

# Intersexual Aggression and Nectar Defense in *Chauliognathus distinguendus* (Coleoptera: Cantharidae)

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## ABSTRACT

The soldier beetle, *Chauliognathus distinguendus*, which defends inflorescences of the tree *Coccoloba floribunda* against intrusion by conspecific individuals, is unusual among insects in that intersexual agonistic behavior is as strong as intrasexual agonistic behavior. Both types of behavior probably result from competition among individuals of both sexes for a common limiting resource. Several lines of evidence suggest that the limiting resource is nectar produced by *C. floribunda*.

MANY INSECTS ACTIVELY DEFEND resources against use by conspecific individuals. Such territorial behavior, which occurs in at least eight orders of insects (Price 1975 and references), most commonly takes one of two forms. In one form, competition among males for access to females has led to the evolution of mating territories, which are often localized around some resource (*e.g.*, oviposition site) used by females. Normally only males interact agonistically (Campanella and Wolf 1974, Jacobs 1955, Otte and Joern 1975, Ziegler 1972). A second common form of territorial behavior of insects is defense by females of a limited or patchy larval food supply. Usually only females interact agonistically in this type of resource defense (Pukowski 1933).

In neither of these forms of resource defense is intersexual competition important. When both sexes compete for the same limiting resource, however, agonistic interactions may be as strong between individuals of opposite sexes as between individuals of the same sex. In this paper we describe resource defense by a soldier beetle, *Chauliognathus distinguendus*. This beetle is unlike other insects that have been studied in that intersexual as well as intrasexual competition for a limiting resource is intense. Intersexual agonistic interactions are consequently as frequent as those between individuals of the same sex.

## METHODS

During the period 3-11 August 1974, *C. distinguendus* was common on *Coccoloba floribunda* Lindau (Polygonaceae) trees growing among the open vegetation bordering a seasonal swamp in Guanacaste Province, Costa Rica. We saw few beetles on other plant species during this period, although they are known to visit flowers of other plants at other times

of the year and in other locations (G. Frankie, pers. comm.). The swamp study site was approximately 2 km southeast of the Palo Verde Field Station, which is operated by the Organization for Tropical Studies.

*Coccoloba floribunda*, a small tree up to 5 m tall, is dioecious with erect inflorescences borne singly at the leaf nodes. Each inflorescence contains many small flowers, only a small fraction of which are open on any one day. *Chauliognathus distinguendus*, a conspicuous yellow and black beetle 13 to 22 mm long, is found from Mexico to Costa Rica (Champion 1914). These beetles frequently confined their activities to a single *C. floribunda* inflorescence for several hours of the day, and while on an inflorescence, a beetle would continually visit flowers and attempt to feed on the nectar they secreted. We never observed any behavior suggesting that these beetles consume pollen or flower parts. Although beetles were found on both male and female trees, we restricted our observations primarily to beetles on male trees.

To facilitate observation of behavior in *C. distinguendus*, we marked individual beetles with spots of red or blue enamel paint. The markings, which we applied with a toothpick while beetles were on a plant, were irregularly shaped, permitting us to identify each beetle individually. We observed a beetle for 10 to 60 minutes. Every interaction with another beetle was recorded by noting the sex of each beetle, which was made possible by differences in the external genitalia. We also recorded, for every interaction, the reaction of the inflorescence occupant toward the intruder (*e.g.*, no visible reaction, approach without contact, approach and momentary contact, and approach followed by sustained contact), the reaction of the intruder (*e.g.*, immediate movement off the inflorescence, movement off inflorescence after brief

contact, movement off inflorescence after sustained contact, movement toward occupant), the duration of the interaction, and the result (*i.e.*, which beetle remained on the inflorescence at the end of the interaction). After ending continuous observation of a beetle, we checked for its presence on the inflorescence every five minutes until it was gone.

For purposes of analysis, we divided interactions between inflorescence occupants and intruder beetles into two types. Aggressive encounters in which the occupant moved toward the intruder or in which occupant-initiated contact between occupant and intruder occurred before the intruder began to leave the inflorescence, and non-aggressive encounters in which an intruder moved onto an inflorescence and then left without being approached or contacted by the occupant.

In order to determine the importance of nectar availability in structuring the activity patterns and agonistic interactions between individuals of *C. distinguendus*, we examined three aspects of beetle behavior. The first was the temporal correlation between agonistic behavior and nectar flow. We measured nectar flow in male *C. floribunda* plants by removing nectar from individual flowers with micropipettes at approximately hourly intervals. The inflorescences were bagged between samplings to exclude beetles and other nectar feeders. We spotted the nectar on Whatman No. 1 filter paper and measured the diameter of the resulting circle. As an estimate of the amount of nectar produced per flower, we averaged the areas of the circles over all flowers in a sampling period. On 7 and 9 August we sampled five flowers on each of two inflorescences from one tree. On 9 August we marked, on the same tree, inflorescences that had been continuously occupied before 0700 hrs by beetles that exhibited frequent agonistic behavior. All 10 inflorescences were then censused at intervals throughout the morning and afternoon for the presence of beetles. The fraction of inflorescences occupied at any census was an estimate of beetle activity on inflorescences at that time.

We next determined whether beetles preferred to defend certain types of inflorescences over others. We reasoned that the amount of nectar produced by an inflorescence would be proportional to the number of open flowers it contained. Moreover, if nectar is a limiting resource, there might be some minimum number of flowers per inflorescence needed to elicit inflorescence defense. At flower numbers below this threshold, the costs of resource defense would outweigh the gains (Carpenter and MacMillen 1976). To determine whether such a threshold existed, we selected a medium-sized tree and marked the

inflorescences beetles actually defended. An inflorescence was considered actively defended if a beetle was present continuously for 30 min or longer and if the beetle reacted aggressively toward other beetles that moved onto the inflorescence. We then counted the number of open flowers on every inflorescence on the tree and recorded which ones beetles actively defended.

Finally, we asked whether increasing the availability of nectar on an inflorescence modified the behavioral interactions between individuals. We selected three inflorescences that had not previously been occupied and defended by beetles. By placing a drop of saturated sucrose solution on three of the flowers on each inflorescence, we artificially increased the amount of nectar available. We then watched each inflorescence for the next two hours and recorded the behavior of all beetles that wandered onto it.

## RESULTS

**GENERAL BEETLE BEHAVIOR.**—During most of the morning, beetles actively defended inflorescences against intrusion by other beetles. When a beetle moved onto an inflorescence occupied by another beetle, it normally began feeding from the lower flowers. Usually, after a few seconds the occupant stopped feeding and moved rapidly toward the intruder. Sometimes the intruder abandoned the inflorescence before being reached by the occupant, which usually continued moving toward the intruder until it reached the bottom of the inflorescence. The occupant returned to the upper portion of the inflorescence and resumed feeding. In other cases, the intruder either did not retreat, or actually moved toward the occupant. This action led to a period of contact that usually lasted less than 10 seconds. During contact each beetle shoved, climbed upon and intensely palpated the other with its antennae, and sometimes bit the other beetle's appendages. We observed several encounters in which the "struggle" between the two beetles was so intense that both fell from the inflorescence to the ground. The advantage during an interaction appeared to be with the occupant: of 238 aggressive interactions, only 5 resulted in the intruder remaining and the original occupant leaving the inflorescence.

Individual beetles successfully defended inflorescences for up to six hours (mean time on inflorescences > 85 min, range: 11-368 min for 22 beetles). While occupying an inflorescence a beetle interacted with intruding beetles once every 3-5 min (for 22 beetles, mean number of aggressive interactions per 10 min was 3.75, range: 1.2-9.1). Over short periods,

interactions were as frequent as one per minute. While individual beetles remained on an inflorescence as long as possible on any one day, we did not find the same beetles on the same inflorescences on the following day.

**BETLE ACTIVITY AND NECTAR PRODUCTION.**—The beetles exhibit a daily cycle of agonistic behavior that is correlated with the periodicity of nectar availability. Individuals spent the night in a quiescent state congregated on the leaves and inflorescences of *C. floribunda*. Shortly after sunrise, normally between 0530 and 0630 hr during our study, the beetles began moving about the tree; they usually occupied suitable inflorescences by 0700 hrs. Flowers opened between 0600 and 0630 hrs and secreted nectar at a decreasing rate until some time shortly after 1000 hrs (fig. 1). While there was some daily variation in the absolute amount of nectar produced, the pattern and timing of decline was similar on both days on which we measured nectar production. Beginning some time after 0900 hrs the fraction of inflorescences occupied by beetles decreased until only 1 in 10 was actively defended by 1400 hrs (fig. 1).

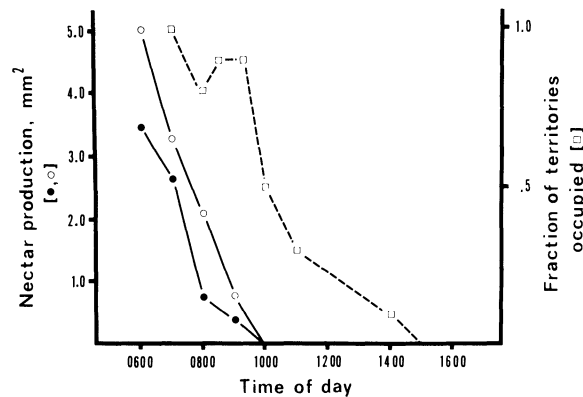


FIGURE 1. Inflorescence defense is confined to the period of nectar production. No detectable nectar production occurred after 1000 hrs on 7 August (open circles) or on 9 August (closed circles). Inflorescence occupation (squares) decreased from 80 to 100 percent before 1000 hrs to 10 percent by 1400 hrs. The sharp decrease in occupancy corresponds with the time at which detectable nectar flow ceases.

The correspondence of a decline in inflorescence occupation with a decline in nectar production was evident from our general observations as well. On each day of our study, beetles that had been occupying and defending inflorescences in the early morning began to leave those inflorescences in late morning. By early afternoon, most beetles had congregated in the shade, often on the underside of leaves, where they remained

until the following morning. The lack of agonistic interactions in these congregations contrasted markedly with the prevalence of such interactions in the early morning when beetles were on inflorescences. Agonistic behavior and inflorescence defense thus seem to be confined more or less to the period of nectar flow in *C. floribunda*.

A minimum nectar production rate seemed to exist, below which an inflorescence is less likely to be occupied and defended by a beetle. *Chauliognathus distinguendus* prefers inflorescences with more than 9 or 10 flowers (fig. 2); beetles actively defended only 6 of 91 inflorescences with fewer than nine open flowers, whereas they defended 28 of 46 with nine or more ( $X^2=24$ ,  $p<.001$ , Kolmogorov-Smirnov Two Sample Test on original data).

Ten beetles wandered onto inflorescences on which the nectar supply had been supplemented with sucrose solution. All 10 behaved differently from those on unsupplemented inflorescences. On unsupplemented inflorescences, a beetle depleted the nectar supply rapidly and because nectar is resecreted slowly, a beetle seldom fed on a single flower for more than five seconds. At supplemented flowers, however, beetles remained feeding for up to 10 minutes. During this time, a beetle did not react toward other beetles that moved onto the inflorescence and began feeding at other flowers. On inflorescence No. 2, for example, a male and two females coexisted without interacting for 2.8 min; on inflorescence No. 3 two males and a female coexisted without interacting for 2 min; on inflorescence No. 2 two females coexisted for 5 min and a male and a female for 8 min without interacting. Only two aggressive interactions occurred. After feeding, each of the other eight beetles left its inflorescence without interacting with the other beetles present and moved to the normal afternoon resting position in the shade. All 10 beetles began resting before 1000 hrs, while the remainder of the beetles on the tree did not begin until 1130 hrs.

**SEX AND INFLORESCENCE DEFENSE.**—Both inter- and intrasexual agonistic behavior was strong in beetles occupying inflorescences (table 1), and both sexes reacted with equal aggression toward intruding females ( $p>.05$ , Fisher Exact Test). On the other hand, while both sexes were aggressive toward intruding males, females were significantly less so ( $X^2=5.5$ ,  $p<.05$ ). We believe that the slightly lower aggressiveness displayed by females toward males can be partially explained by behavioral differences among intruding males. Males that move into an inflorescence occupied by a female can be divided into

two categories. Most entered a female's inflorescence and immediately began feeding. Females eventually

reacted aggressively toward these males and displaced them from the inflorescence. Some males, however, did not begin feeding but immediately approached a female and attempted to copulate. If the mating attempt was unsuccessful, which it normally was, the male often left "voluntarily" before the female initiated any action that we classify as aggressive.

TABLE 1. Number of aggressive and non-aggressive encounters with each sex. Aggressive encounters are those in which the occupant moves toward the intruder or in which occupant-initiated contact between intruder and occupant occurs. Non-aggressive encounters are those in which an intruder moves onto an inflorescence and then leaves without being moved toward or contacted by the occupant.

Defender	encounters with males		encounters with females	
	aggressive	non-aggressive	aggressive	non-aggressive
Males <sup>a</sup>	39	2	9	1
Females <sup>b</sup>	32	10	9	0

<sup>a</sup>Totals for 11 males.

<sup>b</sup>Totals for 10 females.

## DISCUSSION

Agonistic behavior and inflorescence defense in *C. distinguendus* appear to be responses to a limiting resource for which both males and females compete. Several lines of evidence suggest that the limiting resource is nectar produced by *C. floribunda*. First, agonistic behavior is confined to the period of time during which nectar is secreted. Second, the beetles prefer to occupy inflorescences with nine or more flowers, suggesting that an inflorescence with fewer flowers does not provide enough nectar to make defense profitable. Third, agonistic interactions and inflorescence defense can be modified by artificially

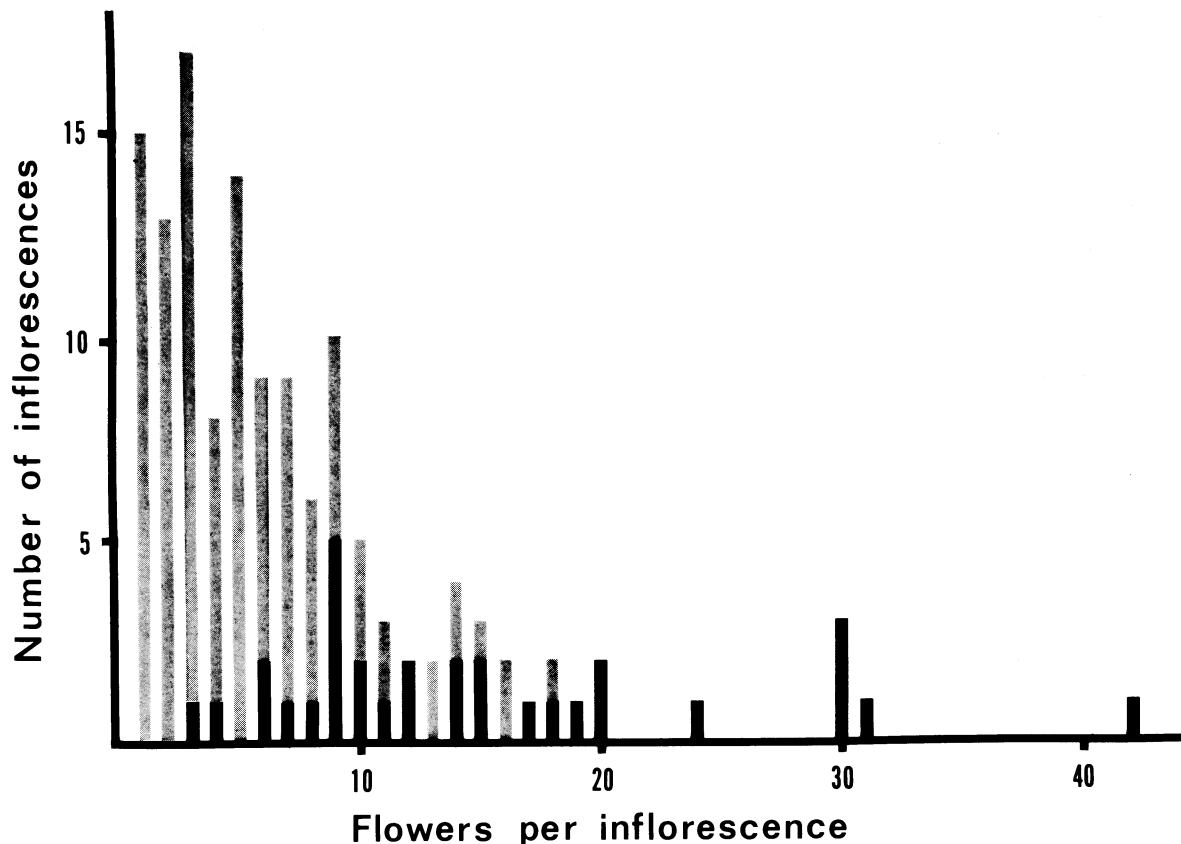


FIGURE 2. Comparison of frequency of inflorescence with a given number of flowers (grey bars) with the number of inflorescences defended (black bars) on plant 4.

increasing the amount of nectar available. Finally, our observations indicate that the beetles occupy and defend inflorescences on both male and female *C. floribunda* trees, suggesting that nectar and not pollen is the resource influencing interactions among these insects. We infer that competition is intense from our estimates that for every beetle occupying an inflorescence there are two to four beetles moving about the tree attempting to gain access to one.

The intra- and intersexual competition for resources in *C. distinguendus* results in agonistic behavior that is equally intense between sexes as it is within a sex. Intersexual aggression is not commonly observed in insects, perhaps because the two sexes rarely compete for the same limiting resource. However, nectar is a resource that both sexes of many insects require. While territorial defense of nectar sources is common in nectarivorous birds (Feinsinger and Chaplin 1975, Feinsinger 1974, Gill and Wolf 1975, Linhart 1973, Stiles and Wolf 1970), it has not previously been reported in insects. This may be because nectar supplies are normally either superabundant or limiting but too diffuse to make territorial defense feasible (Linhart 1973). For *C. distinguendus*, however, nectar is both scarce and clumped, favoring agonistic behavior and inflores-

cence defense. The clumping of flowers in discrete inflorescences on *C. floribunda*, coupled with continual secretion of nectar for three to four hours in the morning, probably facilitates defense of the resource. Furthermore, the *veranillo*, or little dry season, during which our study occurred, appears to be a period of relative nectar scarcity. During our study, few alternative nectar sources were available to *C. distinguendus*. A large population of beetles supported at other times of the year by more abundant nectar resources may experience severe competition as the availability of nectar decreases seasonally and the beetles move onto *C. floribunda*. The natural response appears to be intra- and intersexual agonistic behavior. If so, we would predict that at other times when nectar is more abundant, *C. distinguendus* would exhibit little or no agonistic behavior.

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