

*Section of Neurobiology and Behavior, Cornell University, Ithaca*

**Parent–Offspring Communication in Response to Predators in a  
Subsocial Treehopper (Hemiptera: Membracidae: *Umbonia  
crassicornis*)**

Reginald B. Cocroft

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**Abstract**

The defense of offspring from predators is an important aspect of maternal care in the treehopper *Umbonia crassicornis*. Nymphal offspring develop in a dense cluster around a host plant stem, and laboratory studies show that they can solicit maternal defense using synchronized vibrational signals. Understanding the function of communication, however, requires not only an experimental investigation of the responses of receivers, but also a description of the context in which signaling takes place in nature. In this study I asked how offspring and parents signal in response to natural predators in the field. I filmed parent–offspring groups to record the behavior of *U. crassicornis* and their wasp predators (Hymenoptera: Vespidae: *Pseudopolybia compressa*), along with the substrate-borne vibrational signals produced within the group. I compared the signaling behavior of nymphs, and their mothers, in three contexts: when the family group was undisturbed, when a predatory wasp was present, and when the predator had departed. I assessed the importance of nymphal signals in recruiting the female's initial response by determining whether females or their offspring responded first to a predator's approach. The nymphs produced few synchronized signals when undisturbed, but increased their signaling rate 150-fold in the presence of a wasp. The nymphs continued to signal as long as the wasp was present, and in some cases after it had left, especially if the wasp had contacted or removed a nymph during the encounter. During a wasp's first approach, females responded before the offspring signaled in over half the encounters. Taken together, these results suggest that offspring signals function to influence the mother's behavior throughout a predator encounter, not just to alert her when the predator first appears. Defending females produced signals at a low rate throughout the day and did not significantly increase this rate when a wasp approached. Instead, females began signaling at a high rate only after a wasp had departed. Maternal signals may function to reduce nymphal dispersal after predation events, to reduce the costs of vigilance, or to modify nymphal signaling thresholds in the event of a re-encounter. Both offspring and their

mothers, then, signal in response to predators, but using different signals and at different stages of a predation event. In conjunction with experimental studies of signal function, these results show that communication is important in maternal defense of offspring in these subsocial insects.

R. B. Cocroft, Smithsonian Tropical Research Institute, Unit 0948, APO AA 34002-0948, USA. E-mail: rcocroft@hotmail.com

### Introduction

Predation can provide an important source of selection favoring group living (Hamilton 1971; Alexander 1974). Individuals in groups may benefit if a predator is more likely to take one of the other group members (Foster & Treherne 1981), or if groups are more effective in deterring predators (Henry 1972; Gottmark & Andersson 1984). Group-living individuals may also benefit if their combined vigilance results in earlier detection of predators (Hoogland & Sherman 1976; Bertram 1980; Fitzgibbon 1990). However, the potential benefits of enhanced detection will only be realized if individuals are aware that another group member has detected a predator (Curio 1978a). In some cases, detection of a predator is revealed to other group members indirectly by cues such as escape behavior (Kenward 1978; Treherne & Foster 1981; Lima 1994). In many group-living taxa, however, individuals reveal their detection of a predator by producing signals (Wilson 1975; Curio 1978a; Nault & Montgomery 1979; Klump & Shalter 1984).

Why should an individual that perceives a predator respond by signaling? A signaler might benefit indirectly, by reducing the predation risk for nearby relatives (Hamilton 1964; Maynard Smith 1965; West Eberhard 1975; Sherman 1977; Hoogland 1996). A signaler might also benefit directly. An individual that warns other group members might reduce its current predation risk, if coordinated antipredator behavior reduces the predator's chance of success (Owens & Goss-Custard 1976) or if the behavior of warned individuals redirects the predator's attention (Charnov & Krebs 1975). A signaler might also reduce its future predation risk, if by preventing the predator from making a capture it reduces the predator's likelihood of return (Trivers 1971). Alternatively, signals might warn mates or other group members whose survival benefits the signaler (Williams 1966; Witkin & Ficken 1979; Smith 1986; Alatalo & Helle 1990). Selection could also favor signaling to predators, if they are less likely to attack prey that advertise that they are alerted or in good condition and thus likely to escape (Hasson 1991; Caro 1994).

I have found that offspring in family groups of a subsocial insect communicate in response to predators (Cocroft 1996; 'subsociality' denotes parental care of posthatching offspring). In the treehopper *Umberonia crassicornis* (Hemiptera: Membracidae), family groups consist of a parent female and up to about 100 nymphs, which form a dense cluster around a host plant stem. The nymphs are preyed on by invertebrates, including vespids wasps, predatory Hemiptera, and syrphid fly larvae (Wood 1976, 1983; Dowell & Johnson 1986; Cocroft 1996, 1998). The female's active defense is the nymphs' main protection (Wood 1974, 1976, 1983;

Cocroft 1996, 1998), and disappearance of the female can result in greatly increased predation on the brood (Wood 1976; Dowell & Johnson 1986; Cocroft 1998). Studies in the laboratory show that, when threatened, a nymph produces a brief vibrational signal. Neighboring individuals signal immediately thereafter, and signaling rapidly sweeps through the group. As a result, individual signals combine to form a coordinated, ‘group’ signal. Series of group signals recruit the female’s antipredator behavior (Cocroft 1996).

Several features of communication in *U. crassicornis* families differ from those in other taxa in which antipredator signaling has been studied. First, although signals from offspring can recruit the mother’s antipredator behavior, the mother only responds if individual signals are coordinated to form synchronous, group signals (Cocroft 1996). Coordinated production of antipredator signals does occur in some eusocial insects (e.g. Seeley et al. 1982; see also Kirchner et al. 1994). However, there is more potential for competition within family groups of *U. crassicornis* than in eusocial insect colonies (Trivers 1974; Clutton-Brock 1991). For example, if nymphs within a brood can compete for access to maternal defense, signaling behavior may not be entirely cooperative (Lazarus & Inglis 1986). Second, results to date suggest that only the offspring signal when a predator approaches. In birds and mammals, the group members that produce antipredator signals include adults alone or both adults and juveniles (Curio 1978b; Owings & Virginia 1978; Klump & Shalter 1984; Cheney & Seyfarth 1990; Hoogland 1995). Finally, signals are transmitted in the form of substrate-borne vibrations that travel through the host plant stem (Cocroft 1996, 1998). Unlike the airborne signals of other taxa, the nymphs’ vibrational signals will go undetected by at least some of their major predators, which attack from the air (Dowell & Johnson 1986; Cocroft 1996).

Studies of organisms ranging from honeybees (Seeley 1995) to vervet monkeys (Cheney & Seyfarth 1990) make it clear that many aspects of communication can only be understood in light of observations made under natural conditions. The goal of this study was to describe the communication that takes place within *U. crassicornis* families in response to natural predation events in the field. In this case, observational results may be especially useful in refining the understanding of signal function based on experimental studies in the laboratory. One focus of the study was on the coordinated, group signals produced by nymphs. If nymphal signals do function in recruiting maternal defense, then signaling should be correlated with the presence of a predator. To assess the relationship of nymphal signaling to predation, I compared the rates of coordinated signaling by nymphs among undisturbed periods, predator encounters, and the periods after a predator had departed. Furthermore, if nymphal signals (rather than the female’s own perception of a predator) are important in causing the female’s initial response, then the female should begin to defend only after the nymphs begin signaling. To determine whether nymphal signals precede maternal defense, I examined the timing of responses when a predator approached. The second focus of the study was on signaling by parent females. Adult females can produce vibrational signals, which differ from those of nymphs (Cocroft, unpubl. data), but it is not clear how female signaling behavior is influenced by the presence of a predator. Accordingly,

I also compared rates of signaling by females before, during, and after predator encounters. Identifying how parents and offspring signal in response to predators, and at what stages of a predation event, is important for understanding the function of antipredator communication in these group-living animals.

### Methods

*Umboia crassicornis* can be found from Mexico through to northern South America, with introduced populations in southern Florida and the Caribbean (McKamey & Deitz 1996). Females deposit a clutch of  $\approx 100$  eggs near the apical meristem of a host plant branch (Wood 1974, 1983). Females typically spend the rest of their lives with this brood of offspring, remaining with them until they mature 6–8 wks later and then dying (Wood 1974, 1975, 1983). Nymphs complete their development to adulthood on the same stem on which the eggs were deposited.

This study was conducted from 18 Jul. to 13 Aug. 1996. The study site was at an elevation of  $\approx 700$  m on the Pacific slope of the Cordillera de Tilaran, Puntarenas, Costa Rica. *Umboia crassicornis* is common in the study area during the rainy season, depositing eggs on *Enterolobium cyclocarpum* and *Acacia centralis* saplings (Leguminosae: Mimosoideae) at the edge of clearings and along river banks. Family groups can be found near the tips of branches 1–3 m from the ground on host plants ranging from 2 to 4 m tall.

The most common predator of *U. crassicornis* at this study site is the vespid wasp *Pseudopolybia compressa* (Cocroft 1998; Masters, pers. comm.). Wasps approach from the air, then land on or near the family group and attempt to remove a nymph by biting it and pulling it from the branch (Cocroft 1998). All responses to predation reported in this study involved attacks by *P. compressa*.

Vibrational signals were recorded from aggregations (an 'aggregation' consists of a female and her clustered offspring) using small accelerometers (Knowles BU-1771; weight = 0.28 g) in combination with custom-built amplifiers. Each accelerometer was glued to a small metal clip that was attached to the plant stem 5–10 cm proximal to an aggregation, allowing for clear recordings of vibrational signals. This method of attaching the accelerometer slightly increased the mass loading of the substrate, but was preferred to adhesive attachment because it took less time (< 1 s) and caused minimal disturbance of the aggregation.

The output from the amplifier was routed to a Canon ES 2000 camcorder. Videotapes thus provided not only a record of the behavior of the treehoppers and their predators, but also a record of the vibrational signals produced within the aggregation. The camcorder was mounted on a tripod 1.5–2 m away from the focal aggregation, and observations were made from behind the tripod.

The aggregations observed contained 2nd to 4th instar nymphs. Signaling by 1st instar nymphs has never been observed, and the molt to the adult stage apparently occurs after the 4th stadium at San Luis (pers. obs.). Observations consisted of continuous monitoring of an aggregation for 2–6 h. I began filming when I observed the approach of a predatory wasp, which usually could be detected when it flew within 1–2 m of the aggregation. I continued filming for  $\approx 1$  min after the

wasp departed. I also filmed aggregations for 1 min every 30 min, to provide an estimate of baseline levels of signaling in undisturbed aggregations. Due to technical limitations, filming was limited to daylight hours (including dusk) that were free of rain or heavy wind.

The audio track from the videotapes was digitized at a rate of 22 kHz using a MacRecorder digitizer, SOUNDEDIT software (Farallon, Inc.) and a Macintosh IIsi computer. The signals of nymphs and tending females are distinct from each other and from background sounds. The signals were identified visually from the waveform trace and aurally from playback.

Because only coordinated, group signals are effective in recruiting maternal defense (Cocroft 1996), I focused on the production of these signals by nymphal aggregations. Coordinated signals are produced when signals of one or a few nymphs trigger immediate signaling by neighbors. For this study, a coordinated signal was scored if three or more nymphs signaled in synchrony (the number of individual signals can be distinguished when fewer than four or five nymphs signal together). The onset of coordinated nymphal signals and female signals was scored to the nearest 20 ms, and this record of signal production was used to calculate signaling rates in each context. The timing of predation events was obtained (to the nearest 250 ms) relative to the start of the audio/video recording by playing back the film and using a handheld stopwatch. The precision of measurement thus differed between the video record (predator presence) and the audio record (signals from treehoppers) of the same event, but the error introduced was small relative to the time scale of predator visits.

The signaling rates of the nymphs and their mothers were calculated for each recording for each aggregation. An average rate of signaling was then calculated in each context (baseline, predator present, postpredation) for each aggregation. Statistical comparison of signaling rates between contexts was performed using a Quade test, with a sample size equal to the number of aggregations (Conover 1980). This test is an extension of the Wilcoxon matched-pairs signed-rank test for  $n$  groups and allows for posthoc pairwise comparisons. For the analysis, I assumed that broad trends detected among contexts would not be affected by individual variation among wasps, which were all the same species.

To determine whether the nymphs or their mothers responded first to predatory wasps, I examined videotapes made during the wasp's initial approach. I considered the production of a coordinated signal (defined as above) as a response by the nymphs, and wingbuzzing or approach to the aggregation as a response by tending females. I scored whether the first coordinated nymphal signal occurred before the female's response, after the female's response, or at the same time (this assessment had a resolution of  $\approx 0.5$  s).

## Results

Audiovisual recordings were obtained for 13 *U. crassicornis* aggregations and 176 encounters with predatory wasps. Each nymphal aggregation was tended by a single adult female, and the average number of nymphs per aggregation was

$48.1 \pm 26.3$  at the start of observations (values are reported as  $\bar{x} \pm \text{SD}$ ). Aggregation sizes decreased as nymphs were removed by predators. All aggregations were on *E. cyclocarpum* saplings. Four host plants contained two aggregations each, separated by 1–2 m along the plant surface, and five contained a single aggregation each.

Aggregations were observed for an average of  $9.0 \pm 6.6$  h each, and the number of encounters filmed ranged from 2 to 32 (average =  $13.5 \pm 9.1$ ) per aggregation. Encounters lasted up to 7.5 min, with an average length of  $58.2 \pm 78.3$  s. An 'encounter' began when a wasp arrived within 20 cm of an aggregation, as judged from videotape. During an encounter, a wasp hovered near the aggregation, circling repeatedly and occasionally landing on or near the aggregation. An attacking wasp sometimes moved away from the aggregation for several seconds, then returned; for the purposes of this study, an encounter was considered to have ended at the time when the wasp moved more than 20 cm from the aggregation, if it then remained away for 30 s or more. Defending females moved toward and often on top of the nymphs, wingbuzzed, and kicked at the wasp. Details of female and wasp behavior are described in Cocroft (1998).

The nymphs and their mothers produced substrate-borne vibrational signals in response to predators. Representative signals of nymphs and adult females are shown in Figs 1 and 2. Sequences of signaling, starting when a predator first approached the aggregation, are depicted in Fig. 3 for predator encounters in three different aggregations.

Coordinated signaling by the nymphs was closely associated with the presence of a predator (Fig. 4a). When wasps were absent, the nymphs typically produced no group signals ( $0.15 \pm 0.37$  coordinated signals/min,  $n = 12$  aggregations). In the rare instances when the nymphs did produce coordinated signals, they produced only one or two and then stopped. After the arrival of a wasp, the nymphs began producing coordinated signals at an average rate of  $22.3 \pm 5.2$ /min, a 150-fold increase over baseline levels of signaling. The nymphs continued producing signals as long as the wasp was present at the aggregation (see Fig. 3). After the wasp left, the nymphs either stopped signaling or signaled at a lower rate ( $7.4 \pm 7.5$ /min). There were highly significant differences in signaling rate among contexts (Quade test:  $n = 12$  aggregations,  $t = 35.1$ ,  $p < 0.01$ ). Pairwise multiple comparisons revealed significant differences between the rates of signaling in each context ( $\alpha = 0.01$ , critical  $t = 51.0$  for pairwise comparisons: baseline vs. predation,  $t = 151.5$ ,  $p < 0.01$ ; baseline vs. postpredation,  $t = 69$ ,  $p < 0.01$ ; predation vs. postpredation,  $t = 82.5$ ,  $p < 0.01$ ). Almost all of the coordinated signals appeared to involve many individual nymphs; only 0.6% (26/4141) were produced by only three individuals (the minimum criterion for scoring).

Although undisturbed nymphs did not produce coordinated signals, they usually were not entirely silent. In 84% of baseline recordings, nymphs produced sporadic, individual signals (see Fig. 2a). The rate at which individual signals were produced was variable, ranging from 1 to over 60 signals/min/aggregation.

Physical contact with a wasp was not required for the nymphs to begin signaling. The nymphs produced coordinated signals not only in each of 119 cases

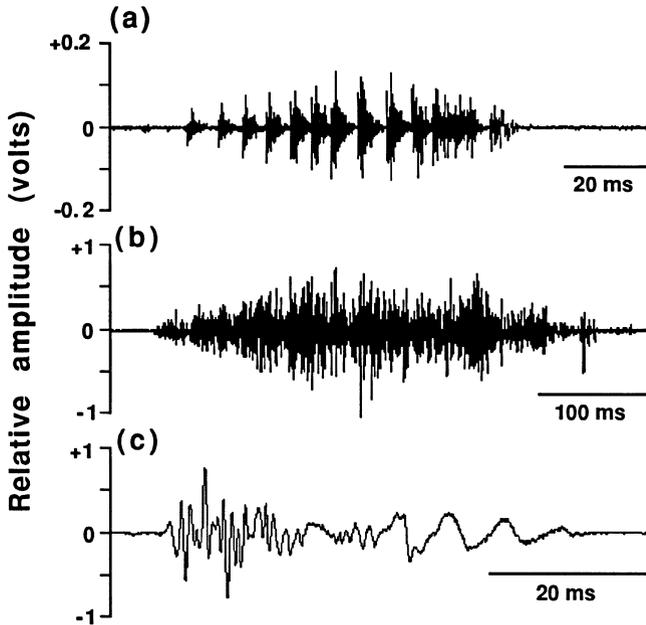
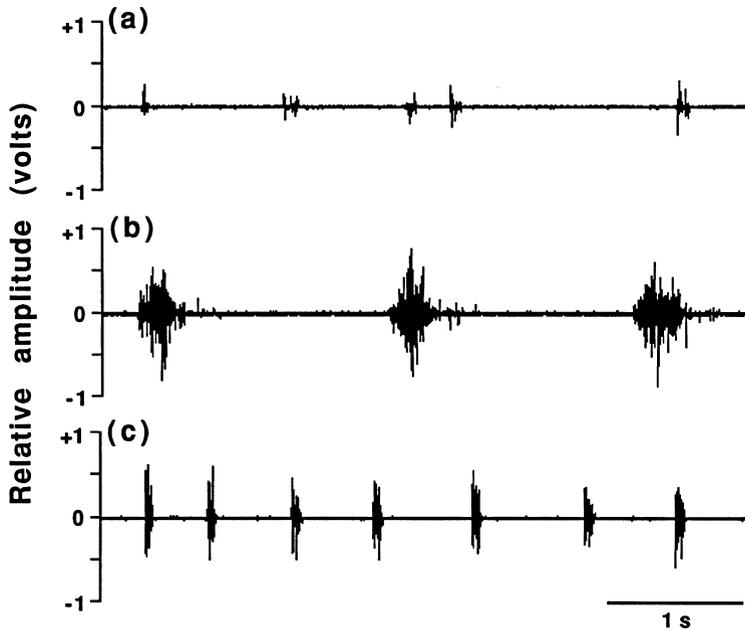


Fig. 1: Substrate-borne vibrational signals of nymphal and parent female *Umberia cras-sicornis*, recorded in the field with an accelerometer on the host plant stem. a. Signal of an individual nymph; b. group signal produced by an aggregation; c. signal from a tending female

in which the wasp contacted a nymph (100%), but also in 45 of 49 cases (91.8%) in which the wasp never contacted a nymph. Even during the encounters in which a wasp did contact a nymph, the nymphs began signaling when it flew near the aggregation, even though it often did not contact a nymph until it had been present for 20 s or more.

The extent to which the nymphs signaled after the departure of the wasp depended on the nature of the encounter. Rates of nymphal signaling were approx. three times higher after encounters in which the wasp had contacted or removed a nymph ( $9.34 \pm 3.97$  signals/min) than after those in which the wasp made no contact ( $3.16 \pm 3.98$  signals/min; Wilcoxon matched-pairs signed-rank test:  $z = 2.67$ ,  $n = 9$  families for which records were available for both kinds of encounter,  $p < 0.01$ ).

Maternal signals were associated with the presence of a wasp, but not in the same way as those of offspring (Fig. 4b). During baseline recordings, the mothers were silent or produced occasional signals, with an overall rate of  $3.3 \pm 3.5$  signals/min. The levels of signaling during wasp encounters were similar to those during baseline periods, with an overall rate of  $5.6 \pm 4.7$ /min. Immediately after the departure of a wasp, the mothers increased their signaling rate 15-fold over baseline levels ( $49.3 \pm 33.3$ /min). The mothers sometimes produced a short burst



*Fig. 2:* Vibrational signals of nymphs and tending females, recorded in three different contexts. a. Sporadic individual signals by nymphs during an undisturbed, baseline period; b. series of coordinated, group signals by nymphs in an aggregation being attacked by a wasp; c. series of signals from a tending female after the departure of a wasp

of signals during gaps when a wasp moved away for a few seconds, becoming silent again once it returned. There were significant differences among contexts (Quade test,  $t = 19.3$ ,  $n = 12$ ,  $p < 0.01$ ). Posthoc multiple comparisons revealed that the rate of signaling in the postpredation context was significantly higher than that during the other two contexts, but that rates of signaling did not differ between baseline periods and predation events ( $\alpha = 0.01$ , critical  $t = 63.8$  for pairwise comparisons; baseline vs. postpredation,  $t = 136.7$ ,  $p < 0.01$ ; predation vs. postpredation,  $t = 97.2$ ,  $p < 0.01$ ; baseline vs. predation,  $t = 39.5$ , not significant).

There was a nonsignificant trend for the rate of maternal signaling to be higher after attacks in which a nymph was contacted ( $n = 10$  females for which records were available for both kinds of attack;  $73.2 \pm 31.4$  signals/min) than after attacks in which no nymph was contacted ( $43.2 \pm 32.3$  signals/min; Wilcoxon matched-pairs signed-rank test:  $z = 1.78$ ,  $n = 10$ ,  $p = 0.07$ ).

Are offspring or their mother more likely to respond first to a wasp's approach? Initial responses could be scored for 78 wasp encounters in 13 aggregations. The mothers wingbuzzed and/or approached the aggregation before the nymphs produced signals in over half ( $56 \pm 33\%$ ) the encounters. The nymphs began signaling before the mother responded in just under a third ( $30 \pm 29\%$ ) of encoun-

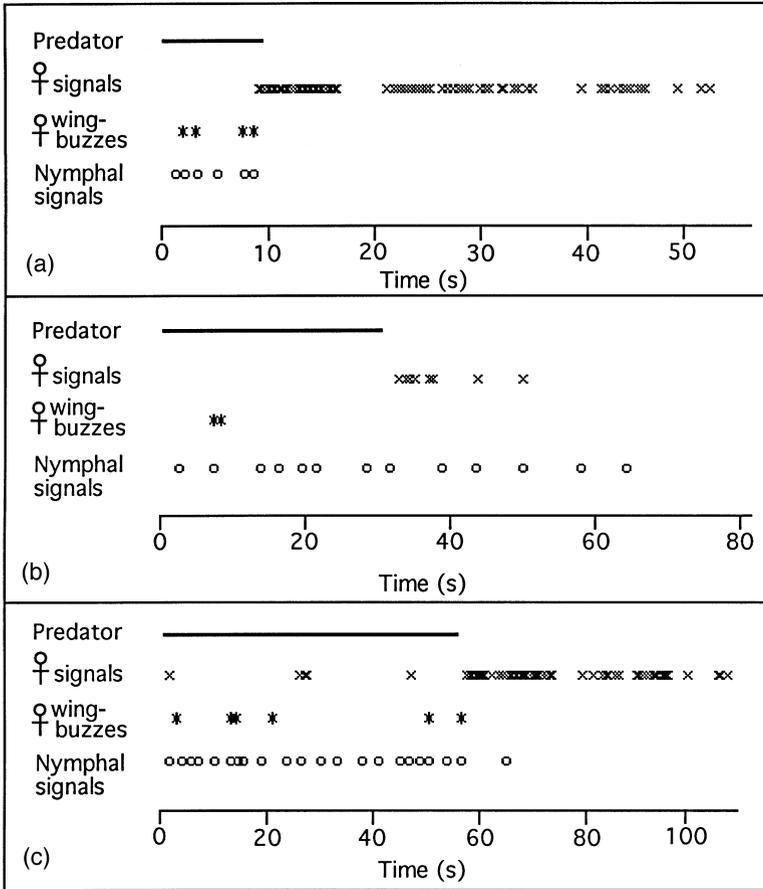


Fig. 3: Timing of signals by nymphs and tending females in three aggregations during encounters with predatory wasps. Also shown are wingbuzzes, a component of the female's defensive behavior. a. The wasp contacted a nymph lightly with its antennae; b. the wasp removed a nymph from the aggregation; c. the wasp made no contact with the nymphs. The predator's presence is indicated by a thick solid line; each × indicates one maternal signal; each \* one maternal wingbuzz; and each ○ one coordinated, group signal from the nymphal aggregation

ters. In the remaining encounters ( $14 \pm 19\%$ ), both nymphs and mothers responded at approximately the same time.

### Discussion

This study under natural conditions has uncovered a complex system of communication between offspring and parents in these subsocial insects. Both

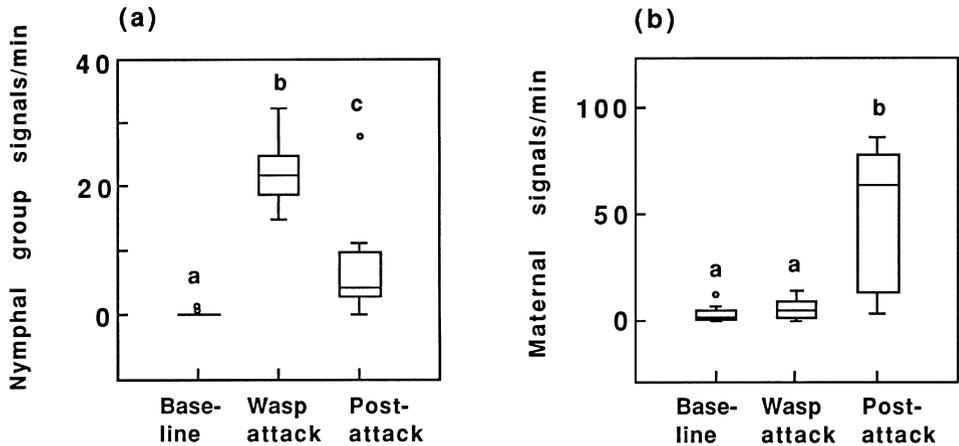


Fig. 4: Context dependence of a. nymphal group signals and b. maternal signals. Signaling rates are shown during baseline recordings of undisturbed aggregations, encounters with predatory wasps, and the periods immediately after the departure of a wasp. Different superscripts indicate significant differences ( $p < 0.01$ )

offspring and their mother signaled in response to predators, but using different signals and at different stages of a predator encounter.

The results of this field study are consistent with experimental laboratory studies showing that coordinated signaling by nymphs evokes maternal defense against predators. Laboratory playback experiments have demonstrated that coordinated signals alone, in the absence of nymphs, can elicit the mother's antipredator behavior (Cocroft 1996). In the field, the nymphs produced a series of coordinated, vibrational signals when approached by predatory wasps. And, as in the laboratory, nymphal signaling was associated with active defense by the mother (Cocroft 1998).

The signals of *U. crassicornis* nymphs may have multiple functions, as do the antipredator signals of other taxa (Greig-Smith 1980; Owings et al. 1986). Although laboratory studies showed that nymphal signals caused the mother to begin defending, this field study showed that the nymphs signaled as long as a wasp was present, not just when it first appeared. Furthermore, the mothers responded before or at the same time as the nymphs in 70% of wasp encounters. Any explanation of nymphal signaling behavior must, therefore, account for the observation that most signals are produced after the mother has already begun defending.

Why might offspring signal throughout a predator encounter? Signaling may be selected for in part because of limits on the female's ability to assess the predator's continued presence or current location. The nymphs form a cylindrical aggregation as they encircle the plant stem. A wasp that has landed behind the female or on the opposite side of the stem may be difficult for her to detect (vision is important in the parent female's defensive behavior; Wood 1976, 1983), but it will be directly perceived by some of the nymphs. Their signals might make it more

likely that the female will keep moving and encounter the wasp. Furthermore, if the individuals closest to the wasp initiate each wave of coordinated signaling, the resulting group signal may contain cues that would allow the female to localize the wasp to a given region of the aggregation. This ‘updating’ role of nymphal signaling might be even more important with predators such as pentatomid bugs that approach along the plant surface. With a walking predator, both its initial approach and its continued location might be more difficult for the female to detect than those of a wasp that orbits the stem in hovering flight, and whose wingbeats induce vibrations in the plant (pers. obs.).

How does an individual offspring benefit by signaling when a predator is present? To the extent that nymphal signals contribute to maternal defense, signaling will reduce a predator’s success. This benefit will be at least partially shared among offspring because the risk itself is distributed: wasps often contact several individuals in different parts of the aggregation before attempting to remove one (Dowell & Johnson 1986; Cocroft 1998). Even if it is not a current target, a nymph whose signals benefit others might reduce its future risk of predation. A group containing more individuals may provide better cover (Hamilton 1971) or a dilution effect (Foster & Treherne 1981), and a predator may be less likely to return after an unsuccessful visit (Trivers 1971). Nymphs may also gain indirect benefits through aiding relatives. Relatedness within nymphal aggregations in the field will vary. Aggregations will often consist of full siblings, because females usually mate only once (Masters 1997) and a host plant stem usually contains only a single aggregation (Cocroft, unpubl. data). However, aggregations may also contain a mixture of half and full siblings and even unrelated individuals, because females sometimes mate more than once (Wood & Dowell 1985; Masters 1997) and aggregations may contain offspring of two females that oviposit on the same branch (Masters 1997; Cocroft, unpubl. data). Although individuals in some taxa may benefit from signaling to the predator (Hasson 1991), these benefits can probably be ruled out in this case, because flying wasps will not perceive vibrational signals traveling through the plant stem. However, the possibility that nymphal signals influence the predator’s behavior cannot be excluded entirely, because the rocking movements associated with signaling could constitute a visual signal, and vibrational signals may be detected by predators that approach along the stem.

Because soliciting maternal protection yields shared benefits and requires collective action – mothers respond to offspring signals only when they are coordinated (Cocroft 1996) – synchronized signaling by nymphs represents a form of cooperation (sensu Dugatkin 1997). In particular, nymphal signaling seems a good candidate for a by-product mutualism (Mesterton-Gibbons & Dugatkin 1992). However, cooperation in these groups may have its limits. Neither maternal protection nor being in a group benefit all offspring equally (Cocroft 1998). There may thus be some scope for competition among offspring, perhaps mediated by signals, for access to maternal defense (Lazarus & Inglis 1986). Noncooperation could be manifested through a failure to signal by nymphs close to the mother, if increased signaling makes the mother more likely to move away (not all individuals signal during every coordinated wave [Cocroft, unpubl. data]). Alternatively, competition

could be manifested by producing signals, if the mother moves to areas in the aggregation containing a greater number of signalers. Evaluating these possibilities will require a more detailed characterization of female responses to signals, and of signaling behavior within aggregations.

The nymphs often continued signaling even after a wasp had departed. Signaling in this context was dependent on the nature of the encounter: the nymphs signaled at a higher rate when the wasp had contacted or removed a nymph during its visit. The function of this postpredation signaling is unclear. It may reflect uncertainty about the predator's continued presence: in this case, signaling would be favored if failing to signal when the predator is present is more costly than signaling when it is absent. A proximate explanation for increased signaling after encounters involving predator–nymph contact is suggested by the existence of chemical cues released from injured nymphs (Wood 1976). These cues can cause a female to behave as if a predator were present (Wood 1976). When *P. compressa* attack a nymph, they usually bite it with their mandibles, sometimes piercing or shearing off parts of the cuticle (Cocroft 1998). If nymphs can detect the chemical cues associated with injury, the presence of these cues after an attack might make nymphs more likely to signal.

Although undisturbed nymphs rarely produced coordinated signals, they produced sporadic, individual signals throughout the day. These signals were similar to those produced by individual nymphs in coordinated displays. It is thus the coordination of signals into group displays, rather than the production of signals per se, that is reliably associated with the presence of a predator. Although spontaneous signals may constitute a substantial fraction of the signals produced by an individual during its nymphal development, their lack of association with any obvious context makes their role in communication unclear. It is possible that they play no role in antipredator communication; they could, for example, provide a cue that triggers production of additional feeding slits by the mother.

Female *U. crassicornis* signaled in an unexpected context. Rather than signaling when a predator approached, the females began signaling at a high rate after the predator had departed. This behavior differs strikingly from antipredator signaling by parents in mammals and birds, which begin signaling when a predator is detected (Klump & Shalter 1984). The closest analog may be the 'jump-yip' call of black-tailed prairie dogs (Hoogland 1995), which is given after a predator leaves (and in other contexts). However, unlike the *U. crassicornis* females in this study, prairie dog adults do produce signals when a predator is detected (Hoogland 1995).

What role does the postpredation signaling of females play in the life of these subsocial insects? There is a range of possible explanations. For example, these signals may advertise the female's continued presence and thereby influence nymphal dispersal. Defense may be risky for females, as wasps foraging for nymphs frequently attack the female (Dowell & Johnson 1986; Cocroft 1998), and some wasps and other predators are capable of preying on adults (Wood 1983; Dowell & Johnson 1986). Because a nymph's probability of surviving a predator attack is dramatically increased by the female's defense (Wood 1974, 1983; Dowell & John-

son 1986; Cocroft 1998), her absence will lower the benefit of being in a conspicuous group and may encourage dispersal. Nymphs do disperse from the aggregation under some conditions, including loss of the female (Wood 1974). Because most of the nymphs in these elongated, cylindrical aggregations probably cannot see the tending female, vibrational signals may be the best means for a female to advertise her presence. At least one other female signal influences nymphal dispersal: when a nymph attempts to walk past the female and out of the aggregation, she uses a tactile signal that causes the nymph to turn around and return to the aggregation (Wood 1974). If nymphs do use the female's vibrational signals to assess her continued presence, this might also explain why females signal at a low rate throughout the day. Another hypothesis for the function of these signals is that they maintain nymphal vigilance, given that a predatory wasp is likely to return to the same aggregation (Cocroft 1998). Alternatively, if there is a cost to vigilance (such as a reduced feeding rate), female signals after the predator has departed could function to decrease nymphal vigilance. Female signals could also facilitate learning by 'labeling' a dangerous predator (as occurs with alarm substance in fish; Chivers & Smith 1994), thereby lowering the nymphs' signaling threshold when they next perceive cues associated with that predator.

Studies of *U. crassicornis* (Cocroft 1996, 1999; this study) provide the first documentation of the role of vibrational signaling in parental care in the Hemiptera, a group in which vibrational mating signals of adults are widespread (Claridge 1985; Henry 1994; Hunt 1994). Parental care is also widespread in the Hemiptera (Tallamy & Schaefer 1997), and parent–offspring communication might prove to be common as well. For example, Keys (1914) described parent–offspring interactions in an aepophilid bug in which tactile signals from the mother, induced by disturbance, appeared to cause nymphs to disperse to a more protected location. The role of vibrational communication between parents and offspring has been little explored in other subsocial insects. The best-known examples are from silphid (Huerta et al. 1992) and passalid beetles (Alexander et al. 1963; Schuster 1983). Signaling in silphids may be involved in parent–offspring interactions (Huerta et al. 1992). Larval passalids possess stridulatory structures that have been hypothesized to function in soliciting food from adults (Schuster & Schuster 1997), and signals of adults may function in avoiding predators (Buchler et al. 1981).

This study shows that communication between parents and offspring is an important feature of maternal care in *U. crassicornis*. The dynamics of communication in these family groups are unexpected, both in the coordination of offspring signals into synchronized displays and in the enigmatic postpredation signaling of mothers. Further investigation is likely to reveal additional complexity, including variation in the signals produced by females and nymphs and an interplay between chemical and vibrational signals. Understanding how signals mediate cooperation and conflict within a brood will require a more detailed characterization of the signaling behavior of individuals during the production of coordinated displays, and of how variation in coordinated displays affects the behavior of defending females.

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