

Dispersal and distribution of adults - In June 1983, 157 (s.d. 54) males and 185 (s.d. 52) females (4 sample periods) were present in the experimental potato field. Recapture of marked adults showed that within-plot movement by males and females was common, and marked individuals were rarely encountered paired with the same partner on subsequent occasions. On one occasion, a male visited 6 different potato plants along a distance of ca. 2 m within half an hour, thoroughly examining each plant before moving to the next one. During this period, he fought with 3 males, one in a pair and 2 individuals. During comparable time intervals, females occasionally traveled short distances, usually from one plant to an adjacent one. From the 170 marked beetles, 82 were recaptured in population counts. However, for both sexes 82 were recaptured once, 19 twice and only 7 three times within 18 days after marking. Of the 2 sexes, males tended to be more mobile: 37 were recaptured once, 7 twice and only 1 three times. Neither sex remained in the area where marked. Of the 35 pairs marked, none were subsequently recaptured while paired with the same partner.

Body weight of field collected males was 130.8 mg (s.d. 18.4, n = 219), with a range of 88 to 182 mg. Males in pairs did not have a higher body weight than non-paired males, 133.8 mg (s.d. 18.2, n = 35) and 130.4 mg (s.d. 20.0, n = 46) respectively. Also, resident males found in combat did not differ significantly in body weight from intruding males: R-males: 134.6 mg (s.d. 19.7, n = 5) vs. I-males: 143.4 mg (s.d. 15.8, n = 5).

In the field, locations of pairs and of individual males and females were significantly different (Table 3). Pairs and individual females were generally observed on plants, while males were frequently found on plants or moving along the soil surface.

DISCUSSION

In a recent paper, Thibout (1982) described the mating of CPB and briefly discussed male aggressive behavior toward other males or toward unreceptive females. My observations were similar to Thibout's. The primary objective of this study was to

Table 3. Distribution of Colorado potato beetle pairs and individuals in a potato field, Institute for Plant Protection, Budapest.

Location	No. observational periods	No. of pairs and individuals	Sex ratio ♂ : ♀
Pairs			
plants	5	73.0 (20.8) a*	1 : 1
ground	5	11.0 (7.9) b	1 : 1
Individuals			
plants			
males	6	47.8 (21.3) ab**	1 : 1.3
females	6	63.3 (35.4) a	
ground			
males	6	24.3 (22.0) bc	2.43 : 1
females	6	10.0 (13.3) c	
Overall sex ratio			1 : 1

*Means (s.d. followed by the same letter are not significantly different at 0.05 Newmans Student t-test).

**Means followed by the same letter are not significantly different at 0.05 (Duncan's Multiple Range Test).

examine mating behavior of the CPB within the context of competitive mate searching (Parker 1978).

When in a post-copulatory guarding position, CPB males actively fought other approaching males. The resident male almost always won, and the intruder invariably retreated. The contest rarely escalated to a level where one male injured another. In Coleoptera, similar guarding of females and/or inter-male fighting has been reported (McCauley and Wade 1978, Lloyd 1979, Brown 1980, Richards 1980). In all these instances, sexual selection acted to provide mates for the most successful males. Generally the successful male was bigger (McCauley and Wade 1978, Borgia 1980, Brown 1980) or had an established territory (Alcock 1979, Gwynne 1980, Fujisaki 1981, Wellington and Fitzpatrick 1981). This was not the case with the CPB.

CPB females could either reject or show a clear preference for individual males. When surplus males were caged with females, certain females and males were never observed as a coupled pair, yet the same individuals were observed paired with others.

A sex ratio skewed toward males seemed more important in intensifying agonistic behavior than either male body size or weight (Tables 1 and 2). The distributions of pairless males and females differed. Males were more mobile than females (Table 3). Possibly, more frequent visitations of males to individual plants increases the probability of finding pairless females. The CPB males did not establish territories. Males and females freely entered and left one area for another; i.e., the situation approached an ideal free distribution (Fretwell and Lucas 1970).

Very little is known about sperm utilization in CPB females. The mere access to a female by a male did not necessarily result in copulation; this was also observed by Thibout (1982). Nevertheless, both sexes showed a high level of polygamy. My laboratory studies showed that individual CPB females copulated about 20 times in less than 2 months. Under these conditions, even if only a fraction of the copulations resulted in sperm transfer, there was an opportunity for the females to utilize various "sperm packages". Sperm competition has not been firmly established in CPB females. The possibility of sperm precedence cannot be ruled out in light of the many matings a female may encounter. Sperm precedence is not common in non-social insects (Walker 1980), although it has been reported in a number of cases (Schlager 1960, Ladd 1966, Bartlett et al. 1968). On the other hand, my preliminary data showed that sperm depletion may occur in CPB females, as some females laid 1/3rd as many eggs if mated only once, compared to those mated 3 times.

Based on available data, two hypotheses for CPB reproductive strategies may be developed. The first one is the competitive mate searching theory (Parker 1978 a,b and others). According to this hypothesis, males make optimal decisions in getting and maintaining a mate. A male's fitness is measured by the number of progeny he produces. A CPB male should make an optimal decision in regard to likelihood of maximizing his own progeny production, between mating with an occupied female, or with other females. This means a male faces conflicting selective pressures to remain with a given female until eggs fertilized by his sperm have been laid, and to leave the female as soon as possible to find a new mate. Remaining with a female is particularly important if sperm precedence occurs in the population. If this were the case, guarding and defending a female would be

beneficial to the R-male in terms of his progeny, but it also would pay for the I-male to take over a female from a resident.

The second hypothesis seems to be simpler, but perhaps more applicable to the CPB. It is proposed that only the number of matings in which a male engages may be maximized. Although females may be capable of storing sperm, they still must remate in order to ensure that the full complement of eggs laid over an extended period of time is fertilized. Under these conditions, the sperm from many males would be used for fertilization. Sperm storage is probable, as mated, overwintered females, after some feeding, can lay eggs without renewed copulation (Jermy and Sáringer 1955). However, it is difficult to explain both the adaptive importance of multiple matings by females and the significance of female-guarding by males within the context of this hypothesis. One of the obvious advantages of multiple mating would be an increased genetic diversity for the progeny (McCauley and Reilly 1984).

The realization of either strategy depends on certain conditions, such as population size, immigration rate, spatial (and especially marginal) position of pairs within an area, etc. Although I have documented the guarding behavior of males, further studies are needed to reveal the significance of this behavior to the CPB.

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