

# Antipredator defense as a limited resource: unequal predation risk in broods of an insect with maternal care

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The allocation of parental investment is a potential source of conflict within broods whenever offspring are able to obtain differential access to the parental resource. Unlike the provisioning of food, parental antipredator behavior is usually considered a resource that benefits all offspring simultaneously. In the thornbug treehopper (*Umboia crassicornis*), offspring form aggregations in exposed positions on host-plant stems. They are subject to intense predation, and maternal defense is their primary means of protection. I examined the distribution of risk within these offspring groups, using natural variation in the outcome of more than 500 predation attempts (324 recorded on videotape) by vespid wasps (*Pseudopolybia compressa*) on 18 *U. crassicornis* aggregations. I found three influences on an individual offspring's risk of predation. The first was the presence of a defending female: as expected, offspring were much more likely to survive contact with a wasp if the female was present than if the female had disappeared. The second influence was position relative to other offspring: when wasps were successful in removing an individual, they almost always removed it from the edge of the group. The third influence was distance from the female: the closer an offspring was to the female at the time it was contacted by a wasp, the higher its likelihood of survival. The distribution of risk is determined largely by the behavior of defending females and the prey-searching behavior of wasps. The nature of risk within these aggregations sets the stage for two forms of sibling rivalry: selfish herd behavior and competition for access to maternal defense. It also raises the question of how a parent should allocate defense among offspring when it is unable to defend them all simultaneously. *Key words*: parental care, predation, *Pseudopolybia compressa*, sibling rivalry, *Umboia crassicornis*. [*Behav Ecol* 13:125–133 (2002)]

The allocation of parental investment within broods of offspring is a source of potential conflict, expressed when siblings compete for a disproportionate share of limited resources (Mock and Parker, 1997; Trivers, 1974). The extent of conflict will be influenced by, among other things, the degree to which individual offspring can monopolize the resource. For example, if a parent bird provisions its brood with a succession of small food items, each of which can be consumed by a single chick, there is the potential, through sibling interactions or parental choice, for some offspring to obtain a disproportionate share (Mock and Parker, 1997). In contrast, if the parental resource benefits an entire brood at once, there may be no opportunity for within-brood competition. Parental vigilance and defense of the brood against predators are often considered to be a form of parental investment that benefits all offspring equally and simultaneously (Lazarus and Inglis, 1986; Ruusila and Poysa, 1998). If this is true, we might expect cooperative rather than competitive behavior among siblings when obtaining access to parental defense against predators.

What is the evidence that parental antipredator behavior benefits all offspring equally? In contrast to the provisioning of food, the allocation of parental defense within broods has received little empirical study. It seems clear that all offspring should benefit when a parent produces an alarm signal (Klump and Shalter, 1984) or intercepts a predator and prevents it from reaching the brood (Owings et al., 1986). However, if parents are not always successful in defending against

predators, there may be two ways in which risk is unequally distributed. First, when broods are relatively large, there may be a selfish herd effect, with individuals on the margins at greater risk of predation (Hamilton, 1971; Krause, 1994; Mooring and Hart, 1992; Rayor and Uetz, 1990). If so, interactions among siblings might determine which individuals are marginal and thus at greater risk (see Kacelnik et al., 1995; McRae et al., 1993). Second, a parent may be unable to defend all offspring at once, depending on the spatial configuration of the brood (Windsor, 1987). Distribution of risk may thus depend both on sibling interactions (i.e., competition for the most protected or defensible locations) and on parental behavior if parents preferentially defend some offspring over others. Parents may also influence the position of offspring within broods, as shown by studies of catfish defense of mixed-species broods (McKaye and Oliver, 1980; McKaye et al., 1992). Adult catfish actively excluded cichlid young from the center of the school, leaving their own young in safer, central positions.

In this study I examined the distribution of predation risk within broods of an insect with extended maternal care. In the thornbug treehopper (Hemiptera: Membracidae: *Umboia crassicornis*), females defend their aggregated offspring from predators (Wood, 1976, 1983). The offspring (or nymphs) are vulnerable to predation by a range of invertebrates (Cocroft, 1996; Dowell and Johnson, 1986; Masters, 1997; McKamey and Deitz, 1996; Wood, 1976, 1983), and loss of the female is associated with greatly increased predation (Dowell and Johnson, 1986; Wood, 1975). Maternal defense is thus an important resource for developing nymphs, as it is in other insects with care of offspring after hatching (Tallamy and Schaefer, 1997).

The protection afforded by female *U. crassicornis* is solicited by means of offspring signals (Cocroft, 1996, 1999a,b), analogous to the food-soliciting signals of altricial birds. However,

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unlike nestling birds, *U. crassicornis* nymphs produce signals in synchronous bursts that exhibit some elements of cooperation (Cocroft, 1996, 1999b). Cooperation would be expected if all individuals benefit simultaneously from maternal defense; however, if maternal defense does not benefit all offspring at once, this coordinated signaling may also contain an element of competition. Understanding the balance of cooperation and noncooperation among offspring in soliciting defense requires clarifying the nature of selection exerted by predators on aggregated offspring.

I investigated three potential influences on predation risk within offspring aggregations, using natural variation in the success rate of predatory wasps (Hymenoptera: Vespidae: *Pseudopolybia compressa*). First, to evaluate the importance of maternal defense against wasp predation, I compared predator success rates between broods attended by a female and those from which the female had disappeared. Second, to assess the potential for spatial inequalities in risk, I asked if an individual's risk of predation is influenced by whether it is on the margin or in the center of the group. Third, to assess a female's effectiveness in defending all offspring at once, I examined the correlation between an individual's risk of predation, once contacted by a predator, and its distance from the female at the time of the attack. I also observed the interactions of females and predators that underlie the observed patterns of risk.

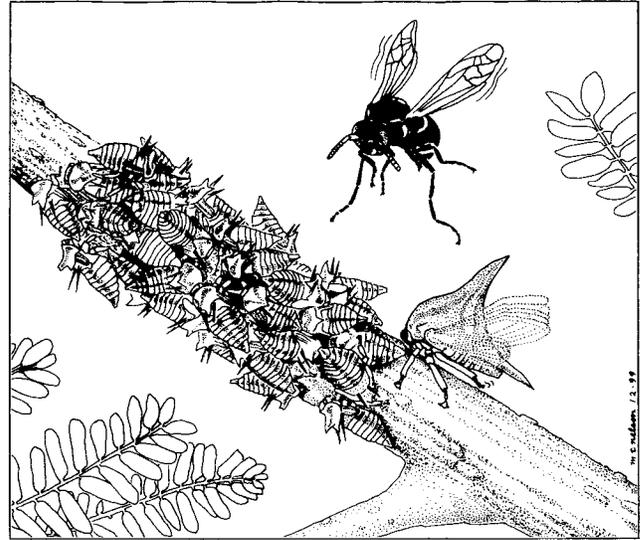
## METHODS

### Study species

*Umbonia crassicornis* occurs from Mexico through northern South America, with introduced populations in southern Florida, USA, and the Caribbean (McKamey and Deitz, 1996). Adults and immatures feed on the sap (presumably phloem) of various trees and shrubs in the mimosoid legumes (McKamey and Deitz, 1996). Females are semelparous, depositing a single clutch of 100 or more eggs into a host-plant stem near the growing tip (Wood, 1974). Females typically spend the rest of their lives with these offspring, often surviving until the offspring reach maturity 6–8 weeks later. Females face the group, usually from below, and periodically cut slits into the bark to facilitate offspring feeding (Wood, 1983). When the nymphs first hatch, they form a group only a few maternal body lengths long (Wood, 1976; adult females are 1–1.5 cm long). However, as the nymphs grow to adulthood during the next 3 or 4 weeks, they form a cylindrical aggregation around the stem, often extending up to 10 or more body lengths away from the mother (Cocroft RB, unpublished data). Nymphs typically complete their development to reproductive maturity on the same stem on which the eggs are deposited.

Aggregations of *U. crassicornis* nymphs often consist of the offspring of one singly mated female (Wood and Dowell, 1984). However, females sometimes mate twice (Masters, 1998). Females also may deposit their egg clutch on the same stem where another female is already guarding eggs; after hatching, the two broods will form a single aggregation attended by both females (Cocroft RB, unpublished data). Furthermore, nymphs occasionally move between aggregations on the same tree (Cocroft RB, personal observation). Group composition can thus range from full siblings to a mix of full siblings, half-siblings, and unrelated individuals. The aggregations used as units of analysis in this study were operationally defined as a cluster of nymphs on a stem, with or without an attending adult female.

The study was conducted near San Luis on the Pacific slope of the Cordillera de Tilaran, Puntarenas, Costa Rica, at an elevation of approximately 700 m. Host plants at the study site



**Figure 1**  
Female *Umbonia crassicornis* with an aggregation of fourth-instar nymphs. The female is buzzing her wings in response to the approach of a predatory wasp (*Pseudopolybia compressa*).

were saplings of *Enterolobium cyclocarpum* and *Acacia centralis* (Leguminosae: Mimosoideae) at the edges of clearings and along riverbanks. Aggregations were found 10–20 cm back from the apical meristem of branches 1–3 m above the ground. *Umbonia crassicornis* is common at the study site during the May–December rainy season (Masters K, personal communication). This study was conducted between 18 July and 13 August, 1996.

The most common predator of *U. crassicornis* nymphs at the study site is a social wasp, *Pseudopolybia compressa* (Cocroft, 1998). Figure 1 shows a female defending an offspring aggregation from a hovering *P. compressa*. Wasps approach from the air, then land on or near the aggregation and attempt to remove a nymph by biting it and pulling it from the branch. Once the wasp returns to its nest, nest mates may cooperate in reducing the nymph to small pieces that will be fed to larvae (Cocroft, personal observation). However, these wasps do not hunt socially.

### Behavioral observations

I videotaped aggregations of *U. crassicornis* to provide a record of predator–prey interactions. All aggregations located during the study were filmed, except those that occurred in windy locations where movement of the stem made observations difficult and filming impossible (those aggregations were not included in the study). The aggregations observed contained second- to fourth-instar nymphs (nymphs at San Luis apparently undergo the final molt to their adult morphology after the fourth stadium, rather than after the fifth as in other localities). To film an aggregation, I positioned a camcorder (Canon ES 2000 Hi-8 with a 20X optical zoom lens) on a tripod 1.5–2 m from the group, with the long axis of the stem in the focal plane of the camera. Observations on a focal aggregation consisted of continuous monitoring for 2–6 h. I began filming when I observed a wasp within 1–2 m of the aggregation, and continued filming for approximately 1 min after the wasp departed. Due to technical limitations, filming was limited to daylight hours (including dusk) that were free of rain or heavy wind. These records were supplemented with field notes on predator encounters that were not captured on

video. I analyzed the behavior of predators and prey using a JVC editing deck and a 12-inch monitor. I measured distance relative to female body length using a clear plastic ruler over the image on the monitor screen. This method can introduce some error due to parallax; however, I assumed the error introduced would be small and unbiased with respect to the analysis.

### Presence of the mother and the predator's success rate

To assess the effectiveness of females in defending against *P. compressa*, I compared the per-encounter success rate of wasps between aggregations tended by a female and those from which the female had disappeared. During an encounter, a wasp arrived at the aggregation, hovered around the aggregation and/or landed on the stem, then left (with or without a nymph). Operationally, I considered an encounter to begin when a wasp approached to within 20 cm of the aggregation (as judged from videotape), and to end when the wasp moved more than 20 cm away, if it then stayed away for 30 s or more.

### Center versus edge positions

Are individuals on the edges of groups more vulnerable to predation than those in the center? If an individual's position influences its predation risk, then the proportion of individuals contacted by predators in center and edge positions should differ from the proportion of individuals available in those positions. For each contact between a wasp and a nymph recorded on film, I scored whether the individual contacted was in the center or on the edge of the group. I then counted the number of individuals in both positions. Because offspring encircle the host plant stem (see Figure 1), only about half of each group is visible on videotape. However, because groups were roughly cylindrical, there should be no systematic bias between the near and far sides of the groups filmed. An individual was scored as in a center position if there was at least one other individual on every side of it and in an edge position if it was exposed on at least one side. Groups were assumed to be symmetrical, so individuals not clearly on an edge, but for which one side was not visible on film, were also scored as center individuals. Sensitivity of the results to potential violations of this symmetry assumption were assessed by conducting two additional analyses, one with these individuals scored as edge and one with them excluded. Field notes clarified the position of these individuals when more of the stem could be seen than was visible from the camera angle. I conducted two separate analyses: one for contacts that resulted in predation, and one for those that did not (the latter may be a better indicator of predator behavior if female behavior influences which individuals are actually preyed on once contacted).

The null hypothesis for this analysis was that predation risk is independent of position. To test this hypothesis, I calculated for each aggregation the probability of observing as many or more edge predations as observed, based on the number of individuals in each position. For illustration, suppose that a total of two predation events were observed for a family group and that both individuals removed were on the edge of the group. If at the time of the first event there were 10 nymphs on the edge and 8 in the center, the probability of an edge predation, given the hypothesis of no effect of position, would have been  $10/(10 + 8)$ , or 0.55. If at the second event there were 9 nymphs on the edge and 8 in the center, the probability that an edge nymph was taken would have been  $9/(9 + 8)$ , or 0.53. The joint probability of the two edge predations is obtained from the product of the probabilities of the individual events:  $0.55 \times 0.53 = 0.29$ . In other words, if predation

risk is independent of position, the probability that both individuals removed from that family would have been on the edge is 0.29. If the individuals removed from another group were 3 edge and 1 center, the probability of observing results as or more extreme would be equal to the joint probability of 3 edge and 1 center predation, plus the probability of 4 edge predations. Results from individual family groups were combined to yield an overall statistic using Fisher's method of combining  $p$  values (Sokal and Rohlf, 1995). Improbable results ( $p < .05$ ) would allow rejection of the hypothesis that predation risk is independent of position.

### Distance from the female at the time of contact

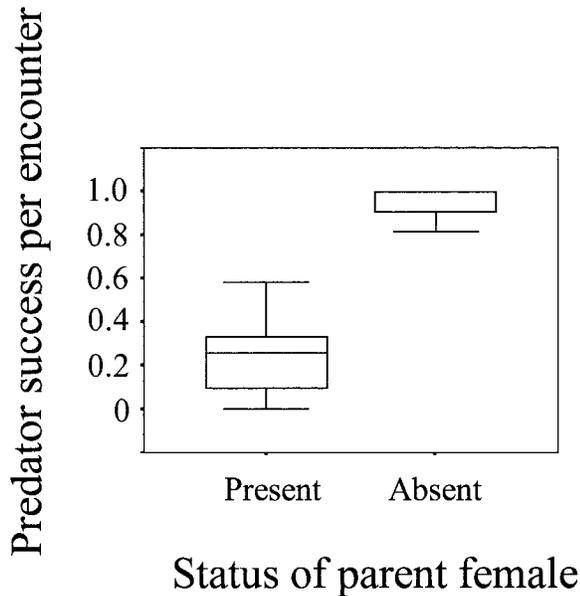
Given that a predator has contacted a nymph, is the nymph's likelihood of capture related to its distance from the female? Distance from the female was measured between the nearest points on the bodies of the mother and the nymph at the time of contact, using a clear plastic ruler placed on the monitor screen. I first measured the female's body length (from the front to the back of the pronotum, the hard shell covering the body; see Figure 1), then made two measurements used in calculating female–nymph distance: distance along the long axis of the stem and distance across the stem. From these I calculated the shortest distance the female would have to travel along the surface of the stem to reach the nymph (expressed in female body lengths and corrected for the stem's cylindrical shape).

Aggregations have an inherent polarity along their long axis, with one end closer to the base of the stem and one closer to the tip. It is conceivable that this could be reflected in spatial structuring within the aggregation if, for example, larger individuals cluster toward one end. To control for the possibility of such structure, I divided each aggregation into thirds on a per-event basis by placing a clear plastic ruler over the image on the monitor screen. The position of each individual contacted by a predator was scored as in the proximal, medial, or distal third of the group, where "proximal" indicates the edge closest to the base of the branch. An individual was considered to be within a given third based on the location of its thorax; if its thorax was equally in two areas, the nymph was scored as being in the third containing the head.

I assessed the relationship between a nymph's predation risk, once it was contacted by a wasp, and its distance from the mother using a multiple logistic regression analysis (Hosmer and Lemeshow, 1989). The dependent variable was the outcome of the contact: captured (1) or not captured (0). In addition to the female–nymph distance, two categorical dummy variables were included to control for possible sources of variation: aggregation, which controlled for differences among family groups (such as variation in maternal behavior or group location) and position, which controlled for the nymph's position within the aggregation. The model was as follows: outcome (captured or not) = constant + aggregation + position (proximal, medial, distal) + mother–offspring distance. The regression analysis was done using SPSS version 10. The model was constructed following the recommendations of Hosmer and Lemeshow (1989)—starting with a basic set of likely explanatory variables and adding or deleting variables based on results of a likelihood ratio test.

### Female and wasp behavior

If there is a relationship between mother–offspring distance and predation risk, the nature of this relationship will be influenced by the behavior of predators and defending females. I measured two aspects of the timing of predator–female interactions: the speed at which females moved across the



**Figure 2**

Proportion of wasp encounters resulting in removal of a nymph in 15 aggregations defended by a female (480 encounters) and 3 aggregations without a female (40 encounters). Aggregations with a defending female experienced an approximately fourfold decrease in predator success rates. Boxes represent interquartile range, vertical lines show the range of values, and a line within the box represents the median.

group, and the time required for a wasp to remove a nymph once contact was initiated. Females may not be able to defend all nymphs simultaneously if their travel time across the aggregation is longer than the time required for wasps to remove a nymph. Furthermore, patterns of vulnerability within the aggregation will depend on how far the female has to

**Table 1**

**Edge bias in predation**

Family	Predation events		Unsuccessful contacts	
	Edge: center	<i>p</i>	Edge: center	<i>p</i>
1	5:0	.11	2:0	.56
2	6:1	$5.0 \times 10^{-6}$	20:1	$1.6 \times 10^{-9}$
3	7:0	.24	22:2	.099
4	11:0	$7.0 \times 10^{-5}$	54:2	$3.8 \times 10^{-20}$
5	7:0	.0018	14:0	$3.3 \times 10^{-6}$
6	14:0	.0002	27:0	$3.3 \times 10^{-6}$
7	3:0	.31	4:0	.016
8	6:0	.022	6:0	.082
9	1:1	.78	5:0	.053
10	7:1	.036	35:1	$1.1 \times 10^{-11}$
11			8:0	.1355
	Combined $p < .001$ ; $\chi^2 = 102.73$ , $df = 20$		Combined $p < .001$ ; $\chi^2 = 259.76$ ; $df = 22$	

Shown is the probability that as many or more edge predation events or contacts would be observed (1) assuming wasps take individuals from center and edge in equal proportions and (2) given the number of edge and center individuals available at the time of each predation event (predation:  $N = 10$  aggregations and 80 predation events; contacts:  $N = 11$  aggregations and 203 contacts).

move to reach a particular location, so I also recorded the females' positions, both during regular censuses and at the times offspring were contacted by wasps. I measured the rate of movement of females across the aggregation in female body lengths per second (body length and distance traveled were measured as above). I also measured the time required for females to turn around ( $180^\circ$  rotation of heading), which they often do while defending. In each case I obtained the time interval by counting the number of full frames (each frame represents  $1/30$  s). I measured the time required for wasps to remove a nymph from the stem for events in which the entire sequence was clearly visible. When removal time was short ( $< 5$  s), I measured its duration to the nearest  $1/30$  s by counting the number of full video frames. For longer removal times ( $> 5$  s), I measured duration to the nearest  $1/4$  s using a hand-held stopwatch.

In most field studies of predation risk, the logistics of the study do not allow determination of the number of individual predators involved in the observed mortality (e.g., Clutton-Brock et al., 1999; Haskell, 1994; McKaye et al., 1992; Rayor and Uetz, 1990; Stamp and Bowers, 1988; Wisenden and Keenleyside, 1995). This knowledge would be useful for an assessment of individual variation among predators. When possible, I marked wasps on the body with a dot of white enamel paint to allow for individual recognition. Wasps were marked when they landed near a group, without capturing them, and were subsequently identified through the location of the paint dot.

## RESULTS

I observed 20 aggregations of *U. crassicornis* and 568 encounters with predatory wasps (*Pseudopolybia compressa*). The number of wasp encounters observed per aggregation ranged from 0 (in two aggregations) to 94 (mean  $\pm$  SD =  $27.0 \pm 26.2$ ). Videotape records were obtained for all or part of 324 of these encounters (the number of encounters used in the following analyses therefore varies depending on whether video analysis was required or whether field notes provided sufficient information). The total observation time was 188 h, with a mean of  $8.9 \pm 6.6$  h per aggregation. All groups consisted of one female and a cluster of immatures, presumably reflecting single-female clutches. One host sapling contained 3 aggregations, 3 contained 2 aggregations each, and 11 contained a single aggregation each. The number of nymphs at the start of observations for each aggregation ranged from 7 to 131 ( $50.1 \pm 36.6$ ); this number dropped as nymphs were lost to predators.

The presence of a defending female was associated with a fourfold reduction in the wasps' per-encounter success rate. In 15 groups attended by a female throughout the study, only 23% of wasp encounters, on average, resulted in capture of a nymph (Figure 2). In three groups observed after the female had disappeared, 94% of wasp encounters resulted in capture of a nymph (Mann-Whitney  $U$  test,  $n_1 = 15$ ,  $n_2 = 3$ ,  $U = 0$ ,  $p < .01$ ). The only individuals that survived wasp encounters in the absence of the female were two nymphs that dispersed to hidden locations on leaves, where wasps searching along the stem failed to locate them.

Videotaped predation events ( $N = 80$ ; this number excludes uninformative events for which there were no nymphs in central positions) provided clear evidence that individuals at the edge were taken preferentially. Out of 80 nymphs removed by a wasp, 77 were removed from edge positions. This proportion is significantly edge-biased compared to the relative numbers of nymphs available in each position (Table 1). The overall proportion of nymphs available in each position (obtained by calculating a proportion for each event, then

averaging means from each aggregation) was 0.523 edge to 0.477 center, and the overall proportion of nymphs taken from each position was 0.963 edge to 0.037 center. These proportions can be used to estimate an odds ratio (Sokal and Rohlf, 1995). When wasps in this study removed a nymph from an aggregation, they were 23.4 times more likely to remove it from the edge of the aggregation than from the center (95% CI = 7.2–76.1).

The proportion of wasp–nymph contacts that did not result in predation was also highly edge biased (Table 1). The odds of being contacted were similar to those of being preyed upon: nymphs that were contacted but not removed by wasps were 25.6 times more likely to be on the edge of the aggregation (95% CI = 10.9–60.0).

I conducted two additional analyses to assess the sensitivity of these results to violations of the assumption that groups were symmetrical (and thus that all of the individuals assigned to center positions were correctly assigned). The results were not affected by this assumption. If individuals for which one side was not visible on the video screen were excluded rather than scored as center, the observed predation was still edge biased ( $\chi^2 = 58.76$ ,  $df = 18$ ,  $p < .001$ ; one aggregation was left out because exclusion of these individuals left an uninformative group of all edge individuals). If the individuals in question were assigned as edge rather than center, predation also remained edge biased ( $\chi^2 = 37.79$ ,  $df = 18$ ,  $p < .001$ ). The results of these additional analyses are the same for contacts that did not result in predation: results remained highly edge biased if the individuals in question were excluded ( $\chi^2 = 148.5$ ,  $p < .001$ ) and if they were scored as edge individuals ( $\chi^2 = 96.6$ ,  $p < .001$ ).

The total number of wasps accounting for the more than 500 predation attempts observed in the study is unknown. However, I was able to individually mark five wasps, and these accounted for 33% (189/568) of the attempts. Repeated observation of these individuals allowed an assessment of individual variation in behavior and a determination of whether pooling data among predators is likely to be misleading. Four marked wasps that successfully attacked nymphs did not differ in the proportion taken on the edge versus the center of aggregations (predation: heterogeneity  $\chi^2 = 0.24$ ,  $df = 3$ ,  $p > .9$ ). There is thus no evidence of individual differences in the likelihood of removing nymphs from the edge of the aggregation (in fact, there was almost no variation in the data). The number of additional, unmarked individuals is unknown, but observations indicate that there were a minimum of two. The encounters observed during the study thus involved seven or more wasps.

Logistic regression analysis revealed that a nymph's risk of capture, once contacted by a wasp, depended on its distance from the mother. Table 2 shows the effect of each variable in the model after the effects of all of the other variables were controlled for. Calculation of an odds ratio (Hosmer and Lemeshow, 1989) revealed that a nymph's chances of being removed increased 3.7-fold (95% CI = 2.2–6.3) for every additional female body length of distance away from the female (after controlling for variation among aggregations and locations within the aggregation). There also was a significant spatial component of the risk of being removed from the stem. Once contacted by a wasp, nymphs in the distal third of the aggregation were three times more likely to be removed than were nymphs in the proximal and medial thirds (after controlling for variation among aggregations and female–nymph distance). Incorporation of an interaction between the nymph's location and its distance from the female did not significantly affect the likelihood of the model; in other words, the relationship between distance and risk was independent of location within the aggregation (likelihood ratio test,  $\chi^2 =$

**Table 2**

**Maximum-likelihood ANOVA table from logistic regression analysis, showing relationship among nymphal predation risk, position in the aggregation, and distance from the parent female ( $N = 12$  aggregations and 351 predator contacts)**

Source	df	$\chi^2$	Probability
Aggregation	11	34.88	.001
Position	2	11.57	.01
Distance	1	29.66	.001

“Aggregation” was a dummy variable included to control for differences among family groups. The  $\chi^2$  values represent the results of log-likelihood tests comparing the likelihood of models with and without that variable.

0.964,  $df = 1$ , ns). Furthermore, there was no significant improvement in the model from adding in nymph age (likelihood ratio test,  $\chi^2 = .637$ ,  $df = 1$ , ns) or the number of nymphs in the aggregation (likelihood ratio test,  $\chi^2 = .235$ ,  $df = 1$ , ns).

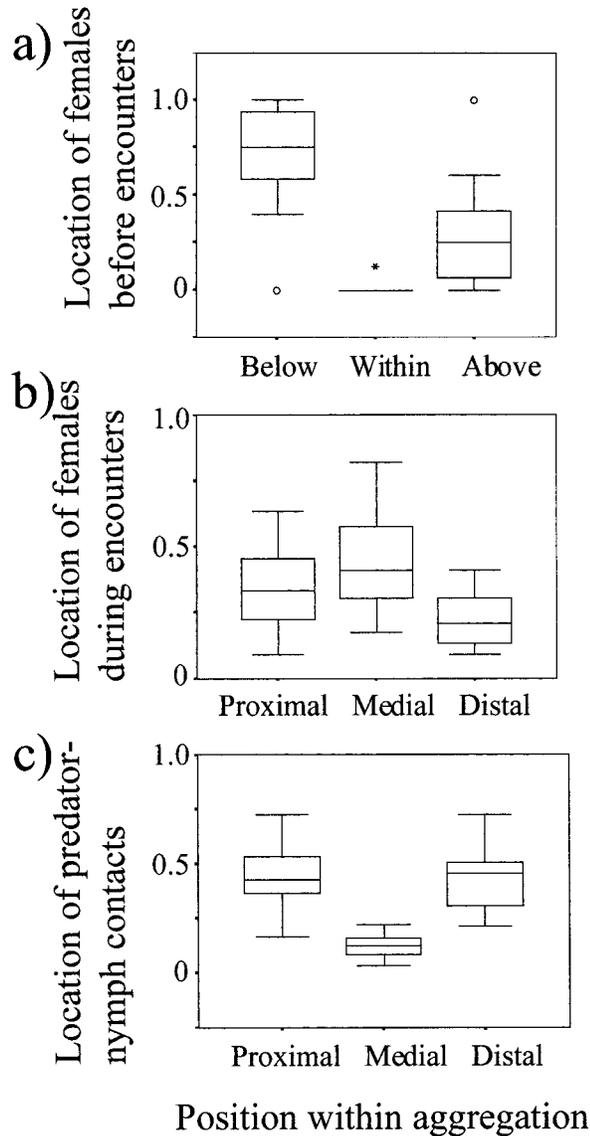
### Female and wasp behavior

Females moved slowly as they walked along the stem or across their aggregated offspring. Females took  $2.6 \pm 1.3$  s (mean  $\pm$  SD) to move one body length ( $N = 11$  females, 32 measurements) in a straight line. Females also took an average of  $2.5 \pm 0.5$  s to turn around, something they often did while defending ( $N = 14$  females, 56 measurements).

Females were most likely to be below the nymphal aggregation (i.e., proximal with respect to the plant) during regular censuses (Figure 3a; replicated chi-square test, total  $\chi^2 = 58.05$ ,  $df = 22$ ,  $p < .01$ ; heterogeneity  $\chi^2 = 31.41$ ,  $df = 20$ , ns, indicating that females were similar in their tendency to be below the group). During encounters, females walked into the aggregation, and at the times when wasps contacted nymphs, females were more likely to be in the medial portion of the aggregation than on one end (Figure 3b; replicated  $G$  test, total  $\chi^2 = 83.9$ ,  $df = 24$ ,  $p < .01$ ; pooled  $\chi^2 = 26.1$ ,  $df = 2$ ,  $p < .01$ ; heterogeneity  $\chi^2 = 57.8$ ,  $df = 22$ ,  $p < .01$ , indicating that not all females were alike).

Wasps began to remove a nymph by biting it on the thorax or abdomen. While holding a nymph in its mandibles (and sometimes its front legs as well), a wasp pushed against the branch with its hind legs. Wasps sometimes pulled one end of the nymph away from the branch, then bit through one or more of the nymph's legs. The wasp then rolled the nymph over by lifting up the side where the legs were severed and quickly pulled the nymph away from the branch. The time involved in removing a nymph from a stem ranged from 0.3 to 33.0 s (mean  $\pm$  SD =  $6.1 \pm 6.35$  s;  $N = 114$  nymphs). Nymphs typically were stationary between and during attacks. However, after a wasp briefly contacted a nymph, that nymph and its neighbors sometimes shifted position. For six aggregations, I observed attacks on both stationary and walking individuals. The amount of time required by a wasp to remove nymphs that were walking was shorter ( $2.5 \pm 1.5$  s) than that required for nymphs that were stationary ( $8.8 \pm 3.9$  s; Wilcoxon matched-pairs, signed-ranks test,  $n = 6$ ,  $T = 0$ , two-tailed  $p < .05$ ).

Wasps made their final approach to nymphs in one of two ways. In 29% (37/129) of the contacts for which the wasp's prior behavior was determined, the wasp landed on the branch above or below the aggregation, then walked along the branch until it reached the aggregation. In these cases the wasp contacted and sometimes removed the first individual



**Figure 3**  
The position of defending females relative to offspring and to the location of predator attacks. (a) The distribution of female locations during regular censuses; (b) the distribution of female locations at the times offspring were contacted by predators; (c) the distribution of predator–nymph contacts within offspring aggregations. The asterisk and circles represent outliers.

encountered on the margin of the aggregation. In the other 71% (92/129) of cases, the wasp simply touched down or landed directly on a nymph. Wasps concentrated their contacts with nymphs at the two ends of aggregations, but they appeared about equally likely to contact nymphs at each end (Figure 3c; replicated  $G$  test, total  $\chi^2 = 160.7$ ,  $df = 22$ ,  $p < 1$ ; pooled  $\chi^2 = 109.1$ ,  $df = 2$ ,  $p < .01$ ; heterogeneity  $\chi^2 = 51.8$ ,  $df = 20$ ,  $p < .01$ , indicating that there was significant variation among aggregations in the distribution of contacts).

In contrast to the slow-moving *U. crassicornis* females, attacking wasps were highly mobile. Flying wasps typically circled the aggregation, moving from one end to the other and contacting up to eight nymphs in the course of a single encounter. While many encounters with female-defended aggregations lasted less than 20 s, some lasted for more than 5 min

(mean =  $51.6 \pm 74.2$  s). Encounters with aggregations without a defending female lasted an average of  $13.0 \pm 10.7$  s. I observed two marked wasps at both female-tended and untended aggregations. Encounters were longer when the female was present, by a factor of 4 in one case (Mann-Whitney  $U$  test,  $n_1 = 22$ ,  $n_2 = 3$ ,  $U = 56$ ,  $p < .05$ , one-tailed) and by a factor of 11 in the other (Mann-Whitney  $U$  test,  $n_1 = 33$ ,  $n_2 = 11$ ,  $U = 322.5$ ,  $p < .01$ , one-tailed).

## DISCUSSION

I found three major influences on the predation risk of offspring. The first was the presence or absence of the mother: defending females substantially reduced the effectiveness of wasps in removing offspring. In this study, wasps were only successful in about one-fourth (23%) of attacks on female-defended aggregations. In contrast, wasps were successful in removing a nymph in 94% of attacks on aggregations without a defending female. These proportions are similar to those found by Dowell and Johnson (1986) in a study conducted with a Florida, USA, population of *U. crassicornis*. Only 19% of attempts by the vespid wasp *Polistes major* to remove nymphs were successful when a defending female was present, as compared to 90% of attempts on nymphs not defended by a female. Maternal defense is important in reducing the success of foraging wasps.

A second important influence on an individual offspring's predation risk was its position relative to other individuals in the group. Almost all of the predation by wasps was on individuals on the margins of groups. This by itself is not necessarily evidence of edge-biased predation: as pointed out by Krause (1994), one limitation of many studies of spatial variation in predation risk is that no information is given on the relative numbers of individuals in center and edge positions. In this study, I estimated the probability of the observed number of edge predation events based on the number of individuals available in each position for each event. Taking into account the relative numbers of individuals in center and edge positions, wasps were approximately 23 times more likely to take an individual from the edge. The same bias was revealed in contacts that did not result in predation. This edge bias occurred in part because wasps often contacted or removed the first nymph encountered as they walked up to the aggregation along the plant stem. There is thus a clear spatial component of predation risk.

The third major influence on offspring predation risk was distance from the mother at the moment of contact by a wasp. Once a nymph was contacted by a predator, its odds of being removed increased by a factor of 3.7 for every female body length away from the female. What accounts for this relationship between survivorship and the female's proximity? Successful defense of nymphs that were being removed by a wasp usually involved approach by the female. Females moved relatively slowly, however, taking 7.7 s, on average, to travel 3 body lengths (one body length is 1–1.5 cm). Females also took an average of 2.5 s to turn around. In contrast, wasps quickly circled the aggregation and moved from one end to the other. Once a wasp contacted a nymph, it required an average of 6.2 s to remove it from the plant stem. A female moving at an average speed toward a wasp taking an average amount of time to remove a nymph would only arrive in time if she were less than 2.4 body lengths away at the time of contact. Because aggregations often extend along the branch for 2–10 female body lengths (Cocroft, unpublished data), a female on one end of the aggregation may not have sufficient time to reach a contacted nymph on the opposite end. The location of the mother is thus an important and dynamic influence on the spatial distribution of risk within the brood.

In species in which parents actively defend a brood, one would expect defense to be less effective when broods are larger. Indeed, constraints on the effectiveness of defense have been proposed to impose an upper limit on brood size (Lack, 1954; Safriel, 1975; Wisenden and Keenleyside, 1995). However, in this study I detected no influence of brood size on the effectiveness of maternal defense. This rather surprising result may have come about because of the extent to which brood sizes were reduced by the time nymphs grew large enough for aggregations to extend long distances along the stem. That is, females may well be less effective at defending long aggregations, but no aggregations spanned sufficient distances in this study to reveal this effect. There also was no effect of offspring age, as reflected by nymphal stage, on predator success rates. Although wasps did not attempt to prey on nymphs in the first posthatching stage, they did prey on individuals at all subsequent stages until they attained the adult morphology.

Results of this study suggest that maternal defense does not benefit all offspring equally and simultaneously. In general, parental resources can be viewed as a continuum with respect to the proportion of current offspring that benefit from an act of parental investment, ranging from provision of a food item to a single offspring to alarm calls that warn the entire brood. Defense by female *U. crassicornis* falls between the two: it does reduce the overall success rate of wasp predators, but at any one time females can only effectively defend offspring in their immediate vicinity. Maternal defense in this species is thus a limited resource. Defense may be similarly limited in other species in which parents protect offspring, as when cichlids defend their fry from predatory fish (Keenleyside and Wisenden, 1995) or ducks defend their brood against gulls (Mendenhall and Milne, 1985).

How should a parent allocate defense within a brood when it cannot protect all offspring at the same time? One possibility is that the parent will always attempt to assess the point of greatest offspring need—for example, by continuously assessing the predator's current location and approaching it. Another possibility is that the parent will favor some offspring by remaining closer to them. These alternatives cannot be distinguished in this study of natural variation in predator success because predator position, offspring signaling behavior (see Cocroft, 1999b), and maternal position and orientation were changing continuously.

What are the consequences for sibling rivalry of this unequal distribution of predation risk? Hamilton (1971) predicted cover-seeking behavior among members of groups vulnerable to a predator that appears within the group and takes the closest individual. This selfish herd model was extended by Vine (1971) to the case of a predator that approaches from outside the group. Studies in a range of taxa have supported the assumption of increased predation on marginal individuals (reviewed in Krause, 1994), and in some cases have shown competitive behavior that gives some individuals access to safer, central positions (Rayor and Uetz, 1993). Other things being equal, competition for central locations might also be expected among individuals within aggregations of *U. crassicornis*. Even in the case of an aggregation of full siblings, competition for secure, central positions should occur. Such competition seems even more likely in broods with lower average relatedness, as when females mate more than once or when broods of more than one female merge into a single aggregation. I have not observed any obvious examples of competitive behavior (e.g., shoving) within nymphal aggregations, and a nymph probably is unable to displace another individual that is securely attached to the stem. Any rivalry is thus more likely to be a form of exploitation competition rather than interference competition; if all central positions are

occupied, an individual seeking a position will have no option but to leave the group or take an edge position.

Offspring in these groups might also be expected to compete for access to the mother's defense (Lazarus and Inglis, 1986). Nymphs use substrate-borne vibrational signals to elicit maternal protection, and these signals are therefore a potential means of competition for the female's proximity. One unusual feature of signaling in *U. crassicornis* offspring groups is that it is coordinated: a wave of signals begins at one point in the group and quickly spreads, with individual signals superimposing into a characteristic group display (Cocroft, 1996, 1999a,b). Furthermore, if multiple individuals signal, they must coordinate their signals to evoke the female's response (Cocroft, 1999a). This coordinated signaling thus contains an element of cooperation, in that maternal defense both benefits the group and requires collective action (see Dugatkin, 1997). However, there may be scope for competition if nymphs can, either by signaling or by withholding signals, influence the female's position within the aggregation. Field observations show that nymphs signal as long as a predator is present, suggesting that signals function to influence the mother's behavior throughout a predator encounter (Cocroft, 1999b).

The characteristics of maternal responses to signals will constrain the ways in which offspring can influence parental behavior. It is thus necessary to understand how female behavior is influenced by variation in signaling behavior within offspring aggregations. It is also necessary to characterize how signaling behavior in aggregations varies in response to predation risk. For example, is the direction of propagation of signals across the aggregation a reliable indicator of the predator's location? Can the mother detect this direction? Previous playback studies with nymphal aggregations have shown that nymphs will signal not only in response to perception of a predator, but also in response to signals from other individuals, even if those signals occur in the absence of a predator (Cocroft, 1999a). Are individuals in more vulnerable positions more likely to signal? Do offspring signal (or fail to signal) in ways that influence the mother's position within the aggregation? It is at least possible that this communication system is completely cooperative, in spite of the unequal distribution of risk. This could occur if predation pressure is sufficiently high and if cooperative communication within the group is important for reducing predator success. If so, selection among groups might oppose selection for selfish behavior within groups, especially where relatedness within groups is high (Sober and Wilson, 1998).

There was a suggestion of additional influences on risk within groups. The first was whether an offspring was stationary or moving. Because defending females move relatively slowly, a nymph's survival depends on its ability to hold onto the branch until the female arrives. Nymphs sometimes changed position during or after a visit by a predatory wasp. Changing position after an attack might be important because wasps can return to the same aggregation (Cocroft, 1998), and thus experience of one attack may indicate the likelihood of subsequent attacks. Changing position entails costs, however, because walking nymphs contacted by wasps were removed in one-third the time it took to remove stationary nymphs. A walking individual may not be as securely anchored to the stem as a stationary individual. A second component of vulnerability to predation was an individual's position along the long axis of the aggregation. Nymphs in the distal third of the aggregation (farthest from the base of the plant) were more likely to be removed, once contacted by a wasp, than nymphs in the rest of the aggregation. The reasons for this are unclear; it was not due to greater distance from the mother because this result was independent of mother-offspring dis-

tance. It is possible that larger or more competitive individuals were clustered in the areas of the aggregation nearer to the female's usual resting position, although no such pattern was obvious within aggregations.

How does defense by female *U. crassicornis* reduce the effectiveness of foraging wasps? Unlike some other subsocial insects that have biting mouthparts and raptorial forelegs (Bequaert, 1935; Kudo et al., 1992), *U. crassicornis* females appear unable to injure an attacking wasp. Instead, females respond to the approach of a wasp by buzzing their wings and by approaching and kicking a wasp that lands on the stem. Given the limitations of female defense, why should a wasp ever end a visit without removing a nymph? In this study, wasps ended about half of their visits without even contacting a nymph. It may be that females can increase the handling time of wasps beyond the point at which it is profitable to continue. For two wasps, attacks on tended aggregations were 4 and 11 times longer than attacks on untended aggregations. During visits to female-tended aggregations, wasps spend most of their time in hovering flight. If this activity is sufficiently energetically demanding, it may sometimes pay wasps to leave an aggregation, especially if untended or less well-defended aggregations may be found elsewhere. In areas with a large number of wasps, repeated visits to the same aggregations will still result in a substantial loss of brood. However, if the female can reduce the rate of loss, the extra time may be sufficient to allow a portion of the brood to reach an age at which they are no longer vulnerable. The wasps observed by Dowell and Johnson (1986) were apparently unable to prey on nymphs once they had reached the fourth or fifth stadium; in this study, wasp predation attempts on newly eclosed or mature adults were invariably unsuccessful (Cocroft, personal observation).

This study describes the behavior of one predator species at one locality. How relevant are these results likely to be for other locations and predator species? In addition to wasps, nymphs of *U. crassicornis* are preyed on by predatory Hemiptera, coccinellid beetles, spiders, neuropteran larvae, and syrphid fly larvae (Cocroft, unpublished data; McKamey and Deitz, 1996; Wood, 1974, 1976). Although the effectiveness of parental defense will vary with the species of predator (Kudo, 1996; Kudo and Ishibashi, 1996), defense by *U. crassicornis* females is likely to be important in reducing the effectiveness of many or most of these predators. For example, Wood (1976) observed predation by coccinellid beetles and predatory Hemiptera on eight first-instar aggregations where females were experimentally removed, and mortality in these aggregations was 100%. Although the role of predation was not documented in that mortality, female-tended aggregations had fewer predators in their vicinity and higher nymphal survivorship. Wood (1976) also observed maternal defense against a syrphid fly larva; however, at my Costa Rican study site, larvae of the syrphid *Ocyptamus phaeoptera* are active at night, when defending females are unable to respond effectively (Cocroft, unpublished data).

Increased risk of marginal individuals has not been examined with other predators of *U. crassicornis* nymphs. Predators that approach the aggregation by moving along the stem (which includes all those listed above, except perhaps wasps) are likely to encounter nymphs on the edges of aggregations. Edge-biased predation may thus be a common pattern for a range of predators. Furthermore, given that the mother must approach the predator to drive it away, the relationship between parent-offspring distance and predation risk may be general feature of maternal defense in this species.

Predation risk is unlikely to be the only important factor influencing choice of position within aggregations. A position in the group is also a feeding position, and it is currently unknown what, if any, differential benefits there may be to

feeding in central versus edge positions or in positions closer to the base versus the tip of the stem. Females continue to make feeding slits in the bark as offspring develop (Wood, 1974), with newer slits being made below the group (i.e., toward the base of the branch). The nutritional quality of these sites may vary depending on the time course of the plant's wound response and of scarring of older slits. There might be trade-offs between foraging and safety, as in some other animal groups (e.g., Petit and Bildstein, 1987; Rayor and Uetz, 1990; Romey, 1995). Information on feeding-site selection is thus needed before predictions can be made about how individuals can optimize their position within a group.

In summary, this study shows that, as in other animal social groups (Krause, 1994), the benefits of group living are unequally distributed among offspring in the maternally defended broods of *U. crassicornis*. Maternal defense in this species lies on a continuum between shared and unshared parental investment (Lazarus and Inglis, 1986). As a result, there is likely to be a complex interplay of cooperation and competition within broods, especially when offspring signal to elicit maternal protection. It also raises the question of how a parent should allocate defense when it cannot defend an entire brood at once.

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