

Negative feedback from maternal signals reduces false alarms by collectively signalling offspring

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Within animal groups, individuals can learn of a predator's approach by attending to the behaviour of others. This use of social information increases an individual's perceptual range, but can also lead to the propagation of false alarms. Error copying is especially likely in species that signal collectively, because the coordination required for collective displays relies heavily on social information. Recent evidence suggests that collective behaviour in animals is, in part, regulated by negative feedback. Negative feedback may reduce false alarms by collectively signalling animals, but this possibility has not yet been tested. We tested the hypothesis that negative feedback increases the accuracy of collective signalling by reducing the production of false alarms. In the treehopper *Umbonia crassicornis*, clustered offspring produce collective signals during predator attacks, advertising the predator's location to the defending mother. Mothers signal after evicting the predator, and we show that this maternal communication reduces false alarms by offspring. We suggest that maternal signals elevate offspring signalling thresholds. This is, to our knowledge, the first study to show that negative feedback can reduce false alarms by collectively behaving groups.

Keywords: collective behaviour; negative feedback; false alarm; information cascade; parent–offspring communication

1. INTRODUCTION

Group-living animals are thought to benefit by using social information, such as behavioural cues or signals from group members, when responding to predators [1–3]. Social information can greatly increase the perceptual range of a group member [4,5]. However, the benefits of social information in predator detection are dependent on the reliability of that information [6–9].

False alarms are common in a variety of group-living taxa [9–11] and can even outnumber correct detections [12,13]. If the first group member to detect a non-threatening stimulus produces a false alarm, this can cause a wave of erroneous decisions to spread, because the first responding individual(s) exerts disproportionate influence on other group members [14]. False alarms may also be costly [9,11], and when false alarms propagate through groups (i.e. 'erroneous information cascades'), most or all group members can lose foraging or mating opportunities [8,9,15]. Yet, any reduction in false alarms comes with a trade-off between sensitivity and accuracy. To reduce false alarms, the group must reduce its sensitivity of response and increase the risk of not detecting a predator [16].

Erroneous information cascades are especially likely in one subset of group-living animals, those that behave collectively. We use the term *collective* in the sense of Sumpter [17], where interacting individuals produce a coherent pattern that exceeds individual interaction

range. Synchronized, or wavelike, collective signalling in particular suggests a strong reliance on social information, because neighbours need to be within sensory range to coordinate synchrony [18–22]. Moreover, such signalling may be repetitive [1–3,23–25], suggesting that the social information necessary for coordinating one group signal also promotes repeated signals, perhaps by lowering response thresholds. Yet, animals that behave collectively in response to predators [23,26,27] are absent from the literature on false alarms and information cascades, and whether such animals behave in ways that limit or reduce false alarms is an open question.

Recent research has focused on general processes by which animals regulate collective behaviour (reviewed in [17,28,29]), some of which could reduce false alarms. For example, if a collectively signalling group had a means of adjusting its response threshold, it might thereby limit false alarms without reducing its overall sensitivity of response. In some group-living (but not collectively behaving) species, an informed subset of individuals (i.e. sentinels) update group members on the background level of predation risk [9,30], including decreases in risk. Such information may elevate response thresholds of group members, making false alarms less likely [9]. Similarly, negative feedback, or behaviour by group members that dampens collective behaviour, is hypothesized to reduce erroneous information cascades by preventing group members from copying errors by other group members [14,31]. In contrast to abundant evidence that positive feedback regulates collective behaviour at all levels of biological organization [28,32–35], negative feedback has only been observed in two collectively behaving animal taxa [36–38]. In honeybees (*Apis mellifera*) and Pharaoh's ants (*Monomorium pharaonis*),

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negative feedback reduces the allocation of foragers to risky or unrewarding patches [36,38], and in swarming honeybees, it also facilitates consensus by decreasing the advertisement of the less-preferred nesting site [37].

Here, we investigate whether a collectively signalling species uses negative feedback to reduce false alarms after a predator encounter. In the treehopper *Umbonia crassicornis*, mothers defend sedentary, clustered offspring groups from invertebrate predators [39]. The offspring produce collective vibrational signals that communicate the predator's presence and location to the defending mother [25]. After offspring produce repeated signals, their signalling threshold drops [40], and the signalling behaviour can become self-perpetuating. As a result, group signalling often continues after the danger has passed, producing false alarms [40]. The mother also produces vibrational signals that are temporally and spectrally distinct from offspring signals (figure 1) [41]. Because mothers signal at a much higher rate after evicting the predator, we hypothesized that maternal signals function to reduce post-predation false alarms by offspring after attacks end.

Our aim in this study was to test the hypothesis that signalling by *U. crassicornis* mothers after predator attacks reduces false alarms by offspring. This hypothesis predicts, first, that maternal and offspring signalling rates will be inversely correlated after a predator encounter, with mothers signalling more while offspring signal less. We tested this prediction by quantifying the signalling behaviour of mothers and group-living offspring in response to predator encounters. The second prediction is that this relationship is causal; that is, that maternal signals inhibit signalling by offspring that are producing false alarms. We tested this prediction by playing back maternal signals to offspring that were signalling after a simulated predator attack. This is, to our knowledge, the first study to investigate the use of negative feedback by collectively behaving animals to reduce false alarms.

2. METHODS

(a) *Insect collection and rearing*

We collected late-instar and teneral adult *U. crassicornis* aggregations from the USDA Subtropical Horticulture Research Station in Miami, FL, USA. We maintained a greenhouse colony on potted *Albizia julibrissin* host plants, at 20–30°C on a 12 L:12 D cycle. To maintain genetic diversity, we collected new aggregations twice a year (December 2007, July 2008, November 2008, May 2009). We separated sexes from each family a few days after adult eclosion, before adults are reproductively mature, and mated males and females from different families to produce subsequent generations. Mating pairs and their offspring were housed on individual potted *A. julibrissin* trees. Each tree with insects was individually caged in fibreglass mesh, and all trees and insects were kept in a large, walk-in cage constructed of wood and fibreglass mesh. In the experiments described later, we used second and third generation *U. crassicornis* families in which nymphs were second through to fourth instar. We were provided with pentatomid predators (*Podisus maculiventris* nymphs) by the USDA–ARS Biological Control of Insects Research Laboratory (Columbia, MO, USA). We maintained a laboratory colony of *P. maculiventris* at approximately 25°C on a 14 L:10 D cycle. Pentatomid

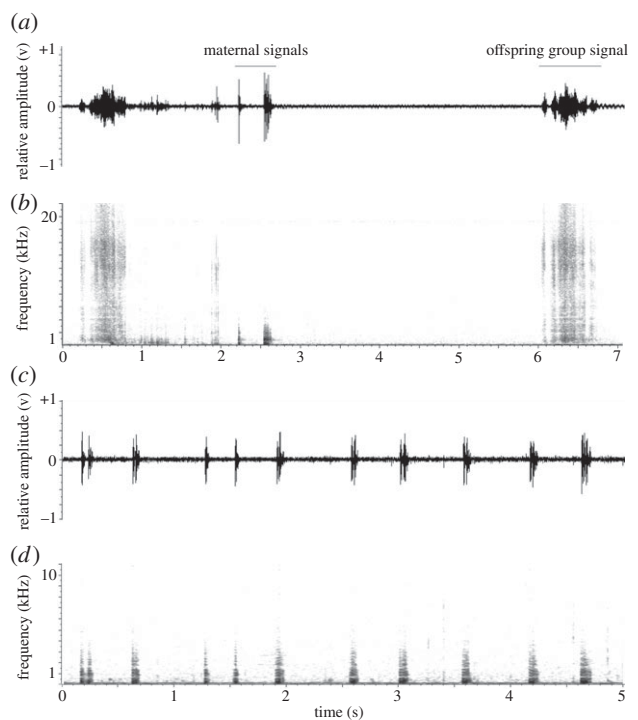


Figure 1. (a,b) Waveform and spectrogram showing *Umbonia crassicornis* maternal and offspring vibrational signals produced during a predator encounter. (c,d) Waveform and spectrogram showing *U. crassicornis* maternal vibrational signals produced after a simulated predator encounter has ended.

nymphs and adults were fed a combination of coddled fourth instar larvae of *Trichoplusia ni* (Hübner) and a zoophylogenous artificial diet [42] and were provided with water via moist dental wicks (Richmond Dental) in small plastic weigh boats (Fisher Scientific). We housed adults of each sex in half-pint paper containers; when females produced eggs, eggs were collected in a new cup in which nymphs developed. New nymphs were provided by the USDA–ARS Laboratory twice a year.

(b) *General methods*

We conducted the experiments described later in the laboratory from July 2008 through to August 2009. We detected maternal and offspring vibrational signals with an accelerometer (PCB Piezotronics, NY, USA; model 352A24, weight 0.8 g, frequency range: from 0.8 Hz to 10 kHz \pm 10%, sensitivity: 10.2 mV per m s^{-2}) attached 4–6 cm from each family using mounting wax and powered by a PCB Model 480E09 ICP Sensor Signal Conditioner. We recorded both offspring and maternal signalling responses and any vibrational stimuli we played on a Marantz PMD660 digital audio recorder at a sampling rate of 44 100 Hz. (For details on vibrational stimuli, see §2e.) We recorded family behaviour using a digital video recorder (Sony Handycam models HDR-HC7 and HDR-SR11). For each family in both experiments, we first set up signal detection and video equipment and allowed the family 1 h to acclimatize. Two families were used in both the predator introduction and playback experiments; all other families were used in one experiment each.

(c) *Prediction 1: maternal and offspring signalling rates diverge after predator encounters*

If maternal signals reduce the false alarms that offspring commonly produce after predator attacks, then there should be an

inverse correlation between maternal and offspring signalling rates after a predator encounter. To test this prediction, we introduced a predator to each family and characterized the family's signalling responses during and after the predator encounter. The predators were juvenile spined soldier bugs (Pentatomidae: *Podisus maculiventris*) that had been fasted overnight, and a different individual predator was introduced to each of 10 *U. crassicornis* families on potted host plants (Mimosaceae: *A. julibrissin*). We allowed the predator to walk up a thin string tied to the treehopper family branch, greater than or equal to 1 cm from the edge of the offspring group, either beyond the end of the aggregation farthest from the mother or on the base of a leaf next to aggregation. Each family also received a control treatment, where we mimicked our movements as in an introduction but did not introduce a predator. We alternated treatment order between families and used each predator only once. We scored family responses (i.e. maternal signals, offspring group signals) for the duration of the predator encounter and for 3 min after the encounter ended. For control treatments (i.e. sham introductions), we recorded family behaviour for 1 h, and scored the production of offspring group signals and maternal signals for the same amount of time as the predator introduction treatment for that family. We scored predator encounters as beginning when a pentatomid made physical contact with one or more *U. crassicornis* nymphs and as ending when a pentatomid terminated contact by moving away from the edge of an offspring aggregation, whether or not the predator was evicted by the mother.

(d) **Prediction 2: playback of maternal signals reduces false alarms by offspring**

If maternal signals reduce false alarms by offspring, then after a predator encounter, offspring collective signalling should decrease in response to the playback of maternal signals. To test this prediction, we simulated predator encounters with 11 offspring aggregations whose mothers had been removed. We then played maternal vibrational signals, wind vibrations or silence to the signalling offspring group (for information on vibrational stimuli, see §2e). Each family received all three playback treatments. The comparison between maternal signals and silence will reveal whether offspring signalling is reduced more if mothers signal than if they do not—i.e. whether maternal signalling after predation events causes a reduction in false alarms. The comparison between maternal signals and wind will further reveal whether maternal signals reduce offspring signals as much as do wind-induced vibrations, which are a common source of noise on plants and have an inhibitory effect on vibrational communication in insects [43,44].

We simulated a predator encounter by presenting a crushed nymph (which had been killed by freezing) from a different *U. crassicornis* family on a dowel approximately 1 cm under the centre of each aggregation; a fresh dowel was used for each presentation. A chemical cue from a crushed nymph acts as a predator cue [45] and reliably elicits group signalling from offspring groups. We elicited 10 group signals from each offspring group and then simultaneously withdrew the crushed nymph and began playing vibrational stimuli or silence for 15 min. Each playback was a loop composed of 30 s of stimulus followed by 30 s of silence; we included silent intervals for scoring of offspring signalling response, in case the presence of playback signals interfered with scoring. However, because offspring group signals

contain energy at higher frequencies than do the maternal signals or wind vibrations, we were able to score all group signals, including those produced during playback stimuli.

We controlled for possible effects of treatment order by randomly assigning each family to one of three possible orders, and by waiting 1 h between treatments.

(e) **Vibrational stimuli and playbacks**

To each group of offspring we played their own mother's signalling response to a simulated predator encounter (as described earlier). To obtain recordings of each mother's vibrational signals, we simulated a predator encounter in the manner described earlier (§2d) with each family one day prior to the playback experiment. When offspring began signalling, mothers patrolled the family, signalled and searched for the source of disturbance. We allowed mothers to find the dowel with crushed nymph that they kicked as they would a predator. As soon as a mother kicked a dowel, we withdrew the predator cue from the aggregation. We used only post- eviction maternal signals for our playback stimuli. We also played wind vibrations and silence as controls: we recorded wind vibrations from one branch each from three trees in the field. For the 'silence' treatment, we generated a silent audio track using audio editing and recording software (AUDACITY v. 1.3.12) and played this as we played vibrational stimuli. We did this to control for any electrical noise generated by our equipment that might influence the behaviour of the insects.

To play vibrational stimuli to the *U. crassicornis* offspring, we glued a small neodymium magnet (United Nuclear Scientific, Laingsburg, MI, USA) to the aggregation's branch at the trunk end of the aggregation, the mother's typical position at rest. We positioned an electromagnet parallel to the magnet at a distance of 1–2 mm. We then transmitted vibrational stimuli to the electromagnet from AUDACITY (v. 1.3.12) on a MacBook (v. 2.4 GHz Intel Core Duo) via a RADIOSHACK 40 W PA amplifier. To ensure that the playback signals had the correct amplitude spectrum, we used a custom program in MATLAB (v. R2008bSV) to assess frequency filtering by the branch and to build an inverse filter [40]. We used this to digitally filter the maternal signals and wind vibrations being played through that branch. To ensure we were playing stimuli at biologically relevant amplitudes, we matched playback stimulus amplitude to signal amplitude from the original field recording.

(f) **Scoring and statistical methods**

We used XBAT (Harold Figueroa, Ithaca, NY, USA) to score the presence of maternal signals and offspring group signals, and then calculated signalling rates for mothers and offspring of each family. We compared signalling responses among treatments in both experiments using the Quade test [46], a non-parametric analogue of a repeated-measures ANOVA. We performed exact Wilcoxon signed-rank tests for *post hoc* comparisons. Comparisons for the predator introduction experiment and offspring signal distribution were two-sided. Comparisons for maternal signal and wind vibration treatments in the playback experiment were one-sided, according to our *a priori* hypotheses. We adjusted comparison *p*-values for false discovery rate (FDR) [47]. To assess whether maternal and offspring group signalling rates diverged among predator encounter contexts, we calculated the difference in signalling rate between contexts for both maternal and offspring signals, and then compared these differences

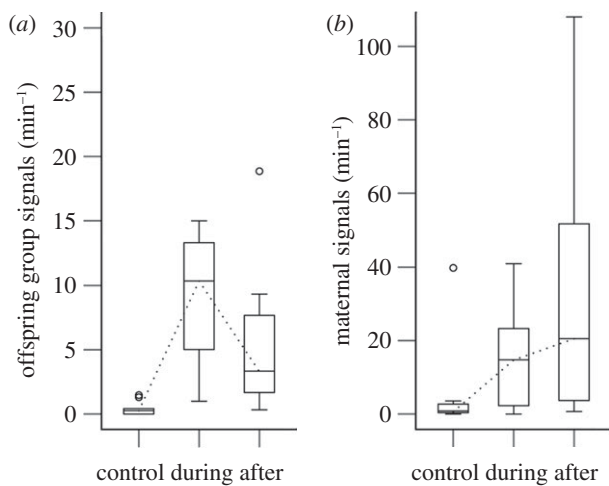


Figure 2. Signalling responses of *Umbonia crassicornis* families to introduced predators. No predators were introduced in control treatments. Box plots show distributions of (a) offspring group signalling rate, and (b) maternal signalling rate (minimum, first quartile, median, third quartile, maximum; open circles represent outliers). Dashed lines indicate how median signalling rates changed with context.

using the Wilcoxon signed-rank test. All statistical tests were conducted with R statistical software (v. 2.13.0).

3. RESULTS

(a) Prediction 1: maternal and offspring signalling rates diverge after predator encounters

The results of this experiment supported the first prediction that maternal and offspring signalling rates should diverge after a predator encounter. Predator encounters lasted 6.21 ± 6.48 min (mean \pm s.d.). Pentatomids contacted greater than or equal to 1 nymph during all predator introductions and attacked greater than or equal to 1 nymph in all but one introduction (nine introductions with attacks, one introduction with contact only). In one-third of introductions where pentatomids attacked nymphs, the pentatomid returned to the aggregation for a second attack after the first attack ended. *Umbonia* offspring always produced group signals before mothers wing-buzzed or approached.

Offspring group signalling rates differed by predator encounter context (Quade test: $n = 10$ aggregations, Quade $F_{2,18} = 12.670$, $p < 0.001$). Mean group signalling rate was 20-fold greater during predator encounters than during control treatments; and offspring produced a substantial number of false alarms, with signalling rates after the encounter that were still 10-fold greater than those during control treatments (control: 0.4 ± 0.5 , during encounters: 9.2 ± 5.3 , after encounters: 5.4 ± 5.6) (control versus during predation, Wilcoxon $W = 0$, $p = 0.002$, $p_{\text{FDR}} = 0.006$; control versus after predation, Wilcoxon $W = 1$, $p = 0.004$, $p_{\text{FDR}} = 0.008$). Offspring signalling rates while predators were in contact with families did not statistically differ from those after predators left (figure 2; predation versus after predation, Wilcoxon $W = 13$, $p = 0.160$, $p_{\text{FDR}} = 0.160$). The peak amplitude of offspring group signals ranged from 0.16 to 0.33 m s^{-2} .

As with offspring group signalling rates, maternal signalling rates were influenced by context (Quade test: $n = 10$ mothers, $F_{2,18} = 3.595$, $p = 0.049$). *Post hoc* comparisons

were not significant after controlling for FDR (control versus during predation, Wilcoxon $W = 11$, $p = 0.106$, $p_{\text{FDR}} = 0.131$; control versus after predation, Wilcoxon $W = 7$, $p = 0.037$, $p_{\text{FDR}} = 0.111$; predation versus after predation, Wilcoxon $W = 12$, $p = 0.131$, $p_{\text{FDR}} = 0.131$). However, the mean maternal signalling rate after predator encounters was more than six times the rate during controls, and twice that during encounters (control: $5.1 \pm 12.3 \text{ min}^{-1}$, during encounters: $17.1 \pm 14.4 \text{ min}^{-1}$, after encounters: $33.0 \pm 39.1 \text{ min}^{-1}$; figure 2). The peak amplitude of maternal signals ranged from 0.11 to 0.20 m s^{-2} .

Maternal signalling and offspring group signalling rates diverged between ‘during encounter’ and ‘after encounter’ contexts (difference between during and after encounter contexts, maternal signalling versus offspring group signalling, Wilcoxon $W = 4$, $p = 0.014$). Maternal signalling rate tended to increase after encounters, whereas offspring signalling rate tended to decrease after encounters (see the electronic supplementary material).

(b) Prediction 2: playback of maternal signals reduces false alarms by offspring

Results of this experiment supported the second prediction that maternal vibrational signals reduce the production of false alarms by offspring. When the post-predation context was simulated experimentally, offspring group signalling rates were decreased by playback of maternal vibrational signals and wind vibrations, but not by silence (Quade test: $n = 11$ aggregations, Quade $F_{2,20} = 5.204$, $p = 0.015$). Offspring produced roughly half as many false alarms per minute when their mother’s vibrational signals or wind vibrations were played than when silence was played (maternal vibrational signals: $2.3 \pm 2.1 \text{ min}^{-1}$, wind vibrations: $1.6 \pm 1.6 \text{ min}^{-1}$, silence: $4.3 \pm 3.3 \text{ min}^{-1}$) (silence versus mother, Wilcoxon $W = 7$, $p = 0.018$, $p_{\text{FDR}} = 0.035$; silence versus wind vibrations, Wilcoxon $W = 1$, $p = 0.001$, $p_{\text{FDR}} = 0.003$; figure 3). There was no difference in false alarms produced during playbacks of wind vibrations or maternal vibrational signals (Wilcoxon $W = 37$, $p = 0.375$, $p_{\text{FDR}} = 0.375$; the electronic supplementary material).

4. DISCUSSION

Group-living animals benefit from incorporating social information in predator detection [4,5], but such benefits are likely to be limited by the common occurrence of false alarms [12,13] and the tendency for potentially costly errors [9,11] to rapidly propagate through a group [6–8]. In this study, offspring groups continued to produce collective anti-predator signals after a predator had left. Mothers signalled at a high rate after predator attacks, and playback of maternal signals reduced the production of those false alarms. This is, to our knowledge, the first evidence of collectively behaving animals using negative feedback to reduce false alarms.

Communicative and defensive roles in *U. crassicornis* families are constrained by the characteristics of each life stage. Offspring cluster in sedentary aggregations and are dependent on their mother for protection against invertebrate predators. Offspring produce collective signals in response to predator attacks, and these signals evoke maternal defence [25]. During attacks, only the

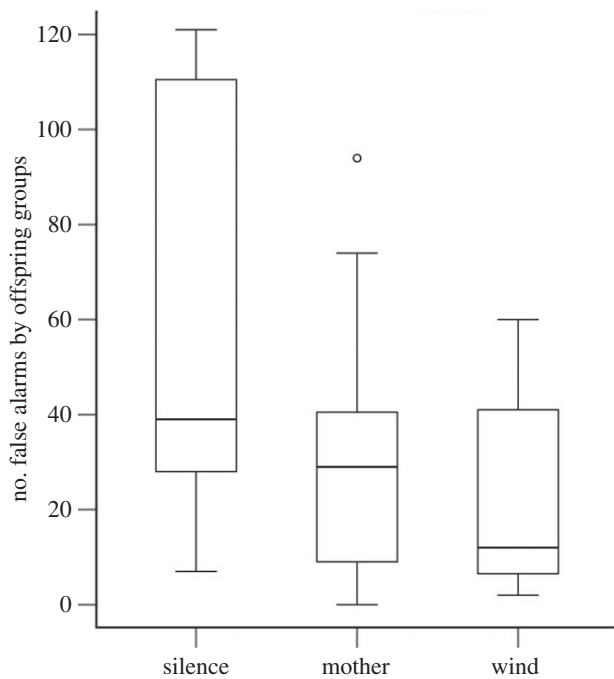


Figure 3. Effect of vibrational playbacks on false alarms by *Umbonia crassicornis* offspring. Box plots show the distribution of all collective offspring group signals produced during 10 min of playback treatments that were started after simulated predator encounters ended (minimum, first quartile, median, third quartile, maximum; open circle represents an outlier).

victim and its nearest neighbours are likely to have personal information about predator presence and location. These individuals are most likely to initiate group signalling; signalling by other group members, or social information, amplifies this response.

While at least some offspring will have reliable information about the predator's presence, no individual offspring can provide reliable information about the predator's absence, because each one scans only a small fraction of the area around the aggregation. By contrast, defending mothers are able to obtain reliable information about predator departure because maternal defences are only effective at close range [48], and mothers must locate and approach predators in order to drive them away. Mothers are thus the only individuals in families likely to have frequently updated personal information on predator presence after attacks. Mothers provide negative feedback: maternal signals dampen collective signalling by offspring as predation risk decreases, at times when mothers have most certain knowledge of predator location and false alarms by offspring are most likely.

Although negative feedback is hypothesized to have important regulatory functions for collective behaviour [31,36], it has, to our knowledge, only been documented in two animal species [36,38] prior to this study. In honeybees (*A. mellifera*), negative feedback promotes consensus decision-making [37] and reduces predation costs [36]. In Pharaoh's ants (*M. pharaonis*), negative feedback deters foragers from unrewarding trails, probably enhancing foraging efficiency [38,49]. This study of *U. crassicornis* adds a third function of negative feedback: it reduces false alarms, possibly allowing these family groups to avoid a trade-off between sensitivity and accuracy in predator detection.

Maternal signals in *Umbonia* probably exert negative feedback on offspring signalling by adjusting offspring response thresholds to social information. *Umbonia* offspring signalling thresholds decrease after a predator attack [40]. Undisturbed offspring aggregations rarely produce group signals [41], but recently disturbed aggregations will continue producing spontaneous group signals (i.e. false alarms) after a predator leaves ([41] and this study). Increasing response thresholds limits false alarms in other taxa [9] and may limit information cascades, possibly by causing individuals to preferentially attend to personal information. By increasing offspring response thresholds, mothers may change the relative influence of social and personal information for nymphs, decreasing the influence of social information provided by other nymphs.

If the function of maternal signals is to inhibit collective signalling by offspring, why do mothers also signal while the predator is present? By providing negative feedback during a predator encounter, maternal signals may enhance a mother's ability to gain information about the predator's position. The rationale for this hypothesis is twofold. First, mothers do not signal during encounters with large, conspicuous offspring predators such as vespid wasps [41]. Mothers often detect and walk towards such predators before their offspring produce any signals, apparently guided by vision [39,41]. By contrast, mothers do signal when responding to small, stealthy predators such as the pentatomids in this study, or when offspring signals are triggered by vibrational playback in the absence of a predator (K. Ramaswamy & R. Cocroft 2009, unpublished data). A mother gains information on the predator's location through a gradient in her offspring's collective signals; offspring farther from the predator are less likely to participate in group displays [22,50]. In the mother's absence, the gradient disappears because individuals farther from the predator are just as likely to signal as those close by [22]. We hypothesize that maternal signals dampen participation by offspring as each collective signal propagates across the group, away from the site of the attack. This hypothesis would explain why mothers signal not only after predators leave, but also while searching for predators that they cannot locate with visual cues.

The finding that mothers reduce false alarms by offspring raises the question of what costs such false alarms may impose on families. Maternal defence in another treehopper species (*Publilia concava*) has metabolic costs, evidenced by trade-offs between duration of care and lifetime fecundity [51]. Metabolic costs may also result in reduced longevity in insect species [52]. If an *Umbonia* mother dies before her offspring reach adulthood, her undefended offspring will be much more vulnerable to predators [39,48,53]. Mothers should limit the metabolic costs of defence. If vibrational signalling is less costly than active antipredator defence, then a mother that has recently evicted a predator will benefit by signalling rather than by continuing to respond to the continuing waves of offspring signals.

In addition to incurring unnecessary metabolic costs for mothers, continued signalling by offspring may also attract other, nearby invertebrate predators or parasitoids, many of which are vibrationally sensitive (e.g. spiders [54], ants (reviewed in [26]), pentatomids [55]) and some of which have been shown to use vibrational cues

[55–57] to locate prey. The study of predator eavesdropping on vibrational signals is a nascent field, but evidence is growing that vibration-sensitive invertebrate predators can home in on prey vibrational signals [58–60]. By reducing offspring signalling after a predator encounter, mothers may reduce the risk of advertising the family's location to additional predators. Continued offspring signalling could also indirectly advertise the family to visually oriented predators (e.g. songbirds). Families are cryptic when stationary (J. Hamel 2008, personal observation), but a mother breaks crypsis by walking and wing buzzing in response to offspring signals. Offspring break crypsis because their collective signals involve both vibration and movement [22,61].

Offspring signalling was reduced not only by maternal signals, but also by wind vibrations. Wind-induced vibrations are the major source of environmental noise for vibrationally communicating insects on plants [62]. Wind vibrations inhibit communication, causing insects to signal during brief wind-free gaps, and diel variation in wind speed is inversely correlated with diel patterns of signalling by some vibrationally communicating insects [43,44]. The importance of wind for antipredator communication by *U. crassicornis* in the field remains to be explored, as does the rate of predator encounters as a function of wind velocity. At higher wind velocities, parent-offspring communication may be limited to wind-free gaps, while at lower velocities, the inhibitory effect of wind-induced vibrations may reduce the need for maternal signalling.

In summary, in *U. crassicornis*, maternal signalling functions as negative feedback and regulates offspring collective signalling. Communicative roles are partitioned between mother and offspring such that the individual(s) with the most reliable information about predation risk provide that information to the rest of the family. Sedentary offspring produce collective vibrational signals that communicate the predator's presence and location to the defending mother. Mothers have the most certain information on predator location after predator attacks, and maternal signals dampen collective signalling by offspring after attacks, thereby reducing false alarms. Maternal signals probably increase offspring thresholds and increase the weight offspring give to personal information. Future studies should investigate the regulation of collective behaviour in other animal groups and further explore the functions and benefits of negative feedback.

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