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Collective signals in treehopper broods provide predator localization cues to the defending mother

Karthik Ramaswamy*, Reginald B. Cocroft

Division of Biological Sciences, University of Missouri

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Many animal groups respond collectively to environmental cues. To understand the function of collective behaviour, an important first step is to establish how it varies in response to differences in the relevant cues. Because collective action arises from individual decisions, this in turn requires characterizing the behaviour of individual group members. In the treehopper *Umberia crassicornis*, offspring live in cylindrical aggregations along a host plant stem. In the presence of a predator, offspring produce synchronized vibrational signals that elicit maternal defence. Predators typically attack the ends of the aggregation; because the mother must approach the predator to defend her offspring, we hypothesized that variation in collective signals reveals not only the predator's presence, but also its location. The defending mother also produces signals, and we hypothesized that maternal cues influence the signalling behaviour of the brood. We simulated predation at either end of the aggregation. In the presence of the mother, (1) offspring closer to the predator were more likely to signal and (2) more offspring contributed to the group signals when the predator attacked the aggregation at the far end from the mother. Differences in group signals, emerging from position-dependent differences in signalling probability of individual offspring, could be used by the defending mother to determine the end of the aggregation being attacked. A loss of these signalling patterns in the absence of the mother reveals that maternal cues are necessary for the establishment of a reliable relationship between collective signalling and predator location.

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Biological systems comprise numerous subunits that coordinate their activities to perform group-level functions (Camazine et al. 2001; Seeley 2002). The subunits that constitute a hierarchical system can be the genes within a genome, the cells within an organism, or the organisms within a society. The hallmark of these systems is the remarkable coordination achieved among the members of the group. Examples of coordinated behaviour in animal societies include house hunting by honeybees (Seeley & Morse 1978), raiding by swarms of army ants (Franks 1989), aggregation and manoeuvring by fish schools (Partridge 1982; Hemelrijk & Kunz 2004) and synchronized flashing by fireflies (Buck & Buck 1976).

Collective behaviour often arises in a decentralized manner (Seeley 2002); that is, individuals experience a stimulus and make decisions in the absence of a global perspective (Camazine et al. 2001). A key property of decentralized collective behaviour is the sensitivity of emergent patterns to changes in the environment (Camazine et al. 2001; Sumpter 2006). Small differences in

environmental parameters can often bring about a large change in global pattern. For example, Hoare et al. (2004) showed that variation in predation risk results in differences in the size of fish schools. In army ants, different foraging environments yield contrasting foraging patterns in species sharing the same underlying set of behavioural rules (Deneubourg et al. 1989). It is thus important to identify context-dependent changes in individual behaviour that yield different group-level responses.

Here we examine the relationship between context-dependent individual behaviour and variation in the collective antipredator signals of a group-living insect. In the treehopper *Umberia crassicornis* (Hemiptera: Membracidae), collective vibrational signalling by offspring alerts the defending mother to the presence of a predator (Cocroft 1996). Because the mother must locate and approach the predator to defend the brood, we hypothesized that collective signals provide information about the location of a predator attack. Offspring live in cylindrical groups around their host plant stems, and predators attack the ends of these groups (Cocroft 2002). Information about which end is being attacked could be provided through a gradient of increased signalling with proximity to the predator, or through an overall difference in signalling level depending on predator location. Furthermore, because offspring behaviour may be influenced by maternal cues during

* Correspondence: K. Ramaswamy, Biology Department, 211 Olin, Augustana College, Rock Island, IL 61201, U.S.A.

E-mail address: karthikramaswamy@augustana.edu (K. Ramaswamy).

a predator attack (Cocroft 1999b), we hypothesized that properties of the collective signal would differ depending on whether the mother was present or absent. We tested these hypotheses by simulating predation on broods and quantifying the signalling behaviour of individual offspring.

METHODS

Study System

Juveniles (nymphs) of *Umbonia crassicornis* develop in a cylindrical aggregation along a stem of their host plant (Wood 1975, 1983, 1985; Cocroft 1999a; Fig. 1); hosts are woody plants in the Mimosaceae, ranging from small shrubs to canopy emergents. The mother sits below the aggregation, which typically extends for 10–15 cm along the stem. Female *U. crassicornis* do not leave the aggregation. Nymphs are subject to intense predation in their exposed locations on plant stems (Cocroft 1996, 2002).

Nymphal *U. crassicornis* are preyed on by a range of invertebrates including vespid wasps, syrphid fly larvae, predatory Hemiptera, coccinellid beetles and neuropteran larvae (Wood 1976, 1983; Dowell & Johnson 1986; McKamey & Deitz 1996; Cocroft 2002, personal observation). The defending female is approximately 1 cm long, while predators range from 0.5 cm to over 1 cm. Flying predators, and probably walking predators, almost always attack the ends of the aggregation (Cocroft 2002).

In response to a predator attack, nymphs produce synchronized vibrational signals that elicit maternal protection (Cocroft 1996). Each individual nymph signal lasts for about 30–40 ms, and consists of a series of pulses (Fig. 2). Nymphal signals have an unusual amount of high-frequency energy, extending to 5 kHz or more (Cocroft 1999a), unlike many insect vibrational signals, for which most of the energy is in the range of a few hundred Hz (Virant-Doberlet & Cokl 2004). This broadband signal is probably produced by a tymbal mechanism (Ossiannilsson 1949). Nymphal (and female) signals produce no detectable airborne sound, and appear to be transmitted entirely through vibration of the host plant stem. Signalling by the one to three individuals closest to the predator elicits signalling from neighbours, leading to a composite group signal that spreads from the source and lasts for 300–600 ms (Fig. 2; Cocroft 1999a). When disturbed, aggregations produce a group signal every 2–3 s (Cocroft 1999a; Fig. 2). Each nymph

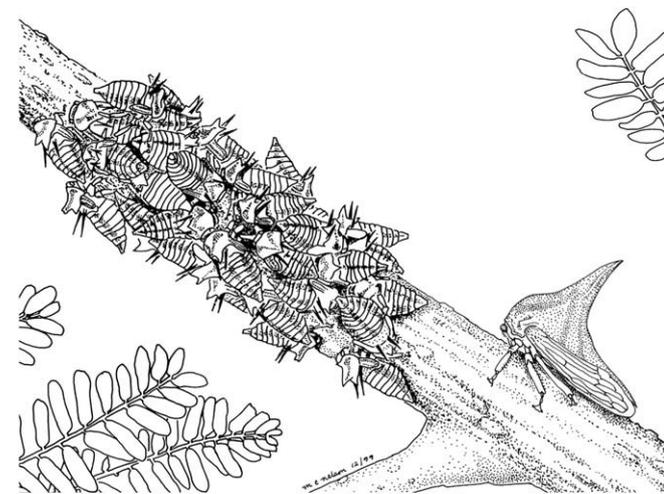


Figure 1. *Umbonia crassicornis* mother below an aggregation of her fourth-instar nymphs (illustration by M. Nelson). Aggregations can extend up to 10 or more of the mother's body lengths away from her.

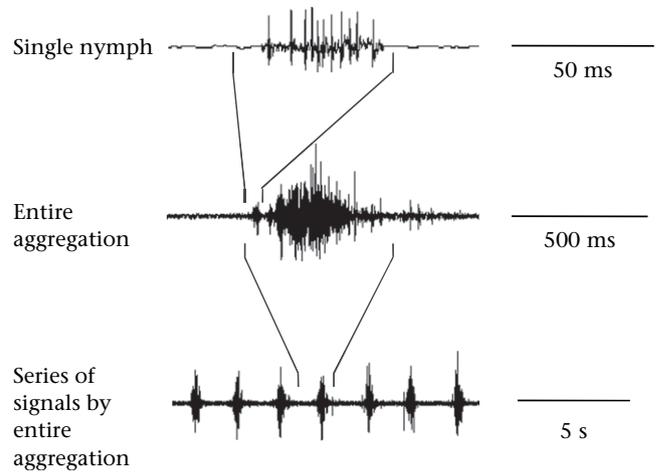


Figure 2. Individual nymph signal and group signals (modified from Cocroft 1999a).

signals only once during a given group signal (Cocroft 1996). Group signals can be detected with an accelerometer up to 1.5 m from the aggregation, depending on host plant structure (R. B. Cocroft, personal observation). However, parent–offspring signalling occurs over much shorter distances, typically less than 15 cm.

Maternal response to offspring signals includes approaching the predator, wing buzzing and kicking at the predator (Wood 1974, 1975, 1983; Brach 1975; Cocroft 2002). All of these defences function at very close range, so the mother must approach to within a few millimetres of the predator. The defending mother also produces her own signals, particularly after the predator departs. Although the function of these signals is not known, their production is correlated with a decrease in nymph signalling (Cocroft 1999b), and preliminary data (J. A. Hamel & R. B. Cocroft, unpublished data) suggest that they increase the nymphs' signalling threshold.

Umbonia crassicornis individuals (late-instar nymphs or teneral adults) were collected in and around Miami, Florida, U.S.A., and used to establish a greenhouse population on potted host plants (Mimosaceae: *Albizia julibrissin*) at the University of Missouri-Columbia in Missouri, U.S.A. The treehoppers were maintained at 20–30 °C on a 12:12 h light:dark cycle. Potted plants 1–1.5 m tall with single-family aggregations were brought to the laboratory 24–48 h before the experiments began.

Individual Signalling Behaviour and Predator Location

If the collective signals of nymphs provide information about predator location, then the signalling behaviour of individuals within the group must differ depending on the location of predator attack. We evaluated two potential mechanisms through which differences in individual behaviour could provide information about the location of an attack.

(1) Signalling probability varies with proximity to the predator

When a predator attacks an *U. crassicornis* aggregation, it attempts to remove a specific individual, and the other nymphs experience the disturbance of the attack in varying degrees. Consequently, the proximity of a nymph to the predator influences the cues that it perceives during an attack, and this variation may influence the individual's probability of producing a signal. The variation in individual signalling probability with distance from the predator may take two forms. As signalling propagates through the group, individuals further from the source may be less likely to

signal. Alternatively, the signals of the few individuals close to the predator may be amplified as the wave of signalling progresses, so that individuals further from the source are more likely to signal.

(2) *The total amount of signalling varies with attack location*

Because the defending mother is typically stationed at the end of the group closest to the base of the stem, there is an inherent asymmetry in predation risk within groups. The best-studied *Umbonia* predator (a vespid wasp) is equally likely to attack either end; but because females must intercept the predator to defend their brood, individuals at the far end of the group are at greater risk (Cocroft 2002). Consequently, since the average risk is higher, we would expect more individuals to participate in group signals when the predator is at the far end of the group.

Maternal Cues and Offspring Signalling Behaviour

If feedback from the mother influences offspring signalling, then either the spatial pattern of signalling or the overall level of signalling may be altered when the mother is absent. Because maternal signals are correlated with a decrease in nymph signalling (Cocroft 1999b), we expected more individuals to participate in group signals in the absence of the mother.

Rationale

If offspring signals provide cues of predator location, how might this make maternal defence more effective? Maternal defence in *U. crassicornis* functions at extremely close range, because females need to contact the predator with kicking legs or buzzing wings in order to drive it away (Cocroft 2002). In undisturbed aggregations in the field, the mother is nearly always found at the base of the aggregation (i.e. nearer the base of the plant). Once alerted to the presence of a predator by offspring signals, the mother walks into the aggregation, locates the predator, and approaches it (Cocroft 2002). The mother's approach to a predator is relatively slow, both because her walking speed is low (~ 2.5 s to travel 1 cm) and because (in the absence of visual cues) her movement is episodic: she walks a short distance after each offspring group signal, then stops until after the next group signal (Cocroft 2002). Some predators, such as large vespid wasps, may be visible to the female even after they have landed on the stem and attacked a nymph; however, even these may not be visible if they land on the opposite side of the stem from the female. Other predators, such as pentatomid bugs, will not be visible to the female if they approach from the far end of the aggregation, or from the base of the stem but on the opposite side of the stem from the female. The female does not appear to detect these walking predators visually from more than a few centimetres away, particularly if there are nymphs between the female and the predator (R. B. Cocroft, personal observation). A nymph's chances of survival, once attacked by a predator, are much higher if the female can intercept the predator. If attacks were concentrated at the far end of the aggregation, rapid female movement to the far end would be an effective strategy, in the absence of localization cues; however, in a field study of over 500 attacks by predatory wasps, the two ends of the group were equally likely to be attacked (Cocroft 2002). Information about predator location is thus important for defence, and in many cases only the nymphs closest to the predator have direct information about its location.

Experimental Design

We simulated predation to elicit signalling. Nymphs will signal when they experience a gentle mechanical disturbance (Cocroft 1999a). A handheld, soft-bristled watercolour brush (referred to

henceforth as the 'predator') was used as a simulated predator to contact a nymph, as in Cocroft (1999a), at one end of the aggregation every 2–3 s. The defending female does not respond to low-amplitude vibrations produced by brush contact: the same brush motion elicits no maternal defence if the brush contacts the stem near the aggregation (Cocroft 1999a). The end closer to the base of the branch (and below which the mother is found) is here referred to as the bottom end of the aggregation, and the opposite end as the top end of the aggregation. To ensure that stimulation by the simulated predator was consistent within and between treatments, a single nymph on the edge of the aggregation was contacted with the brush throughout a treatment. The brush was withdrawn approximately 20 cm from the stem between successive contacts. A contacted nymph will consistently produce a signal, which can (although does not always) initiate a wave of signalling throughout the group. In the field, encounters with predatory wasps last about 1 min (mean = 51.6 ± 74.2 s; range 20 s–7.50 min) (Cocroft 2002); each predation treatment in our experiment lasted for 2 min.

Each individual signals only once during a group signal. Accordingly, an individual's signalling probability for a given treatment was measured as the number of times that it signalled during the 2 min stimulus period, divided by the total number of brush strokes. Because the interval between the brush strokes was equivalent to that between group signals produced in response to a predator (Cocroft 1999a), virtually all collective signals were initiated by a brush stroke. Both treatments, predation at the top and bottom ends, were repeated in the presence and absence of the mother, so each family experienced four treatments. The experiments were performed between October 2001 and July 2002. All experiments were conducted at 24 ± 2 °C.

The experiment was replicated over 12 families. The mean (\pm SD) number of nymphs per aggregation was 41.92 ± 20.16 , with nymphal aggregation lengths of 8.0 ± 2.57 cm (range 4–12 cm). Each family received the four treatments over a 2-day period. On each day, a family received either the mother-present or mother-absent treatments. For the mother-absent treatments, the mother was removed from her aggregation 1 h before the start, placed on another plant, and reunited with her family after the second treatment on the same day. A minimum interval of 3 h occurred between treatments (predation at the top end and predation at the bottom end) on each day. The order of mother-presence/absence treatments was alternated between families, and the order of top/bottom treatments was alternated within the mother-presence/absence treatments. Twelve families experienced predation in the absence of the mother and 11 families in the presence of the mother (one female died during the experiment). Plant-to-plant variation in the transmission properties of the stem will result in differences in the amplitude and frequency characteristics of vibrational signals at a distance from the source (Michelsen et al. 1982; Cokl & Virant-Doberlet 2003; McNett & Cocroft 2008). For a given family, both treatments occurred on the same stem, but this host plant effect may introduce variation in the responses of different families.

The behaviour of the nymphs and the defending mother was recorded using a digital video-camera recorder (Sony DCR-TRV830). The video sequences were digitized using a Macintosh G4 computer and analysed with Final Cut Pro 2 (Apple Inc., Cupertino, CA, U.S.A.). A Knowles BU 1771 accelerometer (Knowles Acoustics, Itasca, IL, U.S.A.), attached to the plant using wax, was used to record vibrational signals. The accelerometer was connected to the digital video-camera recorder through a custom-made amplifier. During video analysis, the number of times that each nymph signalled in response to the brush strokes during the course of a treatment was counted. Each nymph signal is accompanied by a distinct rocking movement of the body (Cocroft 1999b), and this rocking behaviour provides an easily scored, highly repeatable

assay for vibrational signals produced by nymphs. The number of signals produced by each nymph was counted from the video-recordings for each treatment for the 12 families.

The distance of each nymph from the predator was obtained from still images captured at the start of each treatment and calibrated using measurements of total aggregation length. Only one side of the cylindrical aggregation could be captured by the video and only these nymphs were used for the analysis. We positioned the plant such that most nymphs were visible to the camera.

Statistical Analysis

Signalling probability was arcsine transformed for the analysis (Sokal & Rohlf 1969). To avoid issues arising from pooling data from families with different numbers of nymphs, we divided the distance measures into distance bins (width = 1.5 cm) for each family and averaged the signalling probability within each bin for each family.

We performed a multiple regression analysis to assess the relationships between (1) signalling probability and proximity to the predator, (2) the total amount of signalling and attack location and (3) signalling probability and maternal presence/absence. The response variable was the mean signalling probability at each distance bin and the predictor variables were position of the predator (top or bottom), distance from the predator and presence/absence of the mother. Family was treated as a block. Signalling probabilities are presented as means \pm SE.

RESULTS

Summary

The signalling behaviour of nymphs varied with the location of a simulated predator attack, such that group signals provided two potential cues of predator location. These cues were largely lost, however, when the mother was absent.

Individual Signalling Behaviour and Predator Location

When the mother was present, there was a reliable signalling gradient whose slope was correlated with the location of the simulated predator attack. The closer a nymph was to the site of the attack, the more likely it was to signal (Fig. 3a, Table 1). This gradient was steeper when the attack occurred at the top end of the aggregation (further from the female's resting location), in part because many more nymphs initiated signalling at that attack location (Fig. 3a). Note: a second analysis was conducted that compared the signalling probability in the proximal, medial and distal third of each aggregation (effectively normalizing them to the same size) with similar results.

When the mother was present, the overall level of offspring signalling was also correlated with the location of the simulated attack (Fig. 4a, Table 1). On average, nymphs were about twice as likely to signal when the attack occurred at the top end of the aggregation. This difference arose largely from the behaviour of nymphs at the top end, which were more likely to initiate signalling at the onset of an attack than were nymphs at the bottom end (Fig. 3a). The average signalling probability for an aggregation was not correlated with aggregation length or with the number of nymphs it contained ($r^2 < 0.02$, $P > 0.7$ for both variables).

Maternal Defensive Behaviour and Predator Location

Defending mothers responded to the combination of offspring signalling and simulated predator by walking into the aggregation.

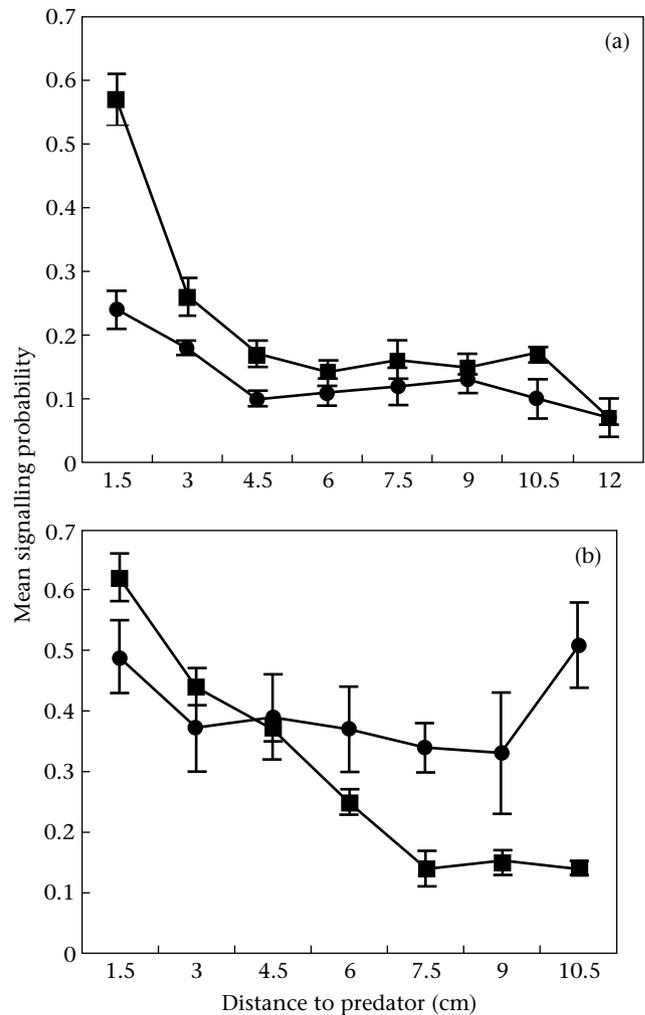


Figure 3. Effect of distance to predator on nymph signalling probability (a) in the presence of the mother and (b) in the absence of the mother. Solid square: predator attacked from the top end of the nymph aggregation; Solid circle: predator attacked from the bottom end of the nymph aggregation.

Mothers approached and kicked at and/or wingbuzzed near the brush when it made contact with a nymph. This close-range maternal defence occurred in both treatments, indicating that some combination of visual and vibrational cues was sufficient to allow the mother to locate the predator.

Table 1

Effect of attack location, distance to predator, mother's presence and their interactions on nymph signalling probability (multiple regression)

Source	df	SS	MS	F	P
Mother presence	1	3.89	3.89	7.10	0.0001
Distance to predator	6	2.99	0.50	10.00	0.0001
Location of predator attack	1	0.71	0.71	14.33	0.0002
Location of predator attack*distance to predator	6	1.02	0.17	3.40	0.0033
Mother presence*distance to predator	6	0.16	0.03	0.52	0.7921
Mother presence*location of predator attack	1	0.08	0.08	1.68	0.1969
Mother presence*distance to predator*location of predator attack	6	0.37	0.06	1.24	0.2870
Family	11	3.89	0.35	7.10	0.0001
Error	191	9.50	0.05	-	-
Total	229	22.61	-	-	-

Values in bold denote a significant effect.

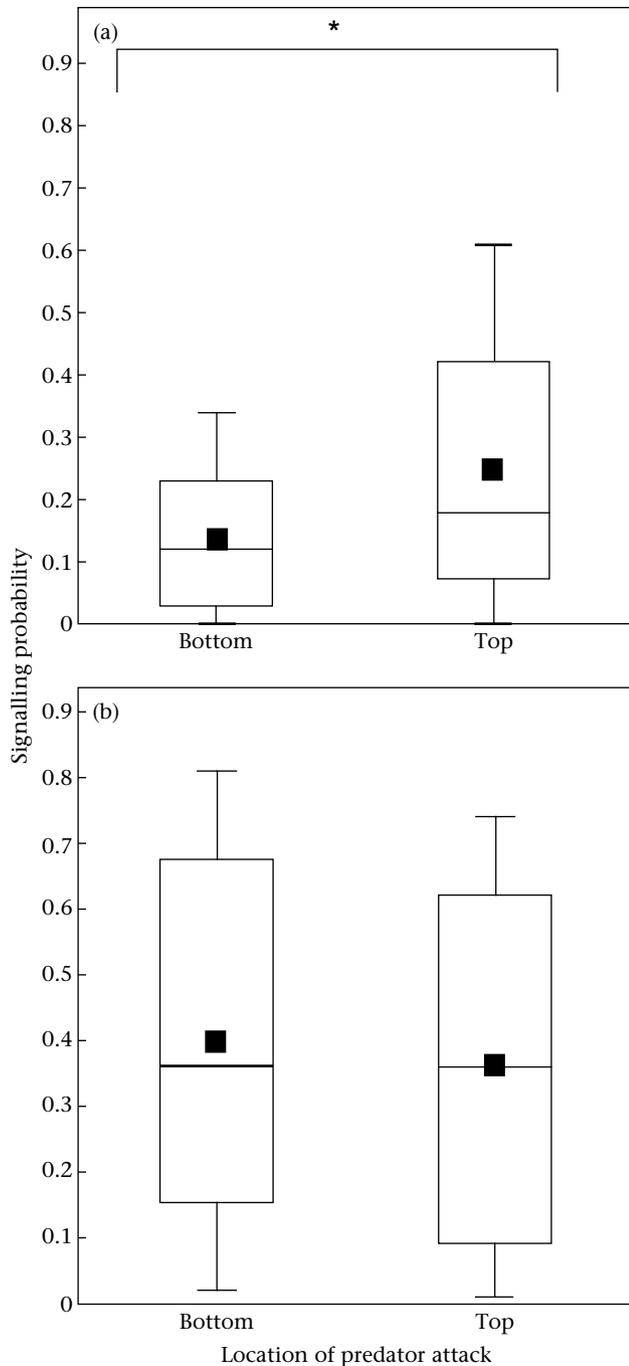


Figure 4. Effect of predator attack location (top or bottom end of the nymph aggregation) on overall signalling probability (a) in the presence of the mother and (b) in the absence of the mother. Box plots indicate median (horizontal line), mean (solid square), second and third quartiles (box ends) and range (whiskers).

Maternal Cues and Offspring Signalling Behaviour

The presence of the mother influenced offspring signalling behaviour: in her absence, significantly more individuals participated in a given group display (Fig. 5, Table 1).

Maternal cues also influenced the relationship between offspring signalling behaviour and predator location. The relationship between a nymph's proximity to the predator and its likelihood of signalling was lost when the attack occurred at the bottom end of the aggregation, although it was retained when the attack

occurred at the top end (Fig. 3b). Although this difference was not reflected in a significant three-way interaction between female presence, attack location and distance of a nymph to the predator (Table 1), there was no longer a consistent signalling gradient that indicated the predator's location.

In the absence of the mother, there was no significant difference in the total amount of signalling between top and bottom attack locations (Fig. 4b).

DISCUSSION

To understand the functional significance of collective behaviour, it is important to know how it varies in response to differences in the relevant cues. And because collective behaviour arises from individual decisions, a focus on the behaviour of individual group members is essential. Here we found that the individual signalling decisions of *U. crassicornis* nymphs are dependent on the location of both the individual and the predator. The resulting group-level patterns contain information about the location of the predator attack. This information may be important in antipredator defence, because the mother must localize and approach the predator in order to defend the brood.

Nymphs closer to the predator are more likely to signal than the nymphs further away, creating a gradient in signalling probability within the aggregation. The nymphs that initiate signalling have direct cues associated with the predator, while other nymphs receive indirect cues, which apparently decay as the signal spreads through the aggregation. Asymmetry in information possession resulting in variation among members of a group is a feature of many group-level behaviours (Beshers & Fewell 2001; Seeley 2002). For animals moving in groups, Couzin et al. (2005) showed that only a small proportion of informed individuals are required to make accurate group decisions. But what cues do nymphs have when they do not perceive the predator? In addition to direct perception of the predator, two sources of input from other

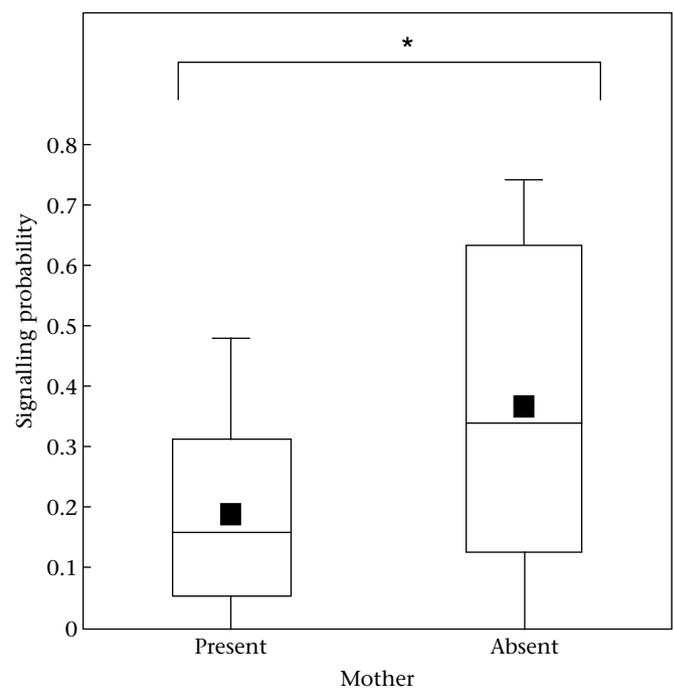


Figure 5. Effect of the mother's presence on the average nymph signalling probability. Box plots indicate median (horizontal line), mean (solid square), second and third quartiles (box ends) and range (whiskers).

members of the brood are likely. First, nymphs have access to the vibrational signals produced by other nymphs, and these alone can evoke signalling (Cocroft 1999a). Second, the production of a vibrational signal is accompanied by a conspicuous rocking movement of the nymph's body (Cocroft 1999a), and this movement may provide visual and/or tactile cues to neighbouring individuals.

Nymphs were more likely to signal when the predator attacked the end of the aggregation that was furthest from the resting female. Although nymphs closer to the predator were more likely to signal regardless of which end of the aggregation was attacked, more individuals initiated signalling when the predator attacked the top end, which was further from the female's pre-attack position. Why would nymphs at the top end of the aggregation have a lower threshold for initiating a group signal? At a proximate level, this decrease in threshold could be due to a relative lack of maternal cues, since these nymphs are furthest from the female. There may also be inherent differences between nymphs in different parts of the aggregation, as suggested by the observation that nymphs on the far end, once attacked, are more quickly removed from the stem by a predator (Cocroft 2002). Such differences in the nymphs' ability to resist a predator attack could arise if there are differences in nutritional resources at the two ends of the aggregation, and/or if there is competition for locations closer to the mother. At an ultimate level, it may be advantageous for nymphs at the far end of the aggregation to have a lower signalling threshold. The mother may be less likely to detect a predator approaching the far side of the aggregation, increasing the importance of antipredator signalling. If distance-dependent attenuation renders the vibrational signals of nymphs further from the female less detectable, a greater number of initiating signals may result in more reliable detection by the female. This could happen because they superimpose to produce a higher-amplitude signal and/or because, given the gradual attrition of signalling with distance, they increase the chances that a group display will include individuals closer to the female. Finally, early detection may be especially critical for preventing predation on individuals at the far end from the female; females move relatively slowly, and delay increases the likelihood that the predator will remove the nymph before the female arrives (Cocroft 2002).

The difference in signalling thresholds between the two ends of the aggregation generates a second potential cue of predator location, since the total amount of offspring signalling is higher when the predator attacks the far end. The presence of a response threshold in the probability of performing a behaviour is an important individual characteristic that can determine the form of a collective behaviour. For instance, differences in response thresholds in workers of social insects is associated with division of labour in insect societies (Beshers & Fewell 2001).

In *U. crassicornis* families, different group-level patterns in response to different environmental conditions will only have functional significance if the mother actually responds differently to signals produced under the two conditions. In our experiment, mothers approached and made contact with the simulated predator, in both attack locations. The available cues, whether visual (simulated predator motion) or vibrational (offspring signalling) were thus sufficient for localization. Female *U. crassicornis* are known to attend to both vibrational (Cocroft 1996) and visual cues (Wood 1976) during defence. Predators such as vespid wasps are large enough to provide potential visual cues to the female, and in such cases offspring signals may function largely as an alerting signal, with the female locating the predator visually from her resting position. A wasp may not be visible, however, if it attacks a nymph on the opposite side of the female, or if it abandons a nymph when approached by the female, and attacks another

nymph behind her (Cocroft 2002). Other predators, such as pentatomid bugs, will often be out of the female's line of vision because they are screened by intervening nymphs and/or are on the opposite side of the stem from the female. There are many situations, then, in which vibrational cues from offspring signalling are available, but visual cues of predator location are not.

What vibrational cues would group signals provide when the predator attack occurs at different ends of the aggregation? Although this study was designed to examine individual offspring behaviour rather than to characterize stem vibrations at different locations in and around the aggregation, a number of differences are likely in the signals evoked by different attack locations. First, the number of individuals participating in the group signal was greater when the attack occurred at the top of the aggregation; more signallers generate a group signal of longer duration and greater total energy, as measured at the location of the resting female (K. Ramaswamy & R. B. Cocroft, unpublished data). Second, because the nymphs closer to the predator are more likely to participate in a group signal than those further from the predator, a female that moves into the centre of the aggregation would experience more signals either in front of or behind her. Third, because the contacted nymphs initiate a group signal, a female that moves into the aggregation would experience signals originating either in front of or behind her.

Given a number of potential vibrational cues of predator location, how likely is it that a female *U. crassicornis* could use such cues to localize the predator? Female movement is episodic, with a burst of walking occurring after a group signal; if females walk further or faster when more signals are produced (as occurs when the attack is at the top end of the aggregation), this would bias her defence towards the end that is attacked. Another possibility, given the gradient of increasing numbers of signallers closer to the predator, would be to assess the direction from which most signals originate; the point at which there are equal numbers of signallers ahead or behind would be closer to the end attacked, at which point the female may be close enough to see the predator. Several species of small insects can localize the source of a vibration on a plant stem (Virant-Doberlet et al. 2006), including nymphs of a closely related treehopper (Cocroft 2005) and males of *U. crassicornis* responding to female replies to advertisement signals (R. B. Cocroft, unpublished data). Female treehoppers move with their front-back axis aligned with the long axis of the stem, and although the intensity and arrival time differences between the front and back legs are small, mechanical directionality in the response to substrate vibration of the body of female *U. crassicornis* provides potential localization cues (Cocroft et al. 2000; Miles et al. 2001). Finally, regardless of the signalling gradient, females could potentially locate the origin of the group signal if there is a precedence effect, such that only the leading signals are localized (Gerhardt & Huber 2002).

It is clear that defending female *U. crassicornis* use multiple cues to locate predators. Wood (1976) showed that visual cues are important in guiding defensive behaviour in *U. crassicornis* females. Field observations also revealed that in some attacks by flying wasps, whose wingbeats induced vibrations in the stem, females begin moving towards the predator before the nymphs signal (Cocroft 2002). The functional significance of vibrational cues for predator localization may thus be to indicate to females which direction to face, or which end of the aggregation to search, while attempting to locate the predator visually.

Nymphs were more likely to signal in the absence of the mother. Defending mothers also produce vibrational signals, especially after the predator has left the aggregation (Cocroft 1999b). Maternal signalling is correlated with a reduction in the rate of nymph signalling. Although the function of maternal signals has not been

investigated, preliminary evidence indicates that they raise nymphal signalling thresholds, which is consistent with the increased signalling seen here in the absence of the mother. However, because most maternal signalling occurs after the predator encounter is over, other cues must be responsible for the change in nymphal thresholds during the encounter. Maternal defence also involves loud wing buzzing and kicking at the predator, and the resulting vibrations can influence nymphal behaviour (Cocroft 1999a, b). In the absence of the mother, there was no signalling gradient associated with distance from the predator when the predator attacked the bottom end of the aggregation. Also, in her absence, there was no relationship between the overall level of signalling and the attack location. Thus, although there is no centralized control, there are two classes of individuals (female and nymphs) whose interaction is required for successful defence.

Signalling systems involving various communication modalities occur in which groups of individuals coordinate their signals temporally (Greenfield 1994). Temporal coordination takes the form of either synchronization or alternation among individuals that form a group. Coordinated signalling behaviour may provide information about the quality of the signallers to the receiver, but often arises as an epiphenomenon of males competing with each other for female attention. When males compete for females using advertisement signals, they may time their signals as in the katydid *Neoconocephalus spiza* such that their signals 'lead' the signals of other males, because females have a preference for leaders (Greenfield & Roizen 1993). Synchronized claw waving by fiddler crabs is also thought to be consequence of male competition to produce leading signals (Pope 2000; Backwell et al. 2006). But there are also examples of cooperative signalling interactions where the members of the group produce temporally coordinated signals. For example, males among some species may seek to maximize the peak signal amplitude, a phenomenon referred to as the 'beacon effect' (Buck & Buck 1976). In some katydid species, synchrony is important because the females only respond to a particular modal rate, and synchronization preserves this rhythm (Greenfield 1994).

The closest analogue of the collective signals of *U. crassicornis* nymphs may be the antipredator 'defence wave' of the giant honeybee, *Apis dorsata* (Kastberger et al. 1998). As in *U. crassicornis*, periodic waves of movement (in this case of the wings and abdomen) travel across the group. However, in *A. dorsata*, the function of the wave is apparently to produce a visual and perhaps auditory signal; although there might be an effect of the visual component of the *U. crassicornis* display on predators, the vibrational signals appear to be the main component perceived by the defending female. Comparison of the mechanisms underlying the transmission of signalling within both *A. dorsata* and *U. crassicornis* groups, as well as the functional consequences of variation in the number and spatial distribution of signallers, could be revealing of the factors shaping the evolution of these collective signals.

The emergence of complex patterns of group behaviour from the actions of individuals has been the subject of much recent investigation in the field of collective behaviour (Camazine et al. 2001). Mathematical models have shown how complex group-level patterns can emerge in a self-organized manner. For instance, Hemelrijk & Kunz (2004) showed how spatial patterns of fish schools can be achieved by attributing the following behavioural rules to individual fish: repulsion (between fish that are close by), aligning (at intermediate distances) and attraction (at greater distances). The phenomenon of how individual behaviour leads to group-level patterns is also of interest in social insects in the context of division of labour among workers (Page & Mitchell 1990). For instance, in the ant *Temnothorax albipennis*, the colony shows a collective ability to choose the best of several new nest sites

without relying on the limited information possessed by individual ants. Pratt et al. (2005), using an agent-based modelling approach, showed how these collective decisions can be made by individual ants following rules based on a strategy of graded commitment to a potential home. By establishing the properties of group signalling in *U. crassicornis* offspring, we can now frame hypotheses about differences in information availability to offspring (with respect to the predator), differences in signalling thresholds, and how information is transferred within an aggregation. This study, therefore, provides us with an opportunity to understand how coordinated group signalling can emerge from signalling by individuals in the absence of centralized control. The emergent signalling patterns are clearly influenced by both the signalling nymphs as well as the mother's behaviour. The need to successfully defend against predators has driven the remarkable coordination between the signalling nymphs and the defending mother. This form of coordination between two classes of individuals (the nymphs and their mother) is analogous to the regulation of worker activity by the queen in many social insect colonies (e.g. Reeve & Gamboa 1983).

A successful paradigm for study of group behaviour includes: identifying the properties of the collective response arising from individual behaviour in response to varying environmental conditions (Sumpter 2006), investigating the adaptive significance of the collective response (Camazine et al. 2001) and understanding how the group-level response arises from individual behaviour (Grimm & Railsback 2005). Insects provide excellent opportunities for studying parent-offspring interactions (Mas & Kölliker 2008), and coordinated group signalling by *U. crassicornis* nymphs is ideally suited for investigating collective behaviour, at both proximate and ultimate levels. Having established group-level properties of nymph signals in response to different locations of predation as a result of differences in individual signalling probabilities, we can now investigate the biological function of differences in properties of group signals associated with predator location, as well as the individual rules that result in group-level signalling patterns.

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