COMMUNICATION ABOUT PREDATION RISK BETWEEN PARENTS AND OFFSPRING GROUPS IN TREEHOPPERS

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by
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The undersigned, appointed by the dean of the Graduate School,

have examined the dissertation entitled

COMMUNICATION ABOUT PREDATION RISK
BETWEEN PARENTS AND OFFSPRING GROUPS IN TREEHOPPERS

presented by Jennifer Anne Hamel,

a candidate for the degree of doctor of philosophy,

and hereby certify that, in their opinion, it is worthy of acceptance.

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DEDICATION

This is dedicated to Tyler, for teaching me about acceptance and reminding me of what's important, and to our families, who put up with an awful lot. It is also dedicated to Tim Forrest, Jim Petranka, and Mike Stuart for encouraging me to pursue a Ph.D., and to Sandi Abell, for teaching me that I didn't know the least thing about teaching.

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Abstract.

False alarms should be common and costly for group-living animals, but to limit false alarms, animals must evade a tradeoff between response sensitivity and accuracy. I investigated this topic in two closely-related species of treehoppers, *Umbonia crassicornis* and *Platycotis vittata*, in which mothers defend their group-living offspring from invertebrate predators. *Umbonia* offspring groups produce synchronous signals to alert their mothers of predator attacks, and *U. crassicornis* offspring groups are known to produce false alarms. I examined a) the function of vibrational signals by *U. crassicornis* mothers after predator attacks, b) the functions of *P. vittata* offspring and maternal signals during predator encounters, and c) the response of a vibrationally-sensitive insect predator to *P. vittata* familial vibrational signals.

Results showed that *U. crassicornis* maternal signals function as negative feedback, dampening the collective signaling of their offspring after predator attacks. This likely reduces false alarms by offspring without reducing the sensitivity of predator detection. *Platycotis vittata* mothers and offspring also partition communicative roles, with offspring signaling predator presence and maternal signals dampening offspring signaling response. However, false alarms are unlikely in this species and thus benefits of negative feedback are unlikely to be the same as for *U. crassicornis*. Finally, *P. vittata* offspring signals attract a species of generalist insect predator, whereas *P. vittata* maternal signals had no effect on the same predator. Predator eavesdropping may favor maternal suppression of unnecessary offspring signaling.

Chapter 1. Introduction

The problem of false alarms for group-living animals

In many group-living animal species, individuals learn about predator approach through social information, in the form of behavioral cues or communication by group members (Wilson 2000; Caro 2005; Zuberbuhler 2009). The use of social information increases an individual's perceptual range (Pulliam 1973; Lima 1995b) and allows group members to dedicate less time to vigilance, per capita, without increasing their risk of being attacked by an undetected predator.

However, in addition to detecting approaching predators, group members also produce false alarms. False alarms can be common and costly (Hoogland 1981; Kahlert 2006; Bell *et al*. 2009; Beauchamp 2010). For example, 27% of alarm calls by group-living African birds with a sentinel system are false alarms (Bell *et al*. 2009). If foragers respond to all alarm calls, they lose an estimated one-quarter of their foraging time. Similarly, 40% of escape flights by Greylag Geese are likely due to alarm calls, and each escape flight costs about 19 minutes of foraging time (Kahlert 2006). Moreover, false alarms can rapidly *spread* through a group where individuals rely heavily on social information (Lima 1995a; Bikhchandani & Hirshleifer 1998; Giraldeau *et al*. 2002; Sirot 2006), and this can cause most or all group members to incur foraging or mating costs (Kahlert 2006; Bell *et al*. 2009).

Group-living animals should limit false alarms. However, any reduction in false alarms increases the likelihood that individuals will not detect a predator (Wiley 1994). An individual's response to a predator stimulus falls into one of four categories. If the predator is really present, the individual either correctly detects the predator or errs. If the predator is not present, then the individual either produces a false alarm or correctly rejects the stimulus. If individuals reduce the likelihood of responding to a stimulus, then they reduce the chance of a false alarm, but also the chance that they correctly detect a predator. The costs of dying from a predator attack are much higher than the costs of false alarms, so in general, reducing the overall sensitivity of response does not pay.

This tradeoff between sensitivity and accuracy could be avoided, if individuals could gain an independent source of information about the background level of risk. For example, the information source could be an environmental correlate of risk, such as time of day. Semipalmated Sandpipers are most likely to respond to alarms at times of day when light levels are low, and this corresponds to the times of day when they are most likely to be attack by a raptor (Beauchamp 2010). The information source could also be in the form of communication from group members. Some group-living species use sentinels, individuals who monitor the area and produce signals that are correlated in some way with the current level of risk (Bell *et al*. 2009). By updating their information on risk level and adjusting their response thresholds, group members respond to alarms when they are most likely to be accurate.

Collective behavior and false alarms

Collectively-behaving species, a subset of group-living animals, should be especially prone to false alarms. I use the term “collective” in the sense of Sumpter (2006): interacting individuals produce a pattern at a spatial scale that is greater than the range of individual interactions. To understand why collectively-behaving species should produce false alarms, consider one type of collective behavior: synchrony. In synchronous behavior, individuals closely coordinate their behavior together in time (Sumpter 2010a). This coordination requires neighbors to be within sensory range of one another (Buck *et al*. 1981; Néda *et al*. 2000; Helbing & Farkas 2002; Ramaswamy & Cocroft 2009; Sumpter 2010a), and suggests that synchronously behaving species rely heavily on social information. Examples of synchronous behavior in the context of predator detection include giant honeybees shimmering to repel marauding wasps (Kastberger *et al*. 2008), oleander aphids waving synchronously to deter parasitoid wasps (Hartbauer 2010), and treehopper nymphs producing collective vibrational signals during predator attacks to elicit maternal defense (Cocroft 1996).

Given their heavy reliance on social information, the occurrence and propagation of false alarms are likely in synchronously signaling animals. Each collective signal begins with signals from just a few individuals and is then amplified, or propagated through the group by other individuals. The individuals that propagate the signal are unlikely to have any direct experience of the stimulus that elicited the first signals.

Regulatory mechanisms of collective behavior: the use of negative feedback

Because distinct forms of collective behavior, such as synchrony, occur in disparate taxa, collective behavior research over the past decade has largely focused on identifying general principles and regulatory mechanisms (Sumpter 2006; Couzin 2009; Sumpter 2010b). For example, positive feedback influences collective behavior at all levels of biological organization, including decision-making by cells and animal groups (Brandman 2005; Sumpter & Pratt 2009), and the behavior of neural networks (Douglas *et al*. 1995) and diverse animal taxa (Sumpter *et al*. 2008; Jeanson & Deneubourg 2009). Positive feedback is important for coordinating synchronous behavior (Collins & Sumpter 2007) and amplifying trails (Sumpter 2006) for group-living animals.

Negative feedback is hypothesized to be important for reducing tradeoffs between response speed or sensitivity and accuracy in collective behavior (Couzin 2009; Nieh 2010). In other words, for predator detection, negative feedback provides the independent source of information described earlier, and may limit false alarms. Despite the potential importance of negative feedback in collective behavior, evidence of it has only been shown in two animal taxa, honeybees (*Apis mellifera*) and Pharoah's ants (*Monomorium pharaonis*) (Robinson *et al*. 2005; Nieh 2010). Additionally, field observations of the treehopper *Umbonia crassicornis* suggest that maternal signals might provide negative feedback to collectively signaling offspring (Cocroft 1999a).

Whereas the same honeybee or Pharoah's ant individual produces multiple discrete signals to communicate recruitment or negative feedback, field data suggest that *U. crassicornis* families partition communicative roles. Offspring collectively signal to communicate predator attacks, or increases in risk, and these signals evoke maternal defense (Cocroft 1996). Mothers walk through offspring aggregations to find predators, because their defenses (i.e., kicks, wing-buzzes) are local (Cocroft 1999a). Maternal signals then increase after attacks end, and are correlated with a reduction in offspring signaling (Cocroft 1999a). I hypothesized that maternal signals reduce offspring signaling after predator attacks end, thus reducing the occurrence of false alarms. To use the vocabulary of the collective behavior literature, maternal signals provide negative feedback to signaling offspring.

After establishing that *U. crassicornis* maternal signals reduce offspring signaling after predator attacks, I investigated whether a closely related species (*Platycotis vittata*) shares the same communicative strategy. *Platycotis* is the sister genus to *Umbonia* (Lin *et al.* 2004), with very similar maternal care (Beamer 1930; Wood 1976a). However, collective offspring signaling in *P. vittata* occurs infrequently when compared with *U. crassicornis,* and maternal signaling occurs at higher rates (Cocroft, pers. comm.; Hamel, pers. obs.). I hypothesized that offspring collective signaling in *P. vittata* should occur in the context of high predation risk (i.e., during attacks) and evoke maternal defense, and that maternal signaling should occur most in the context of decreased predation risk and reduce collective offspring signaling.

Social signals and unintended receivers

In my first two chapters, I consider mother-offspring communication in *U. crassicornis* and *P. vittata* as a sender-receiver dyad. However, vibrational signals can travel through branches, and all invertebrate predators known to predate on *U. crassicornis* and *P. vittata* are vibrationally sensitive (Henry 1980; Pfannenstiel 1995; Hölldobler & Roces 2001; Barth *et al.* 2008; Jeanne 2009). Eavesdropping predators and parasitoids are an important source of selection on communication by prey (*reviewed in* Zuk & Kolluru 1998; Haynes & Yeargan 1999). Although most studies of predator eavesdropping have focused on mate advertisement signals, predators and parasitoids may also eavesdrop on social signals (Allan *et al.* 1996; Haynes & Yeargan 1999; Krams *et al.* 2007; Magrath *et al.* 2010). When multiple animals in close proximity communicate about food or predator discovery, this should provide a robust and persistent source of information to unintended receivers. To better understand the costs and benefits of *P. vittata* maternal and offspring signaling, I examined the responses of one generalist, vibrationally-sensitive predator to *P. vittata* maternal and offspring signals.

Summary of research questions

In this dissertation, I tested the hypothesis that treehopper maternal signals reduce collective signaling by offspring groups in the context of decreased predation risk. I investigated whether a closely-related species shares the strategy of partitioning communicative roles between mother and offspring. Finally, I considered this communication strategy in a community context. I investigated the responses of a vibrationally-sensitive generalist insect predator to *P. vittata* familial signals. Previous work by Tom Wood, Rex Cocroft, and Karthik Ramaswamy have provided a framework for asking these questions in *Umbonia crassicornis* and *Platycotis vittata*, two closely related species of treehoppers.

Focal species

The monophyletic taxonomic group that includes *Umbonia* and *Platycotis* (tribe Hoplophorionini) contains eight genera (Lin *et al*. 2004) (Figure 1). Most species in the group have a neotropical distribution, but *P. vittata* is broadly distributed in North America and Mexico, and an introduced population of *U. crassicornis* has established in south Florida. Hoplophorionine treehoppers do not participate in ant mutualisms, and maternal care of eggs and offspring has been documented in all genera. Maternal signaling has been documented in all genera and collective offspring signaling has been documented in six genera (RB Cocroft, pers. comm.).

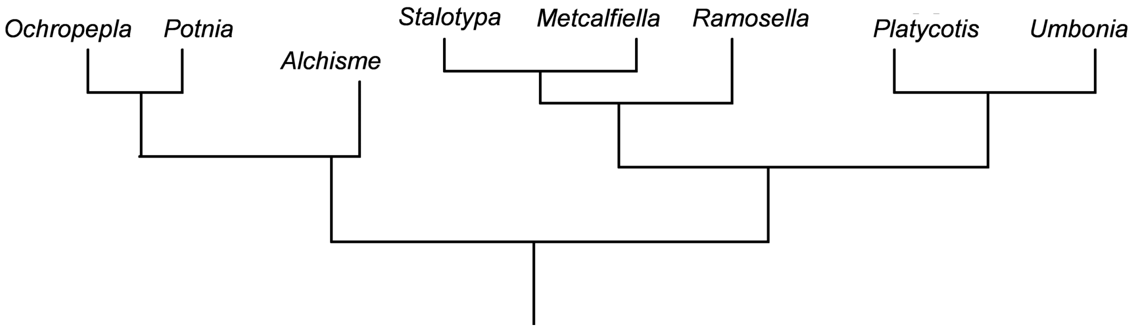

Figure 1. Cladogram showing relationships among the genera of tribe Hoplophorionini. Maternal signaling has been documented in all genera; offspring collective signaling has been documented for all genera except *Stalotypa* and *Ramosella*. Modified from Lin *et al*. (2004).

Umbonia crassicornis families occur on mimosoid legumes (e.g., *Albizia julibrissin*) (Figure 2). Mothers lay one clutch of eggs, and they defend eggs and clustered offspring groups from invertebrate predators until their offspring eclose as adults (Wood 1976b). A family typically consists of 40 to 50 sedentary offspring, arranged around a branch with their mother. Maternal defense is vital for offspring survival (Cocroft 1999a). When a *U. crassicornis* offspring group is attacked by an invertebrate predator, the aggregation produces synchronized, repetitive group signals, and this elicits maternal defense (Cocroft 1996). A mother responds to offspring signals by walking through the aggregation. She must find the predator in order to evict it, because her defenses (i.e., kicking, wing-buzzing) are only effective at close range

(Cocroft 2002). To find a predator amid an offspring aggregation, a mother uses information from her offspring's collective signals (Ramaswamy & Cocroft 2009; Ramaswamy 2010).

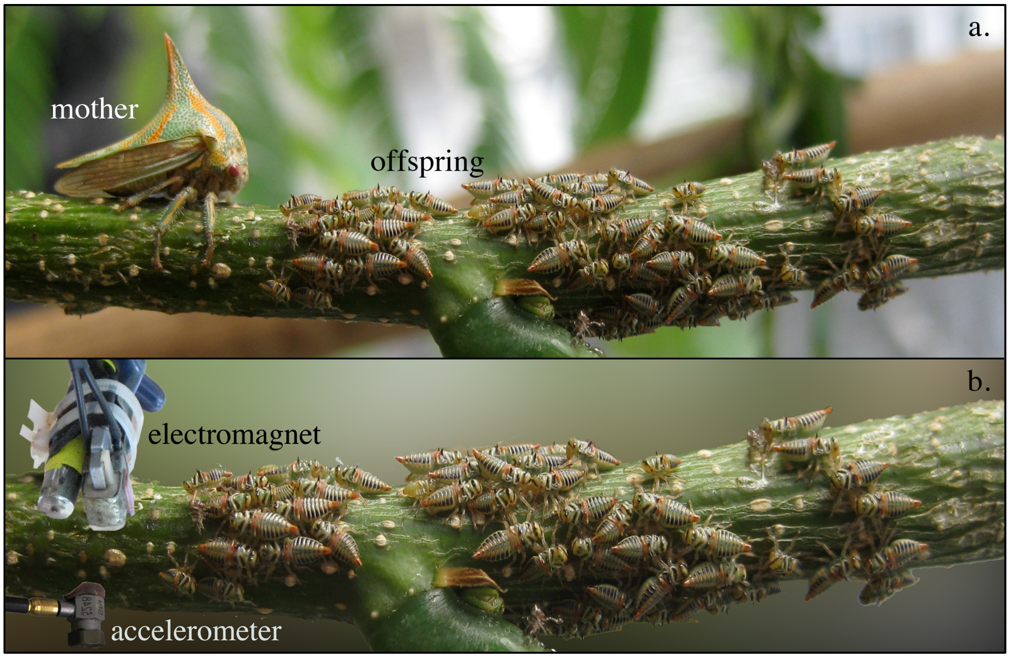

Figure 2. *Umbonia crassicornis* family on *Albizia julibrissin* branch. *(a)* Mother with offspring aggregation; *(b)* Playback apparatus as used in Chapter 2.

After producing repeated signals, the offspring's signaling thresholds drop (Cocroft 1999b). Groups often continue to signal spontaneously after the danger has passed (Cocroft 1999a), and nymphal aggregations signal in response to playbacks of their own signals (Cocroft 1999b). Taken together, this suggests collective signaling can be self-perpetuating. The mother also produces vibrational signals, which are temporally and spectrally distinct from offspring signals (Cocroft 1999a). An increase in maternal signaling after predator encounters end is associated with a decrease in nymphal signaling.

Platycotis is the sister genus to *Umbonia* (Lin *et al*. 2004) (Figure 3), with very similar maternal care (Beamer 1930; Wood 1976a). *Platycotis vittata* occurs on ≥ 30 species of oaks (*Quercus* spp.), and is broadly distributed in North America. Like *Umbonia* mothers, *Platycotis* mothers lay one clutch of eggs (Wood 1976a). A family typically consists of 40 to 50 sedentary offspring arranged around an oak branch with their mother (Wood 1976a). Throughout offspring juvenile development, a mother defends her nymphs from a broad suite of invertebrate predators, including wasps (Beamer 1930), ants, spiders, predatory stink bugs, and lacewing larvae (Hamel, unpub. data). In *P. vittata*, collective offspring signaling occurs infrequently, compared with *U. crassicornis,* but maternal signaling occurs more frequently and at higher rates (Cocroft, pers. comm.; Hamel, pers. obs.).

Figure 3. *Platycotis vittata*. *(a)* Nymphal aggregation with accelerometer, *(b) Podisus maculiventris* nymph feeding on *P. vittata* nymph, next to *P. vittata* mother, *(c)* Ants attacking a *P. vittata* egg clutch, *(d)* spider predating upon *P. vittata* mother, *(e) Platycotis* mother with 2nd instar nymphs, *(f) Platycotis* mother with late instar nymphs. All photos taken at Ordway-Swisher Biological Station, Putnam Co., FL, 2009 and 2010.

Family groups of both *U. crassicornis* and *P. vittata* often develop in the presence of potential invertebrate predators on the same host plant (Hamel, unpub. data), and predation is likely an important selective pressure on these species (Figure 4). All known invertebrate predators of these species are vibrationally-sensitive and use vibrational communication at some life stage (Henry 1980; Pfannenstiel 1995; Hölldobler & Roces 2001; Barth *et al*. 2008; Jeanne 2009). The pentatomid *Podisus maculiventris* is an appropriate focal predator because it is a generalist predator and multiple species of pentatomid nymphs have been observed preying upon *P. vittata* in the field (M. Rothschild, pers. comm.; Hamel, pers. obs.). Moreover, it uses incidental vibrations from caterpillars to locate and prey upon them (Pfannenstiel 1995).

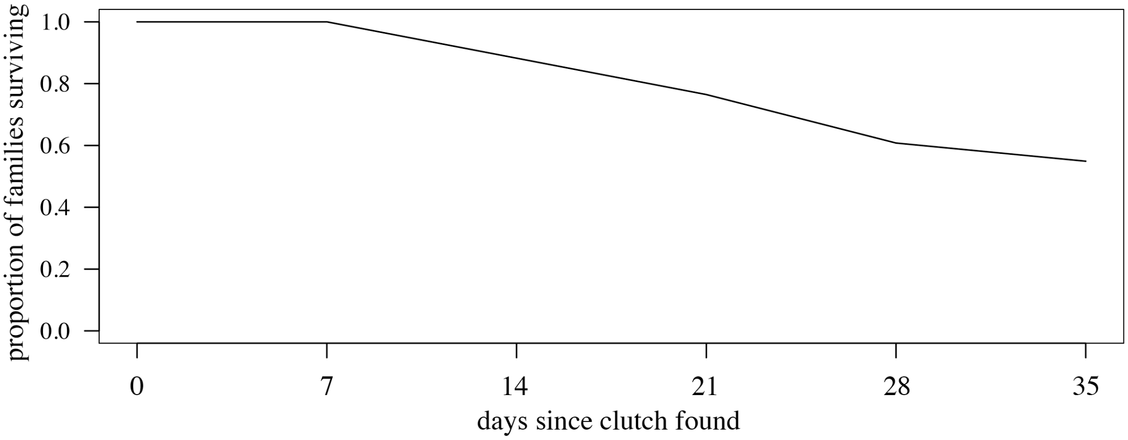

Figure 4. Survivorship of *Platycotis vittata* families in a north Florida population, February to April 2009. Each family consisted of a mother and her aggregated offspring. All families were located as egg clutches and censused every three days. The line shows whole family mortality; surviving families experienced differential survivorship. By day 35, all nymphs were in the 4th or 5th instar. N = 51.

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Chapter 2. Parental signals communicate decreased risk and modify collective signaling behavior of offspring in a group-living insect.

SUMMARY

Within animal groups, individuals can learn of a predator's approach by attending to the behavior of others. The use of social information increases an individual's perceptual range, but can also lead to error propagation. Error copying is especially likely in species that signal collectively, because the coordination required for collective displays relies heavily on social information. Errors could be reduced by modulating individual responses to social information, down-weighting the importance of indirect cues when risk is low. However, this mechanism requires that individuals have information on the current level of overall risk. I tested the hypothesis that partitioning communicative roles allows signaling groups to adaptively modulate their response to social information. 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 I show that this maternal communication inhibits collective signaling by offspring. The results suggest that maternal signals communicate decreased risk, elevating offspring signaling thresholds and possibly causing offspring to down-weight social information. This is the first study to show that collectively signaling groups can manage false alarms and error propagation through partitioning communicative roles.

INTRODUCTION

Uncertainty is a product of a changing environment and contributes to decision-making errors. Group-living animals may reduce uncertainty by integrating social information (Schmidt *et al.* 2010), such as behavioral cues or signals from group members (Wilson 2000; Caro 2005a; Zuberbuhler 2009), with personal information (Danchin 2004; Rieucau & Giraldeau 2011). Social information is especially important in responding to predators because collective detection can greatly increase the perceptual range of a group member (Pulliam 1973; Lima 1995b). However, one potential limit to the benefits of collective detection is that, in addition to correct responses to predators, false alarms can also propagate through a group (Lima 1995a; Giraldeau *et al.* 2002; Sirot 2006; Bell *et al.* 2009). Such errors may be costly (Kahlert 2006; Bell *et al.* 2009). The first individual(s) to respond to a stimulus exerts disproportionate influence on group members and can cause a wave of decisions to spread, producing an information cascade (Bikhchandani & Hirshleifer 1998).

False alarms are common in a variety of group-living taxa (Hoogland 1981; Kahlert 2006; Bell *et al.* 2009) and can even outnumber correct detections (Cresswell *et al.* 2000; Beauchamp 2010). When false alarms propagate through groups, most or all group members can lose foraging or mating opportunities (Proctor *et al.* 2001; Sirot 2006; Bell *et al.* 2009). However, any reduction in false alarms comes with a tradeoff of increased risk of not detecting a predator (Wiley 1994).

What strategies do group-living animals employ to limit false alarms and error propagation while maintaining the benefits of collective detection? Two potentially important strategies are updating information among group members (Sih 1992; Bell *et al*. 2009; Ferrari *et al*. 2010) and modulating response thresholds (Hölldobler 1999; Bell *et al*. 2009). Both of these strategies may involve social communication, whereby signals influence receiver behavior (Wagner & Danchin 2010). Communication that updates group members about decreases in predation risk may elevate response thresholds during periods when false alarms and error propagation are likely (e.g., after predator encounters) (Bell *et al*. 2009). Communication about decreases in risk poses two challenges: individuals must decide when risk has decreased (i.e., a predator is no longer present) (Sih 1992) and receivers must discriminate between signals that communicate increased risk and signals that communicate decreased risk.

One mechanism for modulating response thresholds and updating information is communicative role partitioning, where an informed subset of individuals communicate personal information to group members. Group living species with sentinel behavior partition communicative roles and sometimes solve the challenge of receiver discrimination by using multiple signal types (Blumstein *et al*. 2004; Bell *et al*. 2009). Group members are informed of predator detections with one signal type, and of relative risk level with a second signal type; the second type of signal modifies the likelihood that receivers will respond to the first.

A third strategy for minimizing the false alarms and error copying that promote erroneous information cascades is for individual responses to adjust the relative weight given to personal and social information (Giraldeau *et al*. 2002; Blumstein *et al*. 2004; Nocera & Ratcliffe 2009). For example, if an individual has recent personal information about predator presence, a single alarm cue from a nearby individual may be sufficient to elicit a response. However, if an individual has no recent personal evidence of a predator, it may require multiple alarm cues or signals from group members (i.e., social information) to override its personal information before it will respond (Cresswell *et al.* 2000; Proctor *et al.* 2001; Giraldeau *et al.* 2002; Blumstein *et al.* 2004; Sirot 2006; Beauchamp & Ruxton 2007; Beauchamp 2010). Although much literature on group-living animals is dedicated to alarm signals (Rohrig *et al.* 1999; Blumstein *et al.* 2004; Nocera & Ratcliffe 2009), few empirical studies have explored how communication can modulate the interplay between personal and social information (Blumstein *et al.* 2004; Bell *et al.* 2009).

Studies of group-living animals that produce collective signals in response to predators (Hölldobler 1999; Rohrig *et al.* 1999) are entirely missing from the literature on false alarms and information cascades. I use the term *collective* in the sense of Sumpter (2006), where interacting individuals produce a coherent pattern that exceeds individual interaction range. Synchronized, or wavelike, collective signaling in particular suggests a strong reliance on social information because neighbors need to be within sensory range to coordinate synchrony (Buck *et al.* 1981; Néda *et al.* 2000; Helbing & Farkas 2002; Ramaswamy & Cocroft 2009; Sumpter 2010a). Moreover, such signaling may be repetitive (Cocroft 1996; Schmelzer & Kastberger 2009; Hartbauer 2010a), suggesting that the social information necessary for coordinating one group signal also promotes repeated signals, perhaps through lowering response thresholds. Although communicative role partitioning (Rohrig *et al.* 1999) and threshold modulation (Hölldobler 1999) have been documented in collectively signaling animals, whether these strategies reduce false alarms and erroneous information cascades is an open question.

Here I investigate how the partitioning of communicative roles can allow groups to avoid misleading information cascades after a predator encounter. In the treehopper *Umbonia crassicornis*, mothers defend clustered offspring groups from invertebrate predators (Wood 1976a). The offspring produce collective vibrational signals that communicate the predator's presence and location to the defending mother (Cocroft 1996). However, after offspring produce repeated signals, their signaling threshold drops (Cocroft 1999a), and groups often continue to signal spontaneously after the danger has passed (Cocroft 1999b). The mother also produces vibrational signals, which are temporally and spectrally distinct from offspring signals (Figure 1) (Cocroft 1999b).

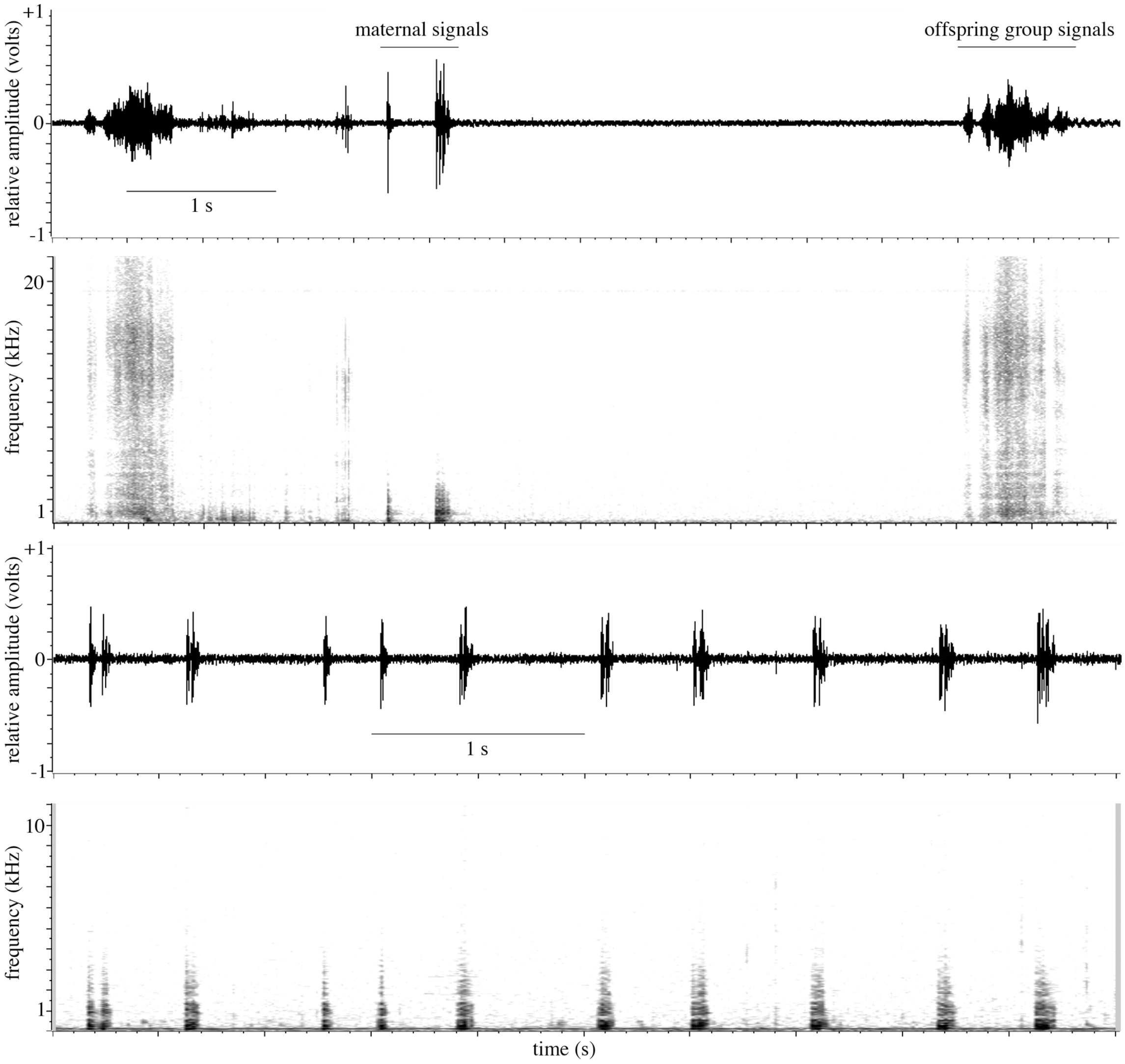

Figure 1. Top two panels: Waveform and spectrogram showing *Umbonia crassicornis* maternal and offspring vibrational signals produced during a predator encounter. Bottom two panels: Waveform and spectrogram showing *Umbonia crassicornis* maternal vibrational signals produced after a simulated predator encounter has ended.

Because mothers signal at a much higher rate after evicting the predator, I hypothesize that maternal signals communicate decreased risk and function to reduce post-predation false alarms among the offspring.

My aim in this study was to test the hypothesis that post-predation signaling by *U. crassicornis* females communicates decreased risk to offspring. I first quantified the signaling behavior of mothers and group-living offspring during predator encounters. I then experimentally tested the prediction that maternal signals reduce the production of spontaneous collective signals after a predator encounter. This is the first study to investigate how the partitioning of communicative roles can allow a collectively signaling group to avoid costs associated with false alarms and error propagation.

METHODS

(a) Insect collection and rearing

I collected late-instar and teneral adult *Umbonia crassicornis* aggregations from the USDA Subtropical Horticulture Research Station in Miami, FL. I maintained a greenhouse colony on potted *Albizia julibrissin* host plants, at 20 to 30°C on a 12:12 h light:dark cycle. To maintain genetic diversity, I collected new aggregations twice a year (Dec 2007, July 2008, Nov 2008, May 2009). I 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 fiberglass mesh, and all trees and insects were kept in a large, walk-in cage constructed of wood and fiberglass mesh. In the experiments described below, I used second and third generation *U. crassicornis* families in which nymphs were 2nd-4th instar. I was provided with pentatomid predators (*Podisus maculiventris* nymphs) by the USDA-ARS Biological Control of Insects Research Laboratory (Columbia, MO). I maintained a laboratory colony of *P. maculiventris* at ~25°C on a 14:10 h light:dark cycle. Pentatomid nymphs and adults were fed a combination of coddled fourth instar larvae of *Trichoplusia ni* (Hübner) and a zoophytogenous artificial diet (Coudron *et al.* 2002) and were provided with water via moist dental wicks (Richmond Dental) in small plastic weigh boats (Fisher Scientific). I housed adults of each sex in half-pint paper containers; when females produced eggs, eggs were collected in a new container in which nymphs developed. New nymphs were provided by the USDA-ARS Laboratory twice a year.

(b) General methods

I conducted the experiments described below in the laboratory from July 2008 through August 2009. I detected maternal and offspring vibrational signals with an accelerometer (PCB Piezotronics, NY, USA; Model 352A24, weight 0.8 g, frequency range: 0.8 Hz to 10 kHz ± 10%) attached 4 to 6 cm from each family using mounting wax and powered by a PCB Model 480E09 ICP Sensor Signal Conditioner. I recorded both offspring and maternal signaling responses and all experimentally generated vibrational stimuli on a Marantz PMD660 digital audio recorder at a sampling rate of 44100 Hz. I recorded family behavior using a digital video recorder (Sony Handycam Models HDR-HC7 and HDR-SR11). For each family in both experiments, I first set up signal detection and video equipment and allowed the family 1 h to acclimate. Different families were used in experiments 1 (predator introductions) and 2 (playback experiment).

(c) Experiment 1: Characterizing signaling responses to increased and decreased risk

I manipulated predation risk by introducing invertebrate predators (juvenile *Podisus maculiventris*) that had been fasted overnight to 10 *U. crassicornis* families on potted host plants (*Albizia julibrissin*). I allowed a predator to walk up a thin string tied to the treehopper family branch, ≥ 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 I mimicked my movements as in an introduction but did not introduce a predator and then recorded family responses for 1 h. I alternated treatment order and used each predator only once. I 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 scored family responses for the same timeframe as during the predator introduction treatment. I 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) Experiment 2: Testing whether maternal vibrational signals communicate decreased risk to offspring

The hypothesis that maternal signals communicate decreased risk predicts that after a predator encounter, offspring signaling should be reduced by maternal signals. To elicit offspring group signaling, I simulated predator encounters with 11 offspring aggregations whose mothers had been removed. I then played maternal vibrational signals, wind vibrations, or silence (generated in Audacity v.1.3.12) to the signaling offspring group. Each family received all three playback treatments. I simulated predation by presenting a crushed nymph from a different *U. crassicornis* family on a dowel ~1 cm under the center of each aggregation. Nymphs were frozen before being crushed and a fresh dowel was used for each presentation. Alarm pheromone from a crushed nymph acts as a predator cue (Nault *et al*. 1974) and reliably elicits group signaling from offspring groups. I 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 comprised of 30 s of stimulus followed by 30 s of silence; I included silent intervals for scoring of offspring signaling response, in case the presence of playback signals on the audio track interfered with scoring. However, because offspring group signals contain energy at higher frequencies than do the maternal signals or wind vibrations, I was easily able to score all group signals, including those produced during vibrational stimuli.

I 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 I played their own mother's signaling in response to a simulated predator encounter (as described above). To obtain recordings of each mother's vibrational signals, I simulated a predator encounter in the manner described above (d) with each family one day prior to the playback experiment. When offspring began signaling, mothers patrolled the family, signaled, and searched for the source of disturbance. I allowed mothers to find the dowel with crushed nymph, which they kicked as they would a predator. As soon as a mother kicked the dowel, I withdrew the predator cue from the aggregation. I used only post-eviction maternal signals for playback stimuli. I also played wind vibrations and silence as controls: I recorded wind vibrations from one branch on each of three different trees in the field and I generated silence in Audacity v.1.3.12. I played silence as I played vibrational stimuli, in order to rule out the possibility that my equipment generated any electrical noise that influenced the behavior of the insects.

To play vibrational stimuli to the *U. crassicornis* offspring, I glued a small neodymium magnet (United Nuclear Scientific, Laingsburg, MI) to the aggregation's branch at the trunk end of the aggregation, the mother's typical position at rest. I positioned an electromagnet parallel to the magnet at a distance of 1 to 2 mm. I then transmitted vibrational stimuli to the electromagnet from Audacity v.1.3.12 on a MacBook 2.4 GHz Intel Core Duo via a RadioShack 40-watt PA amplifier. To ensure that the playback signals had the correct amplitude spectrum, I used a custom program in MatLab v.R2008bSV to assess frequency filtering by the branch and to build an inverse filter (Cocroft 1999a). I used this to filter the maternal signals and wind vibrations played through that branch. To ensure I was playing stimuli at biologically relevant amplitudes, I matched playback stimulus amplitude to signal amplitude from the original field recording.

(f) Scoring and statistical methods

I used XBAT (Harold Figueroa, Ithaca, NY) to score presence of maternal signals and offspring group signals and from these data calculated signaling rates for mothers and offspring of each family. I compared signaling responses among treatments in both experiments using the Quade test (Quade 1979), a non-parametric analog of repeated-measures ANOVA. I 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 my *a priori* hypotheses. I adjusted comparison p-values for false discovery rate (FDR) (Benjamini & Hochberg 1995). All statistical tests were conducted with R statistical software, version 2.13.0.

RESULTS

(a) Experiment 1: Characterizing signaling responses to increased and decreased risk

Predator encounters lasted 6.21 ± 6.48 min (mean ± S.D.). Pentatomids contacted ≥ 1 nymph during all predator introductions and attacked ≥ 1 nymph in all but one introduction (introductions with attacks = 9, introductions with contact only = 1). In 1/3 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 aggregations containing predators.

Offspring group signaling rates differed by predator encounter context (Quade test: N = 10 aggregations, Quade $F = 12.670$, df = 2/18, $p = 0.0004$). Group signaling rate was greater during and after predator encounters than during control treatments (control vs. during predation, Wilcoxon $W = 0$, $p = 0.002$, $p_{\mathrm{FDR}} = 0.006$; control vs. post-predation, Wilcoxon $W = 1$, $p = 0.004$, $p_{\mathrm{FDR}} = 0.008$). Offspring signaling rates while predators were in contact with families did not differ statistically from those after predators left families (Figure 2) (predation vs. post-predation, Wilcoxon $W = 13$, $p = 0.160$, $p_{\mathrm{FDR}} = 0.160$).

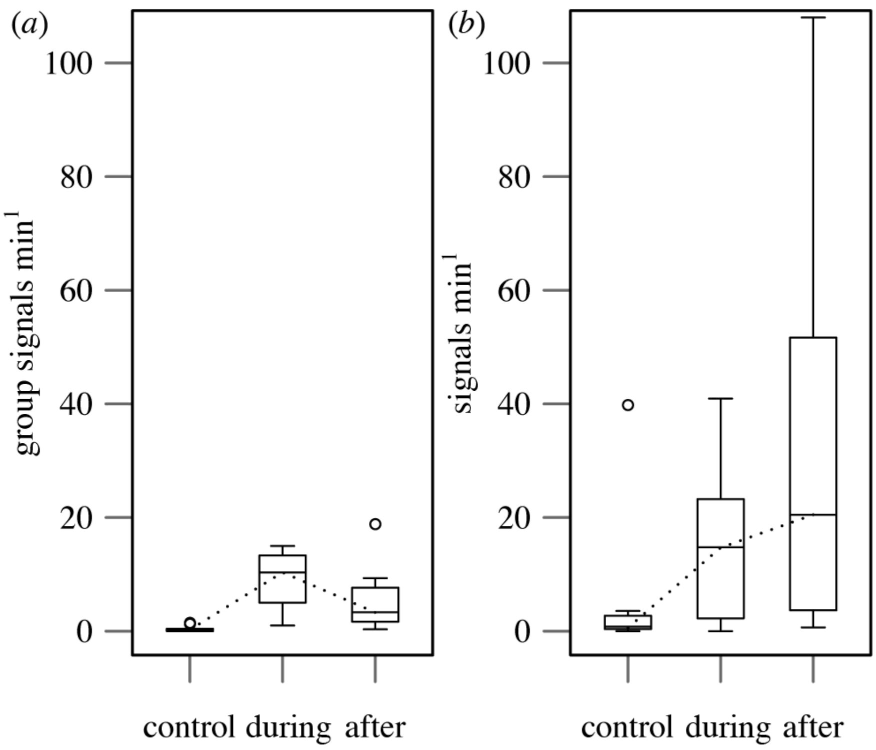

Figure 2. Signaling responses of *Umbonia crassicornis* families to introduced predators. No predators were introduced in control treatments. Box plots show distributions of (*a*) offspring group signaling rate and (*b*) maternal signaling rate (minimum, first quartile, median, third quartile, maximum;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

Like offspring group signaling rates, maternal signaling rates differed among predator encounter contexts (Quade $F = 3.5954$, df = 2/18, $p = 0.049$). Post-hoc comparisons here were not significant after controlling for FDR (control vs. during predation, Wilcoxon W=11, $p = 0.106$, $p_{\mathrm{FDR}} = 0.131$; control vs. post-predation, Wilcoxon $W = 7$, $p = 0.037$, $p_{\mathrm{FDR}} = 0.111$; predation vs. post-predation, Wilcoxon W =12, $p = 0.131$, $p_{\mathrm{FDR}} = 0.131$). However, mothers tended to signal at a higher rate after predator encounters than during controls (Figure 2).

Maternal signaling and offspring group signaling rates diverged between "during encounter" and "after encounter" contexts (difference between during and after encounter contexts, maternal signaling vs. offspring group signaling, Wilcoxon $W = 4$, $p = 0.014$).

(b) Experiment 2: Testing whether maternal vibrational signals communicate decreased risk to offspring

Maternal vibrational signals reduced offspring group signaling. Offspring group signaling rate differed by vibrational playback stimulus (Quade $F = 5.2041$, df = 2 / 20, $p = 0.015$). Offspring produced more group signals during silence and fewer group signals while their mother's vibrational signals or wind vibrations were played (Figure 3) (silence vs. mother, Wilcoxon $W = 7$, $p = 0.018$, $p_{\mathrm{FDR}} = 0.035$; silence vs. wind vibrations, Wilcoxon $W = 1$, $p = 0.001$, $p_{\mathrm{FDR}} = 0.003$). There was no difference in response between wind vibrations and maternal vibrational signals (Wilcoxon $W = 37$, $p = 0.375$, $p_{\mathrm{FDR}} = 0.375$).

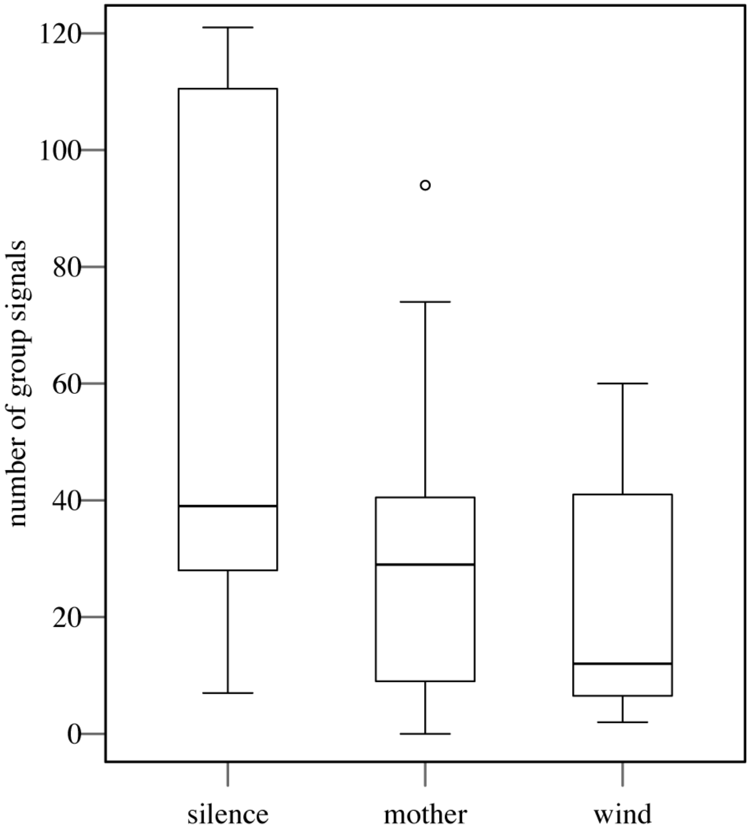

Figure 3. Effect of vibrational playbacks on *Umbonia crassicornis* offspring group signaling. Boxplots show the distribution of all offspring group signals produced during playback treatments (minimum, first quartile, median, third quartile, maximum; open circle represents an outlier).

DISCUSSION

Group living animals benefit from collective detection of predators (Pulliam 1973; Lima 1995b), but such benefits are likely to be balanced against costs associated with the occurrence of false alarms (Cresswell *et al*. 2000; Beauchamp 2010) and the tendency for potentially costly errors (Kahlert 2006; Bell *et al*. 2009) to rapidly propagate through a group (Lima 1995a; Giraldeau *et al*. 2002; Sirot 2006). To limit the occurrence and propagation of errors, individuals should frequently update their information**,** modulate response thresholds according to changes in risk, and preferentially weigh personal or social information, whichever is more reliable. The results of my playback experiment and predator introductions, together with data from field observations (Cocroft 1999b) and experiments testing the function of offspring group signaling (Cocroft 1996; Cocroft 1999a; Ramaswamy & Cocroft 2009) provide strong evidence that *U. crassicornis* families partition communicative roles to accomplish these tasks.

Communicative and defensive roles in *U. crassicornis* families are constrained by life stage characteristics. 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 defense (Cocroft 1996). During attacks, only the victim and its nearest neighbors are likely to have personal information about predator presence and location. These individuals are most likely to initiate group signaling; signaling by other group members, or social information, should amplify this response.

Whereas 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 scans only a small fraction of the area around the aggregation. Additionally, the only mechanism for communicating decreased risk would be a complete cessation of offspring signaling. In contrast, defending mothers are able to obtain reliable information about predator departure because maternal defenses are effective only at close range (Cocroft 2002), 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.

The results of this study suggest that maternal signals after attacks communicate decreased risk and elevate offspring response thresholds. Offspring signaling thresholds decrease after a predator attack (Cocroft 1999a). Undisturbed offspring aggregations rarely produce group signals (Cocroft 1999b), but recently disturbed aggregations will continue producing spontaneous group signals (i.e., false alarms) after a predator leaves (Cocroft 1999b; this study). Increasing response thresholds limits false alarms in other taxa (Bell *et al*. 2009) 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.

Mothers may also decrease the influence of social information from other nymphs *during* attacks. When a predator attack is simulated in the presence of the mother, there is a gradient of signaling within the offspring group, such that individuals closer to the predator are more likely to participate in collective signals (Ramaswamy & Cocroft 2009). The mother uses this signaling gradient to locate the predator (Ramaswamy 2010). In the absence of the mother, the gradient is no longer reliably present because individuals farther from the predator are just as likely to signal as those nearest to the predator. In other words, nymphs that are relying entirely on social information are as likely to signal as those with personal information. Some cue associated with the mother reduces the nymphs' response to social information from other nymphs; this cue may be maternal vibrational signals.

Umbonia crassicornis families are attacked by several different types of invertebrate predators (Wood 1976a; Dowell & Johnson 1986; Cocroft 1996). The directional information provided by offspring signals may be more important to mothers searching for cryptic predators (e.g., pentatomids) than to mothers defending against conspicuous predators (e.g., wasps). This idea is supported by a difference between my results and those of a field study by Cocroft (1999b). In over half of encounters with wasps, *U. crassicornis* mothers responded to attacks before offspring began signaling. However, mothers never responded to pentatomid attacks before offspring began signaling. Mothers also signaled more during pentatomid attacks than during wasp attacks, and offspring signaled less (Appendix 1, Table I). Although a comparison between results from a field study and a laboratory study must be treated cautiously, these observations fit what one would predict if maternal signals during attacks enhance directional information in the collective signals of offspring.

If vibrational signaling is less costly than active antipredator defense, then maternal signaling that reduces false alarms will also reduce the overall costs of defense.

Maternal defense in another treehopper species (*Publilia concava*) has metabolic costs, evidenced by tradeoffs between duration of care and lifetime fecundity (Zink 2003). Metabolic costs may also result in reduced longevity in insect species (Okada *et al.* 2011). The maximum observed lifespan for an *Umbonia* female in our greenhouse colony is 100 days; minimum generation time is eight weeks (56 days) (Cocroft, unpub. data). Given that her nymphs will be vulnerable to invertebrate predators throughout their month-long juvenile development, a mother should limit the metabolic costs of defense. If a mother dies before her offspring reach adulthood, her undefended offspring will probably perish (Wood 1976a; Dowell & Johnson 1986; Cocroft 2002).

In addition to incurring unnecessary metabolic costs for mothers, continued signaling by offspring may also attract other, nearby invertebrate predators or parasitoids, many of which are vibrationally-sensitive, such as spiders (Barth 1998), ants (*reviewed in* Hölldobler 1999), and pentatomids (Pfannenstiel 1995), and some of which have been shown to use vibrational cues (Pfannenstiel 1995; Djemai *et al.* 2004; Fertin & Casas 2007) 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 (Narhardiyati & Bailey 2005; Roberts *et al.* 2007; Virant-Doberlet *et al.* 2011). By reducing offspring signaling after a predator encounter, mothers may reduce the risk of advertising the family's location to additional predators. Continued offspring signaling could also indirectly advertise the family to visually-oriented predators (e.g., songbirds). Families are cryptic when stationary (Hamel, pers. obs.), 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 (Brach 1975; Ramaswamy & Cocroft 2009).

Group signaling by *U. crassicornis* nymphs is a synchronized collective behavior in the sense of Sumpter (2006). To the best of my knowledge, this is the first example in any species of collective signaling being modified by an individual that does not participate in the collective behavior. To limit the duration of offspring signaling after an attack and prevent sporadic group signals from beginning again after signaling ceases, social information from another party is necessary. Nymphs engaged in collective signaling are necessarily relying on social information and nymphal signals only communicate increased risk.

In summary, *U. crassicornis* offspring collective signaling, together with maternal signaling, constitute a reciprocal communication system. Communicative roles are partitioned in a way where the individual(s) likely to have the most reliable information about predation risk provides that information to the rest of the family. Mothers have the most certain information on predator location after predator attacks, and maternal signals function to reduce offspring signaling after predator encounters end. Maternal signals likely increase offspring thresholds and increase the weight offspring give to personal information. Promising avenues of research to pursue in future studies include exploring whether maternal signals elicit or enhance directional information in offspring group signals and investigating the influence of personal and social information on offspring and maternal behavior.

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Chapter 3. The use of role-partitioning and negative feedback to regulate collective signaling in group-living treehoppers (Hemiptera: Membracidae).

SUMMARY

Collective behaviors, including group movement and synchrony, occur in numerous and divergent taxa. In a search for general principles, recent effort has focused on mechanisms that regulate collective behavior, such as positive feedback. Negative feedback is also hypothesized to be important as a means of minimizing investment in unprofitable group decisions, but its role has only been documented in three taxa. I investigated whether a communication strategy, where one individual provides negative feedback to a collectively behaving group, is shared between two closely-related species of insects (*Platycotis vittata* and *Umbonia crassicornis*). In both species, mothers defend offspring groups from invertebrate predators. In *U. crassicornis*, previous work has shown that offspring groups produce synchronous signals that elicit maternal defense, and maternal signals inhibit offspring signals after attacks end, likely reducing false alarms. I found that collective offspring signaling, its function, and the use of role-partitioning are shared between these species. However, differences in signaling rates, as well as differences in the stage of predator attack when offspring and maternal signaling occur, suggest that negative feedback may not provide the same benefits in both species.

INTRODUCTION

Collective behavior (*sensu* Sumpter 2006) is a general term describing interactions among group members that result in patterns at spatial scales greater than the individual interaction range. Examples include coordinated group movement (e.g., flocking, swarming, schooling), living structures (e.g., ant rafts and bridges), and synchronous signaling (e.g., katydid choruses, synchronized fireflies, shimmering by giant honeybees) (*reviewed in* Sumpter 2010). Because each form of collective behavior is documented in diverse taxa, there has been strong interest over the past decade in identifying predictors of convergence; a search for general principles (Camazine *et al*. 2003; Couzin *et al*. 2005; Sumpter 2006; Couzin 2009; Sumpter 2010). Much of this effort has focused on mechanisms that regulate collective behavior, such as positive feedback, negative feedback, and response thresholds (Sumpter 2006; Sumpter *et al*. 2008b; Jeanson & Deneubourg 2009; Sumpter & Pratt 2009; Nieh 2010a).

Positive feedback regulates collective behavior at all levels of biological organization, including decision-making in cells and group-living animals (Brandman 2005; Sumpter & Pratt 2009), neural networks (Douglas *et al*. 1995), physiological homeostasis (Lam 2010), and social groups in diverse animal taxa (Sumpter *et al*. 2008a; Jeanson & Deneubourg 2009). Positive feedback generally functions to propagate a response past a certain threshold (Plenz & Thiagarajan 2007) or through a group (Ward *et al*. 2008). In animal groups, positive feedback is important for coordinating synchronous behavior (Collins & Sumpter 2007) and amplifying trails that promote group movement (Sumpter 2006).

Negative feedback is hypothesized to be important for reducing tradeoffs between response speed or sensitivity and accuracy in collective behavior (Couzin 2009; Nieh 2010a). Consider a group that performs a synchronous behavior to deter attacking predators (Kastberger *et al*. 2008; Hartbauer 2010). One or a few individuals produce a predator detection signal. This signal is propagated by neighbors and rapidly spreads through the group. To be effective at deterring predators, this group response requires that individuals both detect predators and respond to the signals of other group members with high sensitivity. However, as group members are more prone to respond to a stimulus, they are also more likely to make errors and respond to spurious stimuli, that is, to produce false alarms (Wiley 1994). If group members had an independent source of information on the background level of risk, they could avoid this tradeoff between sensitivity and false alarm rate by limiting responses to situations in which the likelihood of producing false alarms is low. Such an information source could be a correlate of predation risk, such as light level (Beauchamp 2010), or it could be signals by some group members that have access to information about the current level of risk (Bell *et al*. 2009).

Despite the potential importance of negative feedback in collective behavior, so far it has been shown to influence collective behavior in only three animal taxa. Honeybee *(Apis mellifera)* workers dampen recruitment to foraging sites where they have experienced simulated attacks (Nieh 2010a), and a model suggests that negative feedback prevents colonies from robbing other well-defended colonies against which they are unlikely to prevail (Johnson & Nieh 2010). Pharoah's ants *(Monomorium pharaonis)* mark unrewarding trails with deterrent pheromone (Robinson *et al*. 2005). A model suggests that without negative feedback, foraging trails that are no longer profitable continue to be re-marked with trail pheromone by Pharoah's ants during random encounters. These workers reinforce and amplify the trail pheromone, maintaining a trail without reward (Robinson *et al*. 2008). Finally, thornbug treehopper (*Umbonia crassicornis*) mothers produce vibrational signals to reduce collective signaling by their offspring after predator attacks (Chapter 1). For both honeybees and Pharoah's ants, negative feedback permits colonies to rapidly cease allocating foragers to a resource when costs likely outweigh benefits.

Whereas a single Pharoah's ant or honeybee worker may provide both positive and negative feedback through dedicated signals, *U. crassicornis* families partition communicative roles: only one party provides negative feedback. When a *U. crassicornis* offspring group is attacked by an invertebrate predator, the aggregation produces synchronized, repetitive group signals which elicit maternal defense (Cocroft 1996). A mother responds to offspring signals by walking through the aggregation. She must find the predator in order to evict it because her defenses (i.e., kicking, wing-buzzing) are effective only at close range (Cocroft 2002). To find a predator amid an offspring aggregation, a mother uses information from her offspring's collective signals (Ramaswamy & Cocroft 2009; Ramaswamy 2010).

Offspring groups of *U. crassicornis,* however, are prone to signaling after an attack, and nymphal aggregations signal in response to playbacks of their own signals (Cocroft 1999a). Taken together, these observations suggest collective signaling can be self-perpetuating. Moreover, false alarms, in the form of signaling after the predator's departure, are observed (Cocroft 1999b). Mothers are mobile, searching for and evicting predators (Wood 1976a; Cocroft 1999b) and thus have more certain knowledge of whether a given predator has been evicted than does any individual nymph. Mothers produce vibrational signals during and after attacks (Cocroft 1999b). After predator attacks, an increase in maternal signaling rate inhibits offspring signaling (Chapter 1). In this way, negative feedback is a rapid response to decreases in predation risk that limits false alarms, even as offspring respond to increases in predation risk with high sensitivity.

Because maternal defense is vital for offspring survival (Cocroft 1999b), offspring signaling is likely adaptive. Offspring signals must be produced collectively to elicit maternal defense (Cocroft 1996); mothers do not respond to a single nymphal signal, or to several nymphs producing uncoordinated signals. Thus selection should favor not only sensitivity for predator detection, but also for signal propagation through offspring aggregations. By providing an independent source of information on the background level of risk, *U. crassicornis* maternal signaling allows a family to escape the tradeoff between high sensitivity and high false alarm rate (Chapter 1).

Here I investigate whether a closely related species shares the antipredator communication strategy of *Umbonia crassicornis*. *Platycotis* is the sister genus to *Umbonia* (Lin *et al*. 2004), with very similar maternal care (Beamer 1930; Wood 1976b). However, in *P. vittata*, collective offspring signaling occurs infrequently, compared with *U. crassicornis,* but maternal signaling occurs more frequently and at higher rates (Cocroft, pers. comm.; Hamel, pers. obs.).

To investigate antipredator communication in *P. vittata*, I first characterized family responses to changes in predation risk by introducing generalist insect predators to families. With a playback experiment, I next tested whether collective offspring signals function to evoke maternal defense, as they do in *U. crassicornis*. With a second playback experiment, I tested whether maternal signals provide negative feedback and reduce offspring signaling.

METHODS

(a) General methods

I conducted all experiments in the field at the University of Florida's Ordway-Swisher Biological Station (OSBS) (Putnam Co., FL) February to April in 2009 and 2010. I located *P. vittata* mothers on eggs in February 2009 and 2010 by scanning branch ends of several oak species (*Quercus virginiana*, *Q. geminata*, *Q. laurifolia*, and *Q. nigra*). In 2010, I protected each mother and egg mass with a predator exclusion cage made of fine mesh. I used only 2nd to 4th instar nymphal aggregations in all experiments. Each family was used in only one experiment.

I detected maternal and offspring vibrational signals with an accelerometer (PCB Piezotronics, NY, USA; Model 352A24, weight 0.8 g, frequency range: 0.8 Hz to 10 kHz ± 10% or Vibra-Metrics, NJ, USA; Model 9002A, weight 0.8 g, frequency range: 8 Hz to 18 kHz ± 10%) attached < 10 cm from each family using mounting wax and powered by a signal conditioner and power supply (PCB Model 480E09 or Vibra-Metrics Model P5000). I recorded both offspring and maternal signaling responses and any vibrational stimuli I played on a Marantz PMD660 digital audio recorder at a sampling rate of 44100 Hz. I recorded family behavior using a digital video recorder (Sony Handycam Models

HDR-HC7 and HDR-SR11). For each family in all experiments, I first set up vibration recording and video equipment and allowed the family 1 h to acclimate.

I obtained predators (the pentatomid *Podisus maculiventris*) from the USDA-ARS Biological Control of Insects Research Laboratory (Columbia, MO) and transported them to OSBS. This pentatomid is an appropriate species for exploring the response of *P. vittata* families to predation because it is a generalist predator, and pentatomids have been observed preying upon *P. vittata* in the field (Hamel, pers. obs.; M. Rothschild, pers. comm.). I maintained a laboratory colony of *P. maculiventris* at OSBS at ~25°C on a 14:10 h light:dark cycle. Pentatomid nymphs and adults fed on a combination of coddled fourth instars of *Trichoplusia ni* (Hübner) and a zoophytogenous artificial diet (Coudron *et al*. 2002) and obtained water via moist dental wicks (Richmond Dental) in small plastic weigh boats (Fisher Scientific). I housed adults in half-pint paper containers; eggs were collected and transferred to a new container in which nymphs developed.

I carried out all statistical analyses using R (available at www.r-project.org/).

(b) Experiment 1: How do mothers and offspring respond to predator attacks?

I quantified family response to a predator attack by introducing invertebrate predators to six *P. vittata* families on oak tree branches. Predators were juvenile *Podisus maculiventris* that had been fasted overnight. I introduced a predator to a family's branch by allowing it to walk up a 1/4" poplar dowel and touching the dowel gently to the branch near the edge of the aggregation. I used each predator only once.

I used JWatcher (v. 1.0) to score offspring signaling rate, maternal signaling rate, and the time mothers spent walking. In the closely related *Umbonia crassicornis*, in which communication has been more extensively studied, mothers respond not to individual signals, but to collective signals produced by three or more individuals (Cocroft 1999a). To enable comparison of responses of *P. vittata* families during predator attacks with those of *U. crassicornis* families, I scored collective signals using Audacity (v. 1.3.13 beta) to verify that offspring group signals contained at least three overlapping individual signals. I compared signaling responses among predator encounter stages using the Quade test (Quade 1979), a non-parametric analog of repeated-measures ANOVA.

(c) Experiment 2: Do offspring vibrational signals communicate predator presence to mothers?

Based on observations from the predator introductions in this study (Experiment 1) and from a preliminary study with a separate *P. vittata* population (Appendix 2, Figure 1), I hypothesized that offspring signals communicate predator presence in the aggregation to mothers. If so, then offspring signals should be sufficient to evoke the mother's antipredator behavior, which includes walking and signaling. To test this prediction, I played offspring vibrational signals to family groups (consisting of a single mother and her offspring) in the field. As a control, I used silence, played as described in Chapter 1. Each family received both playback treatments. I controlled for treatment order by alternating the order between families and by waiting 30 min between treatments.

To obtain recordings of each family's offspring vibrational signals, I simulated predation one day before the playback experiment. I presented a crushed nymph from a different *P. vittata* family on a stainless steel probe ~1 cm under the center of the aggregation. A chemical cue from a crushed nymph acts as a predator cue (Nault *et al.* 1974; Cocroft 1999b) and reliably elicits collective signaling from offspring. Nymphs were frozen before being crushed and presented to offspring, and the probe was rinsed with 70% etOH after each presentation.

To play vibrational stimuli to the *P. vittata* offspring, I glued a small neodymium magnet (United Nuclear Scientific, Laingsburg, MI) to the aggregation's branch. I attached the magnet in the center of each aggregation. Nymphs did not move more than 1 to 2 cm during this procedure and the family remained aggregated around the magnet. I positioned an electromagnet 1 to 2 mm from the magnet so that faces were parallel. I then played vibrational stimuli to the electromagnet from Audacity v.1.3.12 on a MacBook 2.4 GHz Intel Core Duo via a RadioShack 40-watt PA amplifier. (See Appendix 4, Figure 1 for photo and diagram of playback apparatus.) To ensure that the playback signals had the correct amplitude spectrum, I used a custom program in MatLab v.R2008bSV to assess frequency filtering by the branch and build an inverse filter (Cocroft 1999a). I used this to filter the offspring signals being played through that branch. To ensure I played stimuli at biologically relevant amplitudes, I matched playback peak acceleration to signal peak acceleration from the original field recording.

Wind poses a challenge for delivering and recording vibrational playbacks through vegetation in the field, both because it is the main source of environmental noise (McNett *et al.* 2010) and because any change in relative position between electromagnet and magnet would cause frequency filtering to change (the frequency response of the system is dependent on the distance between the magnet and electromagnet). To reduce the influence of wind, I conducted playback experiments during early mornings when wind speed was lowest. In addition, I used aluminum construction tripods (DeWALT DW0737) and laboratory clamps to fix each family branch in position. To improve the stability of the apparatus, I fixed weights to the tripod legs (Appendix 4, Figure 1).

I scored offspring group signals, maternal signals, and maternal walking as in Experiment 1, but used QuickTime Player (v. 7) and Audacity (v. 1.3.13 beta). I compared responses to playbacks of offspring signals against those produced during silence with the Wilcoxon Signed-Rank test; all comparisons were two-sided. Because I scored both walking and signaling by mothers to test whether offspring signals elicited maternal defense, I adjusted comparison *p*-values for false discovery rate (FDR) (Benjamini & Hochberg 1995).

(d) Experiment 3: Do the mother's post-search vibrational signals reduce offspring signaling?

Data from the predator introductions in this study (Experiment 1), and from additional predator introductions with a separate *P. vittata* population (Appendix 2, Figure 1) suggest that maternal signal rates increase after mothers have searched for predators and after attacks have ended. However, data from a preliminary playback study suggest that whether or not maternal signals are played, offspring produce few signals after simulated predator attacks end (Appendix 3, Figure 1). I hypothesized that maternal signals reduce offspring signaling, but do so during attacks. To test this hypothesis, my experimental approach was to remove the mother from a family; cause the offspring to begin signaling by simulating predation; and then play back either the mother's signals or silence.

To conduct this experiment, I first obtained a recording of each mother's signals. To record the mother's vibrational signals, I simulated predation with each family one day before the playback experiment, as described for Experiment 2. When offspring began signaling, mothers patrolled the family, signaled, and searched for the source of disturbance. I allowed mothers to find the probe with the crushed nymph, which they kicked as they would a predator. As soon as a mother kicked the probe, I withdrew it from the aggregation, simulating a predator eviction. At this point, mothers walked back to their resting position and produced steady bouts of signals. I recorded maternal signals from the start of the simulated attack until after each mother located and evicted the simulated predator.

Mothers produced short (20 to 200 ms) and long (200 to 1800 ms) syllables in their vibrational signals (Figure 4). Before searching and during the first minute of searching for predators, mothers produced mostly short syllables; after ending the search, mothers produced both short and long syllables. I therefore used two playback treatments: one with short syllables only from maternal signals early in the simulated attacks (hereafter referred to as "early-encounter signals"), and one with post-search maternal signals, which typically contained semi-continuous trains of long and short syllables (hereafter referred to as "post-search signals").

For each family, I returned the following day, removed the mother, and simulated a second predator encounter with only the offspring aggregation. I presented the predator cue and simultaneously began playing vibrational stimuli or silence for 10 min. To play vibrational stimuli to the *P. vittata* offspring, I glued the magnet to the branch at the trunk end of the aggregation, the mother's typical position at rest. I played vibrational stimuli using an electromagnet as described for Experiment 2. I controlled for possible effects of treatment order by randomly assigning each family to one of six pre-determined treatment sequences, and by waiting 1 h between treatments.

I used Audacity (v. 1.3.13 beta) to score offspring group signaling rates for each family in response to each playback treatment. Because I had a greater sample size for this experiment than for Experiments 1 and 2, I assessed the effect of early encounter and post-search maternal signaling on offspring signaling with a generalized linear mixed model (GLMM) (package glmmadmb, http://glmmadmb.r-forge.r-project.org/) fitted to the negative binomial error distribution. This enabled me to account for experimental design parameters and environmental factors that might have influenced offspring signaling response. I included the following fixed effects: playback treatment, carryover effects, treatment sequence, temperature, total energy from wind-induced vibrations within each playback, and interactions between temperature and playback treatment and temperature and carryover effects. Because this was a repeated-measures design, I included family nested within playback sequence as a random term. To define a baseline for offspring signaling rates, I set contrasts in the model to compare responses from the other playback treatments against those from the silence treatment.

RESULTS

(a) Experiment 1: How do mothers and offspring respond to predator attacks?

Nymphal *P. vittata* produced collective signals in response to a predator attack: one or more individuals at the site of the attack produced signals, triggering a rapid signaling response from other nearby individuals. The result is a combined, 'group' signal, and alarmed groups may produce such coordinated signals every few seconds. *Platycotis* mothers also produced vibrational signals, both during and after their search for the predator (Figures 1 and 2).

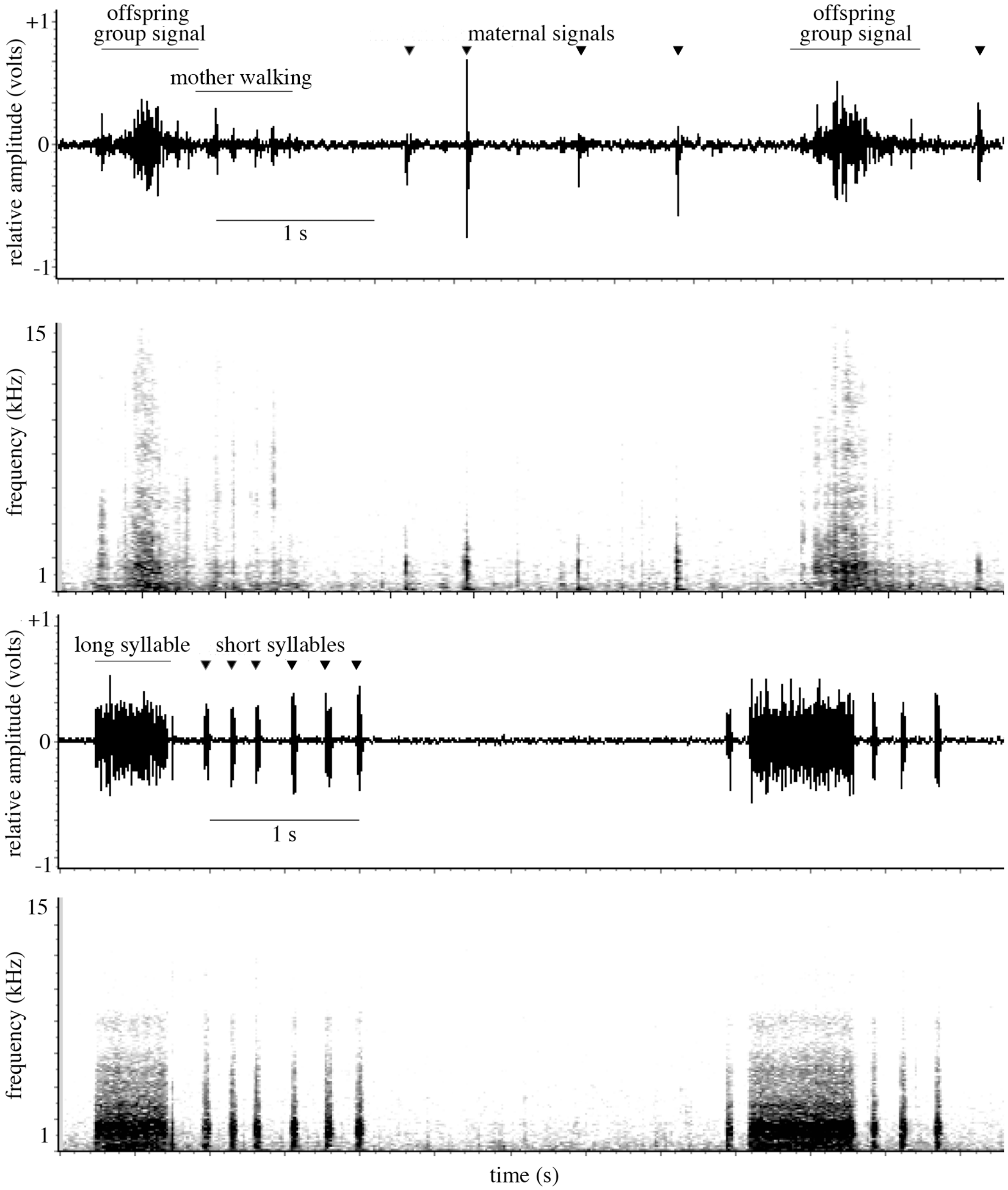

Figure 1. *Top two panels:* Waveform and spectrogram showing *Platycotis vittata* offspring collective vibrational signals, vibrations from mother walking, and maternal vibrational signals (marked with triangular points) produced during the early stages of a predator encounter. *Bottom two panels:* Waveform and spectrogram showing *Platycotis vittata* maternal vibrational signals with long and short syllables produced after a mother has searched for a predator.

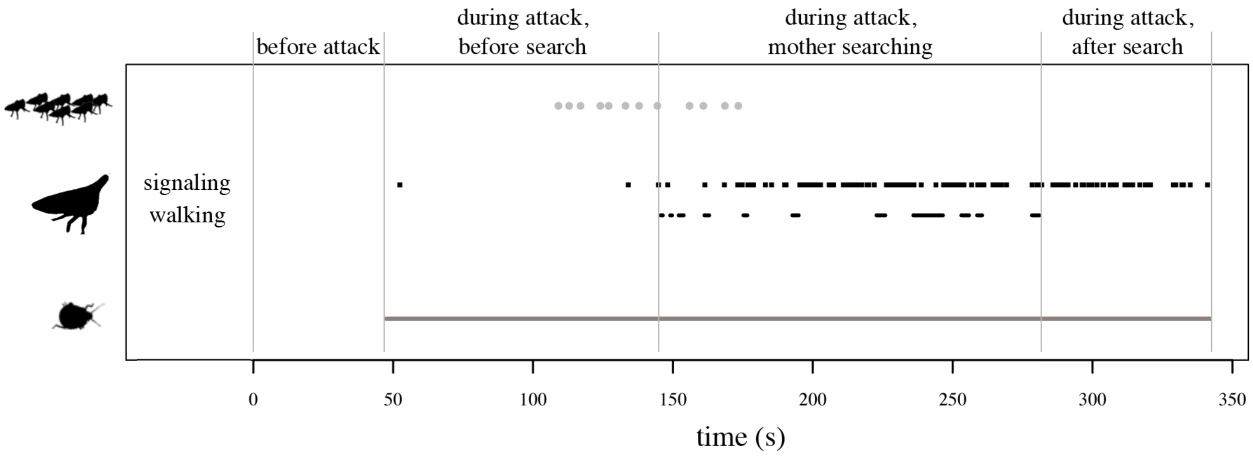

Figure 2. Family response to pentatomid predator introduction, categorized into four phases based on maternal and predator behavior. Top row: grey points represent group signals by *P. vittata* nymphs. Middle rows: upper broken black lines represent signaling by mother; lower broken black lines represent walking by mother. Bottom row: solid grey line represents period during which pentatomid was feeding on a nymph within the nymphal aggregation.

During preliminary observations of predator introductions, the mothers' behavior was consistent. During an attack, each mother walked through the nymphal aggregation, producing vibrational signals. After walking through the entire aggregation one to several times, mothers returned to their original position between the trunk and the aggregation and continued to signal for several minutes; this occurred whether or not the mother found and evicted the predator. I used the mother’s walking behavior to divide each predator encounter into four periods: from the predator introduction until the predator attacked a nymph; from predation until the mother began walking; from the time the mother began walking until she stopped; and from the time the mother ceased walking until the end of the predator attack (Figure 2).

Offspring never signaled before a predator attack. In four out of six families, offspring produced collective signals during attacks, either before or while their mother walked through the aggregation. In one out of six families offspring signaled after their mother walked through the aggregation. There were no significant differences in signaling rate among contexts (Quade $F = 2.4591$, df = 2/10, $p = 0.1353$). However, given that 100% of collective signals were produced before or during the mother's search, the lack of significance is likely due to the small sample size (N = 6).

Maternal signaling rate differed among contexts, with most signaling occurring while the mother searched, and after she returned to her original position (Figure 3; Quade $F = 21$, df = 2/10, $p = 0.0003$). However, *Platycotis vittata* maternal signals are comprised of short and long syllables (Figures 1 and 4), while *U. crassicornis* maternal signals contain only one syllable type (Cocroft 1999b).

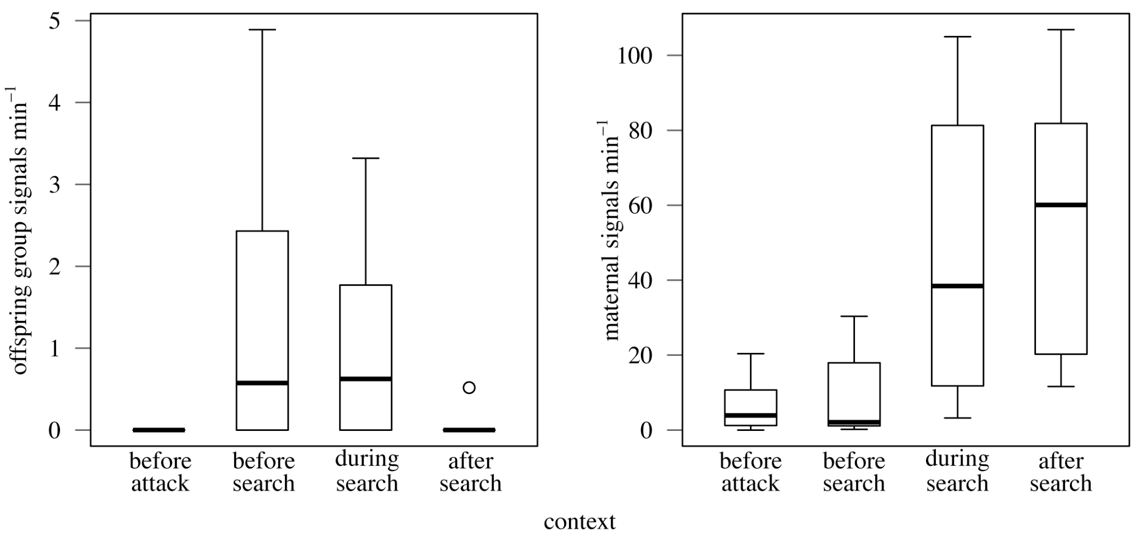

Figure 3. Signaling responses of *Platycotis vittata* offspring and mothers to introduced pentatomid predators during four stages of encounters: from the predator introduction until the predator attacked a nymph *(before attack)*; from predation until the mother began walking *(before search)*; from the time the mother began walking until she stopped *(during search)*; and from the time the mother ceased walking until the end of the predator attack *(after search)*. Box plots show distributions of (*left*) offspring group signaling rate, (*right*) maternal signaling rate (minimum, first quartile, median, third quartile, maximum; open circles represent outliers).

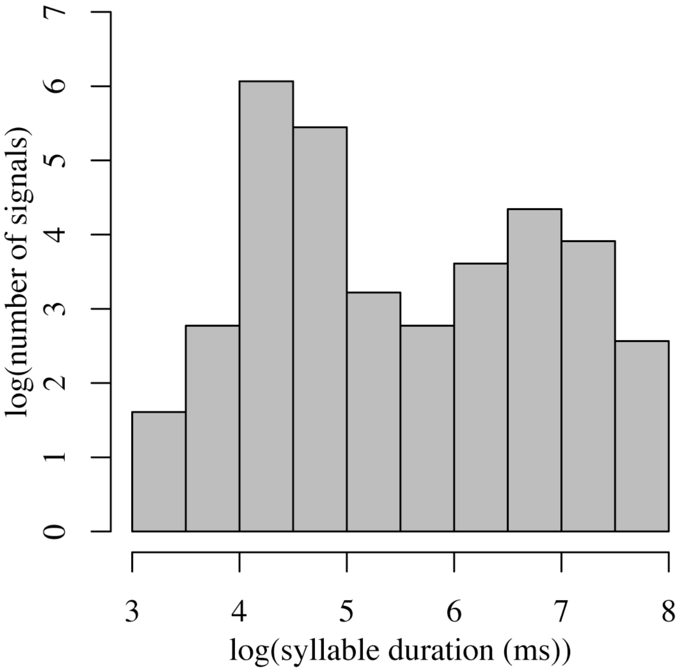

Figure 4. Distribution of syllable lengths in *Platycotis vittata* maternal vibrational signals. Data are from nine *P. vittata* mothers responding to playbacks of offspring signals in Experiment 2.

During the four introductions where offspring aggregations produced group signals, one mother began walking before offspring began signaling. Three of these mothers never found the predators; one mother evicted the predator. During the two introductions where offspring produced no group signals, mothers found and evicted predators, but in both cases, the pentatomids returned to the family for multiple attacks before being evicted (one attacked twice, one attacked three times).

(b) Experiment 2: Do offspring vibrational signals communicate increased risk to mothers?

Mothers signaled at a higher rate when offspring signals were played than when silence was played (signals vs. baseline, Wilcoxon $W = 0, p = 0.008, p_{\mathrm{FDR}} = 0.016$). Mothers walked for a greater proportion of time when offspring signals were played than when silence was played (signals vs. baseline, Wilcoxon $W = 0, p = 0.008, p_{\mathrm{FDR}} = 0.016$) (Figure 5). Nymphs produced some signals in response to playbacks, at rates similar to those in Experiment 1.

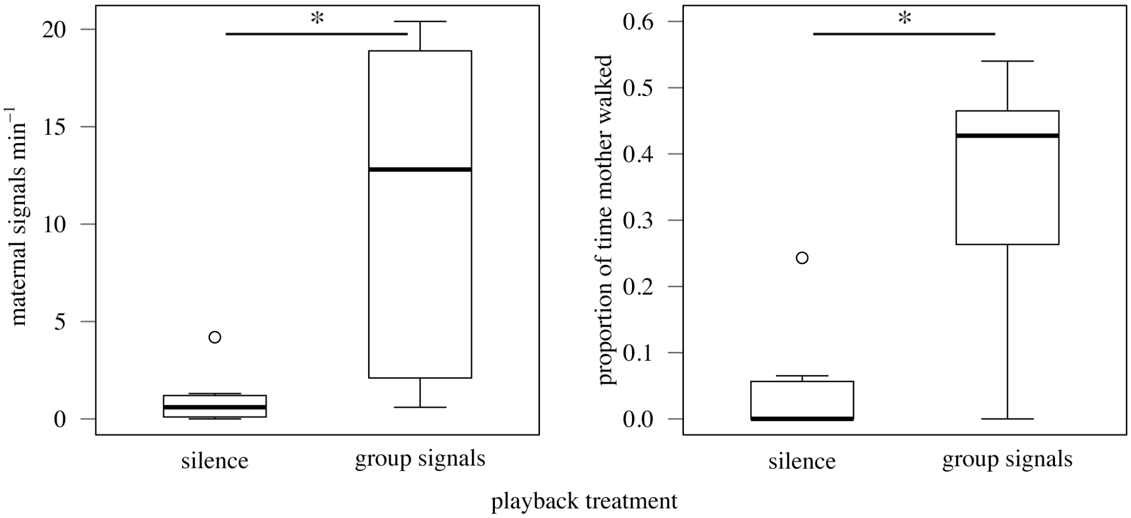

Figure 5. Signaling and walking response of mothers to playbacks of silence and offspring group signals. * represents $p_{\mathrm{FDR}} < 0.05$, Wilcoxon Signed-Rank Test. Box plots show distributions of (*left*) maternal signaling rate, (*right*) proportion of time mothers walked (minimum, first quartile, median, third quartile, maximum; open circles represent outliers).

(c) Experiment 3: Do the mother's post-search vibrational signals communicate decreased risk to the offspring?

Maternal post-search vibrational signals reduced offspring collective signaling during simulated predator attacks. The full model explained 68% of the variation in offspring signaling rate. After accounting for the effect of temperature on offspring behavior (GLMM, coefficient = 0.8009, SE = 0.2412, $p < 0.001$), offspring aggregations signaled at lower rates during playbacks of maternal post-search signals (GLMM, coefficient = -0.6085, SE = 0.1945, $p = 0.002$; Figure 6) than during silence. Playbacks of maternal signals from the early stages of simulated predator attacks had no significant effect on offspring group signaling (GLMM, coefficient = -0.2673, SE = 0.1767, $p = 0.130$; Figure 6). The experimental design parameters that I expected would influence offspring signaling response accounted for a total of 7.03% of variation (carryover: 4.89%; sequence: 2.14%), and interactions between temperature and design parameters another 11.53%.

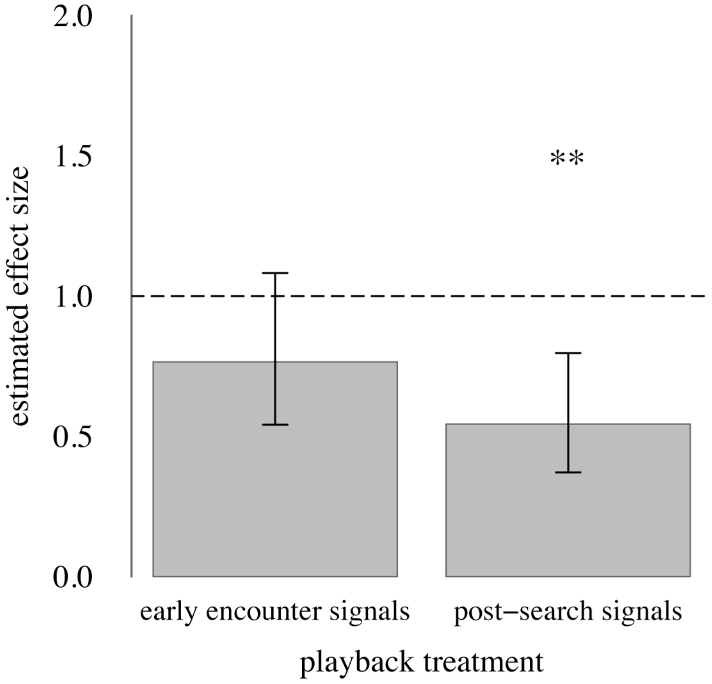

Figure 6. Predicted number of offspring group signals in response to playbacks of maternal early encounter and post-search signals, contrasted against predicted response during silence treatments (dashed line). Grey bars show exponentiated coefficents (± 95% CI). For every offspring signal produced during 10 minutes of silence, the model predicted 0.54 signals would be produced during post-search signals, and 0.77 signals would be produced during early encounter signals. ** represents $p < 0.01$, GLMM

DISCUSSION

In this study, I investigated whether a collective behavior and a mechanism for regulating it are shared between two closely related species. As do *U. crassicornis* families, *P. vittata* families partition roles when communicating about predation risk. That is, each party communicates either predator presence or predator absence, unlike species where the same individuals communicate both predator presence and absence, by using two or more dedicated signals (Robinson *et al*. 2005; Bell *et al*. 2009; Nieh 2010b). Offspring collectively signal in response to attacks by insect predators, and these signals evoke defensive behaviors by their mother in both *P. vittata* and *U. crassicornis* (Cocroft 1996, 1999b). In both species, mothers signal while searching for predators and continue signaling after search and eviction (Cocroft 1999b; Chapter 2)**,** and maternal signals reduce offspring signaling after mothers have searched for and / or evicted predators (Chapter 2).

However, differences exist between these species in the rates of offspring and maternal signaling responses during predator attacks (Table 1). Because one of the *Umbonia* studies involved a different predator type (wasps) (Cocroft 1999b) and the other was a laboratory study (Chapter 1), neither is directly comparable to the current study. In both cases, however, offspring signaling rate in *U. crassicornis* was more than nine times greater than that in *P. vittata,* and *U. crassicornis* maternal signaling rate was lower than that in *P. vittata*. Studies with simulated predator attacks suggest there are also differences in offspring signaling rates *after* attacks: offspring signaling rate in *U. crassicornis* was higher than that in *P. vitata* (Table 2). Taken together, these data suggest that *U. crassicornis* offspring have a higher propensity to signal during and after predator attacks than do *P. vittata* offspring, and that *P. vittata* mothers signal at higher rates during attacks than do *U. crassicornis* mothers.

Table 1. Comparison of *U. crassicornis* and *P. vittata* maternal and offspring signaling *during* attacks by insect predators (mean ± SD).

	offspring signals/min	maternal signals/min
Umbonia crassicornis		
field study, vespid wasps*	22.3 ± 5.2	5.6 ± 4.7
laboratory study, pentatomids**	9.2 ± 5.3	17.1 ± 14.4
Platycotis vittata		
field study, pentatomids***	0.9 ± 1.4	37.4 ± 37.0

* Data from Cocroft (1999b).
** Data from Chapter 1, this dissertation.
***Data from Experiment 1, this study.

Table 2. Comparison of group signaling responses (mean ± SD) by *P. vittata* and *U. crassicornis* offspring *after* simulated predator attacks, during playback of maternal signals, wind vibrations, and silence. The study with *U. crassicornis* was conducted in the laboratory; the study with *P. vittata* was conducted in the field.

	maternal signals	wind vibrations	silence
*U. crassicornis**	2.34 ± 2.12	1.57 ± 1.55	4.25 ± 3.26
*P. vittata***	1.17 ± 1.07	0.44 ± 0.40	1.53 ± 1.41

* Data from Chapter 2.
** Data from Appendix 3.

The main hypothesized benefit of negative feedback in regulating collective behavior in animal groups is to reduce tradeoffs between response speed or sensitivity and accuracy (Couzin 2009; Nieh 2010a). Maternal signaling in *U. crassicornis* supports this hypothesis, as it dampens synchronous behavior by a group and prevents false alarms, thus increasing accuracy without sacrificing sensitivity. In *P. vittata*, maternal signaling dampens synchronous behavior by a group, but I found no evidence that false alarms occur in this species, and thus no evidence that offspring signaling accuracy is increased by negative feedback.

Although maternal signals reduce offspring signaling in both *U. crassicornis* and *P. vittata*, this occurs at different predator encounter stages for each species. *Platycotis* offspring do not signal after attacks end, whereas *U. crassicornis* offspring frequently do, thereby producing false alarms. Thus, when *U. crassicornis* maternal signals reduce offspring signaling after attacks, they are increasing the accuracy of predator detection via offspring signals, consistent with the hypothesis that negative feedback improves the accuracy of collective behavior while maintaining sensitivity. In contrast to *U. crassicornis* nymphs, *P. vittata* nymphs produce few signals during predator encounters, and I never observed false alarms. Rather than inhibiting offspring signaling after evicting the predator, *P. vittata* mothers inhibit offspring signaling while searching for the predator.

In this study, *Platycotis vittata* mothers did not always find or evict predators. After responding to offspring signals and patrolling the aggregation, mothers resumed their resting positions and increased their signaling rates, whether or not they located the predator. *Platycotis vittata* offspring did not continue signaling throughout searches by their mothers. In contrast, *U. crassicornis* offspring signals continued as *U. crassicornis* mothers searched for predators, and *U. crassicornis* mothers used information in these signals to locate predators (Ramaswamy & Cocroft 2009; Ramaswamy 2010). *Platycotis* mothers may rely on offspring signals to detect predator arrival, but they may then use information other than offspring signals to locate predators (e.g., visual cues, which are seldom provided by stealthy pentatomid nymphs).

To understand if negative feedback enables *P. vittata* families to avoid a tradeoff between sensitivity and accuracy in predator detection, future research should ask why maternal signals reduce offspring signals in *Platycotis vittata*. Maternal signals might increase the accuracy of offspring signals; they might provide other benefits by reducing offspring signals during attacks; or they might provide only marginal benefits but persist with low costs. All genera in this taxonomic group exhibit maternal signaling, and collective offspring signaling has been documented for most (Cocroft and Lin, unpub. data); this would be an ideal study system for a broader comparative study of collective behavior and its regulatory mechansisms.

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Chapter 4. Unintended receivers and the costs of parent-offspring vibrational communication in a group-living insect.

SUMMARY

A principal benefit of group living is reduction of individual predation risk. However, group-living animals communicate about environmental factors, including food and predators, and predators and parasitoids may eavesdrop on social signals. Most studies on predator eavesdropping have focused on mate advertisement signals, but social signals are concentrated in space and time and provide a persistent source of information, making within-group communication especially vulnerable to eavesdropping. I tested whether a generalist invertebrate predator (*Podisus maculiventris*) eavesdrops on vibrational communication between parents and offspring groups in a species of treehopper (*Platycotis vittata*). In *P. vittata*, clustered offspring produce collective vibrational signals during predator attacks, eliciting defense from their mother. Mothers also signal, after searching for a predator, and maternal signaling inhibits offspring signaling. I found that *P. maculiventris* homes in on *P. vittata* offspring signals, but not maternal signals. This is the first study to show that invertebrate predators eavesdrop on vibrational social signals by group-living prey.

INTRODUCTION

Within many animal social groups, individuals communicate about important aspects of the environment, such as predators and food resources (Wilson 2000; Caro 2005a; Hauber & Zuk 2010). Establishing the costs and benefits of social signals is challenging, however, because it requires understanding how the signals influence the many possible receivers within a complex social and ecological network (Peake 2005). A first step is to assess whether any individuals outside the group are receiving within-group signals and to investigate how such signals influence their behavior. Such unintended receivers can include predators, whether attacking (Hasson 1991; Caro 2005b; Shelley & Blumstein 2005) or not yet attacking, but located nearby (Chivers *et al*. 1996), as well as mutualists (Morales *et al*. 2008), and other, nearby heterospecifics not engaged in obvious symbioses with the group (Hauser 1988). Here, I focus on how within-group communication can influence the behavior of one type of unintended receiver: nearby, eavesdropping predators.

Eavesdropping predators and parasitoids are an important source of selection on communication by prey (*reviewed in* Zuk & Kolluru 1998; Haynes & Yeargan 1999), even causing the loss of long-range signaling (Zuk *et al*. 2006). Most studies of predator eavesdropping have focused on mate advertisement signals, but predators and parasitoids also may eavesdrop on social signals such as aggregating signals (*reviewed in* Haynes & Yeargan 1999), offspring begging signals (*reviewed in* Magrath *et al*. 2010), alarm signals (Allan *et al*. 1996), and mobbing signals (Krams *et al*. 2007). When multiple individuals signal in close proximity, as when social groups communicate about food or predator discovery, this should provide an amplified and persistent source of information to unintended receivers.

Platycotis vittata is a treehopper with maternal care of clustered offspring. Mothers and offspring groups communicate with one another through substrate vibrations during predator encounters. A family typically consists of 40 to 50 sedentary offspring arranged around an oak branch with their mother (Wood 1976). Throughout offspring juvenile development, a mother defends her nymphs from a broad suite of invertebrate predators, including wasps (Beamer 1930), ants, spiders, predatory stink bugs, and lacewing larvae (Hamel, unpub. data). During predator encounters, offspring groups produce synchronous vibrational signals (Chapter 2). Offspring signals elicit maternal defense behavior, including searching for and evicting the predator. Mothers also produce vibrational signals during and after encounters (Chapter 2). As encounters progress, the maternal signaling rate increases, and after encounters end, mothers produce semi-continuous trains of interspersed short and long syllables for several minutes (Hamel, unpub. data). Maternal and offspring signals are temporally and spectrally distinct (Chapter 2, Figure 2). Maternal signals reduce offspring signaling during simulated predator encounters (Chapter 2).

Family groups of *P. vittata* often develop in the presence of potential invertebrate predators on the same host plant (Hamel, unpub. data). All known invertebrate predators of *Platycotis vittata* are vibrationally-sensitive and use vibrational communication at some life stage (Henry 1980; Pfannenstiel 1995; Hölldobler & Roces 2001; Barth *et al.* 2008; Jeanne 2009). During predator attacks, *P. vittata* maternal and offspring signals may both be beneficial; offspring signals alert the mother to predator presence and maternal signals limit unnecessary signaling by offspring. However, family signals could be costly if they attract additional predators; or they may have additional benefits if they repel predators. To understand the costs and benefits of *P. vittata* maternal and offspring signaling, it is important to determine if predators attend to signals elicited by another predator's attack. In this study, I examine the responses of one generalist, vibrationally-sensitive predator to *P. vittata* maternal and offspring signals. The pentatomid *Podisus maculiventris* is an appropriate focal predator because it has been observed preying upon *P. vittata* in the field (M. Rothschild, pers. comm.), and because it uses incidental vibrations from caterpillars to locate and prey upon them (Pfannenstiel 1995). *Platycotis vittata* maternal and offspring signals have different functions and acoustic properties, and may differ in their salience to a predator. If signals do elicit responses, they may attract or repel predators.

METHODS

(a) Predator rearing

I was provided with pentatomid nymphs by the USDA-ARS Biological Control of Insects Research Laboratory (Columbia, MO). I maintained a laboratory colony of *P. maculiventris* at ~ 25°C on a 14:10 h light:dark cycle. Pentatomid nymphs and adults were fed a combination of coddled fourth instar larvae of *Trichoplusia ni* (Hübner) and a zoophytogenous artificial diet (Coudron *et al*. 2002) and provided with water via moist dental wicks (Richmond Dental) in small plastic weigh boats (Fisher Scientific). I housed two adults of each sex in half-pint paper containers; eggs were collected and transferred to a new container in which nymphs developed.

(b) Experiment 1: Do offspring signals influence the behavior of potential predators?

In June 2009, I assessed the behavioral responses of naïve pentatomid nymphs to vibrational signaling by *Platycotis vittata* offspring aggregations. In the laboratory, I allowed each pentatomid nymph to walk up a thin string tied to the center of a branch of a potted oak (*Quercus alba*) sapling, where offspring vibrational signals, wind vibrations, or silence were played for 3 minutes in a continuous loop. For all experiments, I used a different pentatomid nymph for each treatment and each replicate. For playback exemplars, I recorded offspring signals from two families and wind-induced vibrations from two trees (see *"Vibrational stimuli and playbacks"* for details on exemplars). The silence treatment provided a baseline and a control for any effect of equipment setup or electrical noise that might influence pentatomid behavior, and the wind treatment provided a vibration control, using a common environmental source of non-prey-generated vibrations.

(c) Experiment 2: Do maternal signals influence the behavior of potential predators?

From February to May 2009, I assessed the behavioral responses of naïve pentatomid nymphs to vibrational signaling by *Platycotis vittata* mothers. I introduced pentatomid nymphs to the branch of one of three potted *Q. alba* saplings, as in Experiment 1. For playback exemplars, I recorded signals from five mothers and wind vibrations from five trees (see next section for details on exemplars).

(d) Vibrational stimuli and playbacks

For playback stimuli, I recorded signals from *Platycotis* mothers and group signals from *Platycotis* offspring aggregations, all from a field population near Gainesville, FL (Chapter 2). To record familial signals, I attached an accelerometer (PCB Piezotronics, NY, USA; Model 352A24, weight 0.8 g, frequency range: 0.8 Hz – 10 kHz ± 10%) to the branch ≤ 10 cm from each family using mounting wax. The accelerometer was powered by a PCB Model 480E09 ICP Sensor Signal Conditioner. I recorded offspring and maternal vibrational signaling responses to simulated predator attacks, using a Marantz PMD670 digital audio recorder at a sampling rate of 44100 Hz. To simulate predator attacks, I presented a crushed *P. vittata* nymph on a dowel ~ 1 cm under the center of the aggregation. A chemical cue from a crushed nymph acts as a predator cue (Nault *et al*. 1974; Cocroft 1999b) and reliably elicits collective signaling from offspring. Sacrificial nymphs were frozen before being crushed and the probe was rinsed with 70% etOH after each presentation.

I played wind vibrations and silence as two separate control treatments. I recorded wind vibrations from branches of *P. vittata* host trees (*Quercus laurifolia* and *Q. virginiana*) at the same field site mentioned above, using the same equipment with which I recorded familial signals. Wind-induced vibrations were recorded from branches similar in diameter to those used by *P. vittata* families. I assembled playback stimuli in Audacity v.1.3.12. For the silence treatment, I used the same playback methods as in the signal and wind vibration treatments, but played a track of silence that I generated using Audacity.

To play vibrational stimuli through a potted oak branch (Figure 1), I glued a neodymium magnet (1/8" Dia. x 1/16" thick Disc; United Nuclear Scientific, Laingsburg, MI) to the underside of the branch, < 10 cm from where the branch met the trunk. I positioned an electromagnet parallel to the magnet at a distance of 1 to 2 mm. I then played vibrational stimuli to the electromagnet from Audacity on a Macintosh 1.66 GHz PowerPC G5 via a RadioShack 40-watt PA amplifier. To ensure that the playback signals had the correct amplitude spectrum, I used a custom program in MatLab v.R2008bSV to assess frequency filtering by the branch and to build an inverse filter (Cocroft 1999a). I used this to filter the maternal and offspring signals and wind vibrations being played through the branch. To ensure I was playing stimuli at biologically relevant amplitudes, I matched playback peak acceleration to that of the original field recordings of maternal and offspring signals. For playbacks of wind vibrations, I matched playback peak acceleration to that of the maternal or offspring signals being played.

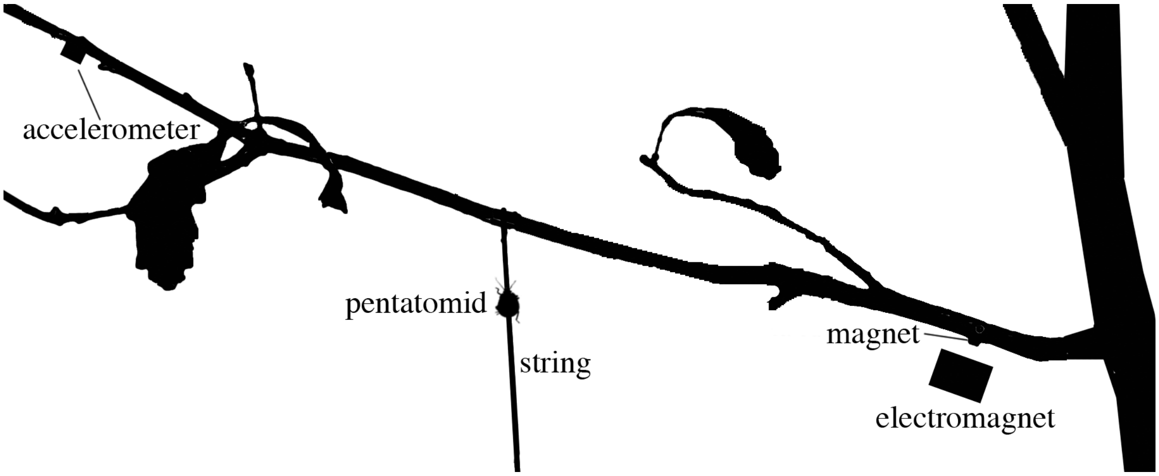

Figure 1. Playback setup. In both experiments, pentatomid nymphs were introduced to string and allowed to walk up to the branch of a potted *Q. alba* sapling. Vibrational stimuli were imparted into the branch from an electromagnet and detected via an accelerometer.

(e) Scoring and statistical methods

I recorded pentatomid behavior using a digital HD video recorder (Sony Handycam Model HDR-SR1 or HDR-SR11). Scoring began when all of a pentatomid's legs made contact with the branch and ended after 180 s or when the pentatomid dropped from the branch. Because pentatomids detect substrate vibrations with sensory organs in their legs (Čokl & Virant-Doberlet 2003), they remain still when attending to vibrational stimuli. Furthermore, because *P. maculiventris* nymphs are stealthy predators, they typically intersperse longer stationary periods with short bouts of movement as they approach prey (Hamel, pers. obs.). Accordingly, I scored the proportion of time each pentatomid remained stationary as an index of attentiveness to the stimulus. As an index of stimulus attractiveness, I scored the proportion of time each pentatomid spent near the vibration source (i.e., on the half of the branch nearer the playback vibration source).

I fitted a binomial regression model for the proportion of time pentatomids remained stationary. I set contrasts so the model compared individual responses during signal and wind vibration treatments against responses during silence (baseline) treatments. The second response variable, proportion of time spent near the vibration source, had a nearly binary distribution, with most individuals spending all or none of the observation time near the vibration source. I therefore treated these responses as binary data (success: individuals spend ≥ half the observation time near the vibration source) and fitted a logistic regression model, with contrasts set as in the first model. For both response variables, I first tested for effects of playback exemplars. I found no significant exemplar effects (all $p > 0.15$), thus I pooled data within each playback treatment (silence, wind vibrations, and maternal or offspring signals). Because there were two measures of pentatomid behavior, I corrected p-values for false-discovery rate (FDR) (Benjamini & Hochberg 1995). All models were fitted with R statistical software, version 2.13.0.

RESULTS

(a) Experiment 1: Do offspring signals influence the behavior of potential predators?

Playback treatment influenced the proportion of time pentatomids were stationary (analysis of deviance, $p_{\mathrm{FDR}} < 0.001$). Pentatomid individuals were stationary for more time when offspring signals were played than when silence or wind vibrations were played (offspring signals vs. silence: $p < 0.001$; offspring signals vs. wind vibrations: $p < 0.01$) (Table 1; Figure 2). There was a non-significant trend for the overall effect of playback treatment on the proportion of individuals spending more time near the vibration source (analysis of deviance, $p_{\mathrm{FDR}} = 0.068$). On closer examination, the proportion of individuals spending more time near the vibration source was higher during playbacks of offspring signals than during silence ($p = 0.033$). The proportion of individuals spending more time near the vibration source did not differ between offspring signal and wind vibration treatments ($p = 0.185$) (Table 2; Figure 3).

(b) Experiment 2: Do maternal signals influence the behavior of potential predators?

Playback of maternal signals did not influence the proportion of time pentatomids remained stationary (analysis of deviance, $p_{\mathrm{FDR}} = 0.274$) (Table 1; Figure 2) or on the proportion of individuals spending ≥ 50% time near the vibration source (analysis of deviance, $p_{\mathrm{FDR}} = 0.346$) (Table 2; Figure 3).

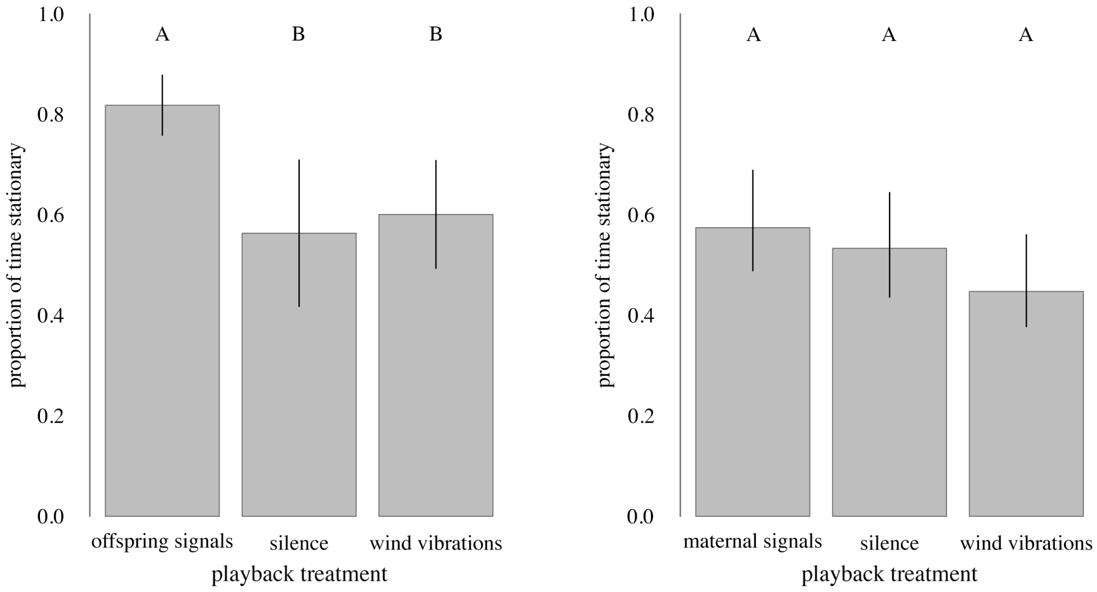

Figure 2. Mean proportion of time stationary (± 95% CI) by pentatomid nymphs in response to playbacks of silence, wind vibrations, and *(left)* offspring or *(right)* maternal vibrational signals. Means with different letters are significantly different (binomial regression model, $p < 0.001$).

Table 1**.** Binomial regression models of whether playback treatment influenced the proportion of time pentatomids remained stationary. $N = 30$ for offspring signaling experiment; $N = 51$ for maternal signaling experiment.

	estimate	SE	*t*	*P*
Nymph signals	1.224	0.322	3.799	0.0008
Wind vibrations	0.232	0.294	0.789	0.4369
Maternal signals	0.114	0.310	0.367	0.715
Wind vibrations	-0.458	0.308	-1.487	0.143

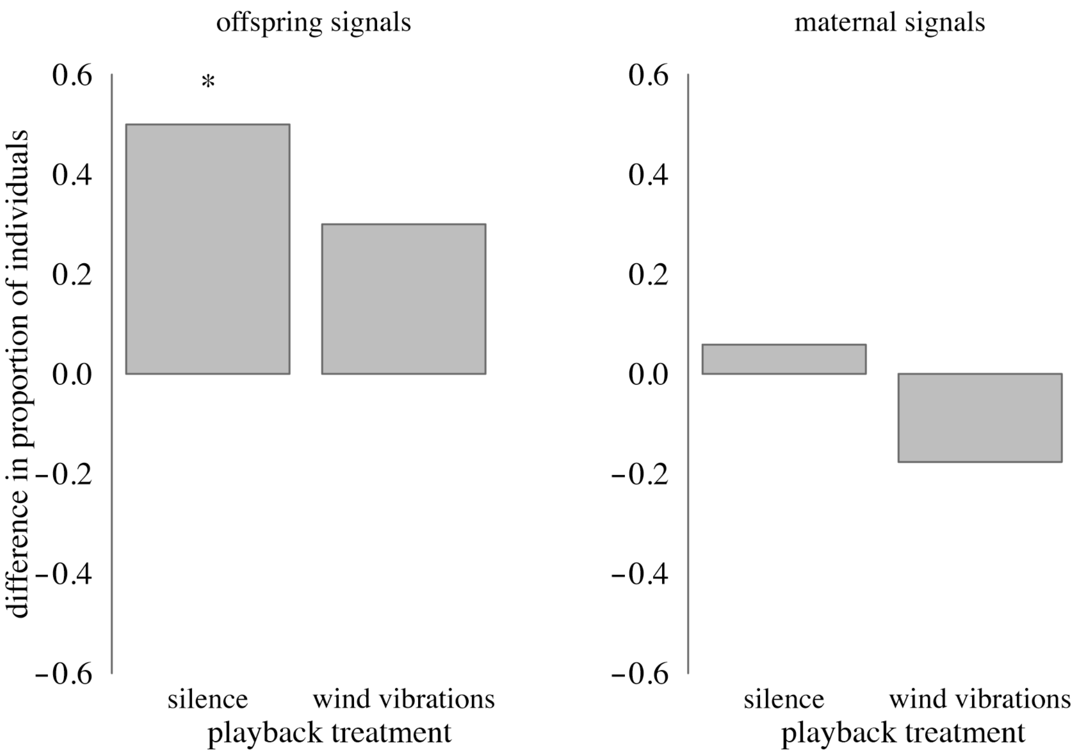

Figure 3. Differences in the proportion of pentatomid individuals that spent more time near the vibration source. Differences were calculated between playbacks of silence and wind vibrations and *(left)* offspring or *(right)* maternal vibrational signals. * represents $p < 0.05$, logistic regression model.

Table 2**.** Logistic regression models of whether playback treatment influenced the proportion of individuals spending most time near the vibration source. *N* = 30 for offspring signaling experiment; *N* = 51 for maternal signaling experiment.

	estimate	SE	*z*	*P*
Nymph signals	2.234	1.049	2.128	0.033
Wind vibrations	0.981	1.021	0.961	0.336
Maternal signals	0.236	0.687	0.343	0.732
Wind vibrations	0.993	0.721	1.378	0.168

DISCUSSION

I investigated whether within-group vibrational signals by *Platycotis* mothers and offspring during predator attacks influence the behavior of nearby potential predators. The results of this study suggest that the collective vibrational signals of *P. vittata* offspring attract a species of generalist invertebrate eavesdropping predator. Pentatomids attended to offspring group signals with a stationary 'listening' posture. Pentatomids also spent more time near the vibration source when offspring signals were played than during silence, though this response did not differ between playback of offspring signals and wind vibrations. In contrast to playback of *P. vittata* offspring signals, playback of *P. vittata* maternal signals had no effect on predator behavior.

Although this study focused on receivers outside the social group, it provides insights into within-group interactions. Maternal signaling in *P. vittata* (Chapter 2) and closely related *Umbonia crassicornis* (Chapter 1) inhibits offspring signaling in the context of predator attacks. Most maternal signaling takes place after a mother has searched for (Chapter 2) or evicted (Chapter 1) the predator. One likely benefit of reducing offspring signals after a predator attack is the prevention of false alarms, especially in *U. crassicornis*, where offspring signaling often continues after a predator has been evicted. This study suggests that another function of inhibiting offspring signals is to reduce the risk of advertising family location to eavesdropping predators.

Predation is one of the major factors that favors group-living in animals (Barbosa 2005; Caro 2005c). However, the per-capita risk for group-living animals is a function not only of the number of individuals in the group, but also of the extent to which predators are attracted to the group (Mooring & Hart 1992). This study supports evidence from studies on begging by nestling birds (*reviewed in* Magrath *et al*. 2010), avian mobbing calls (Krams *et al*. 2007), and chemical communication by ants (Allan *et al*. 1996) that social signals attract predators to groups. Although most studies of predator eavesdropping focus on mate advertisement signals (Zuk & Kolluru 1998; Haynes & Yeargan 1999; Peake 2005), social communication produces a concentrated and persistent source of signals and may be especially vulnerable to eavesdropping. Adaptations to reduce the apparency of social signals to predators are likely to be a general, if often overlooked, feature of social communication.

This study is one of the first to suggest that plant-borne vibrational communication is subject to predator eavesdropping. Among insects that communicate using some form of mechanical waves transmitted through a medium, most do so at least in part through substrate vibrations (Cocroft & Rodriguez 2005). Although the vibrational modality has been described as a private channel where insect signalers escape eavesdroppers (Henry 1980; Zuk & Kolluru 1998; Römer *et al*. 2010), Cocroft and

Rodriguez (2005) argued that predator eavesdropping was likely, given the abundance and diversity of vibration sensitive invertebrate predators present in the environments where communication occurs. Recently, Virant-Doberlet *et al*. (2011) used molecular data to establish the predator-prey relationship between theridiid spiders and a species of leafhopper. The authors then showed that the spiders responded to playbacks of male leafhopper advertisement calls, but not to controls, by spending more time on the playback plant, and sometimes by orienting toward the playback source. Roberts *et al.* (2007) showed that jumping spiders attend to the vibrational component of a multimodal signaling display by their wolf spider prey. Laumann *et al*. (2007) showed that small wasps that parasitize pentatomid eggs home in on the vibrations produced by females. Invertebrate predators can home in on incidental vibrations generated by walking or chewing prey (Pfannenstiel 1995; Barth 1998; Meyhofer & Casas 1999), and it is becoming clear that invertebrate predators home in on vibrational communication signals as well (Cocroft 2011).

Many insects are group-living for at least one life stage (Costa 2006), and vibrational communication is widespread in group-living insects (Cocroft & Hamel 2010). A group of insects produces a steady and robust stream of information for predators. Predation risk is likely to be an important cost of vibrational communication and group movement, and eavesdropping predators and parasitoids may exert strong selection on within-group signaling.

This study assessed naïve predators for response to prey signaling, but the influence of vibrational communication on invertebrate predators may depend on associative learning (Jackson & Li 2004; Guillette *et al*. 2009). It is likely that *P. vittata* families experience multiple attacks by some individual predators. During a study on a closely related species (*Umbonia crassicornis*) with antipredator communication and defense similar to that of *P. vittata*, five individual vespid wasps accounted for 189 attacks (Cocroft 1999b). Some invertebrate predators assess food availability before selecting foraging sites (Uetz 1992), and the costs of *P. vittata* offspring signaling may become amplified if local predators associate offspring signals with a persistent food source. However, because most offspring signals occur during attacks, a recurring predator may also associate offspring signals with the maternal defenses (i.e., kicking and wing-buzzing) the signals evoke. Similarly, maternal vibrational signals may be associated with maternal defensive behavior and with reduced profitability from increased handling time. Although *P. vittata* maternal vibrational signals by themselves had no influence on pentatomid nymphs, the possibility that maternal signals deter experienced predators from attacking an offspring aggregation remains to be tested.

In summary, within-group communication in an insect species in which groups use collective detection influences the behavior of potential predators, and eavesdropping predators likely contribute to the costs and benefits of family vibrational communication. *Platycotis vittata* offspring signaling inadvertently advertises family presence and location to pentatomid predators. A probable benefit of maternal signaling is reduction in the risk of a family being discovered by eavesdropping predators. I suggest that predator eavesdropping is a widespread cost of within-group communication for invertebrate groups using vibrational signals, and that future studies should examine the role of predator experience and associative learning in this context.

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Chapter 5. Discussion.

At the beginning of my dissertation studies, I observed a group-living animal that produced synchronous signals during predator attacks. This led me to the intersection of three different areas of contemporary biological theory: antipredator behavior in animal groups, collective behavior, and animal communication. An area of overlap shared by all three bodies of literature is the problem of false alarms.

In group-living, but not necessarily collectively behaving animals, we have evidence that false alarms can be common and costly (Hoogland 1981; Kahlert 2006; Bell *et al*. 2009; Beauchamp 2010) during predator encounters. Additionally, false alarms during predator encounters can spread through animal groups (Lima 1995; Bikhchandani & Hirshleifer 1998; Giraldeau *et al*. 2002; Sirot 2006), with costs for most or all group members (Kahlert 2006; Bell *et al*. 2009). Collectively behaving animals, a subset of group-living animals, rely heavily on social information (Sumpter 2010). During synchronous collective behavior, animals use social information to closely coordinate their behavior in time (Buck *et al*. 1981; Néda *et al*. 2000; Helbing & Farkas 2002; Ramaswamy & Cocroft 2009; Sumpter 2010). Because of this, false alarms are highly likely for synchronously behaving animals.

The communication literature describes an inherent trade-off between sensitivity and accuracy for the detection of predators or signals. Group-living animals should limit false alarms, but by doing so they will also limit their ability to make correct detections (Wiley 1994). The collective behavior literature suggests that negative feedback, a source of information that dampens collective behavior, should reduce tradeoffs between sensitivity and accuracy (Couzin 2009; Nieh 2010). However, prior to this work, negative feedback had only been documented as a regulatory mechanism of collective behavior in two animal taxa (Robinson *et al*. 2005; Nieh 2010).

In the preceding chapters, I found that two closely-related animal species dampen collective signaling with negative feedback, and to do so they partition communicative roles between mother and offspring. Only one party produces collective signals, and only one party provides the negative feedback that dampens those signals. In at least one of these species, maternal signals likely reduce false alarms and the propagation of errors, and this is consistent with hypothesized benefits of negative feedback for collective behavior (Couzin 2009; Nieh 2010). However, although *P. vittata* maternal signals dampen collective offspring signaling, there is no evidence that this reduces false alarms or error propagation. This suggests that there is a different benefit associated with reducing offspring signals, or that maternal signals have an unknown function, and that offspring signaling is dampened as a by-product.

In Chapters 2 and 3, I focused on mother-offspring communication in *U. crassicornis* and *P. vittata*. In Chapter 4, I considered mother-offspring communication in a community context. To understand the costs and benefits of familial signaling, it is necessary to assess whether family signals have unintended receivers, such as eavesdropping invertebrate predators. For plant-living invertebrates producing vibrational social signals, predator eavesdropping is highly likely. For example, *P. vittata* offspring aggregations often develop on plants where their predators also occur (Hamel, unpub. data), and all invertebrate predators of *U. crassicornis* and *P. vittata* use vibrational communication during at least one life stage (Henry 1980; Pfannenstiel 1995; Hölldobler

& Roces 2001; Barth *et al*. 2008; Jeanne 2009). I found that *P. vittata* maternal signals had no effect on one species of naïve insect predator, but that *P. vittata* offspring signals attract the same insect predator. I suggest that unintended receivers may favor maternal behavior that suppresses unnecessary offspring signaling, and that future studies should investigate eavesdropping by experienced predators and explore the role of associative learning.

In summary, in two species of collectively-signaling animals for which false alarms are likely to be common and costly, negative feedback dampens collective signaling. The ability to dampen collective signaling may enable one species to reduce false alarms, thereby sidestepping a tradeoff between predator detection sensitivity and accuracy. In a closely-related species, negative feedback dampens collective behavior, but does not appear to reduce false alarms. This begs consideration of alternative benefits that could be associated with negative feedback. Predator eavesdropping may select for maternal behavior that reduces offspring signaling. In both collectively-signaling species, mother and offspring partition communicative roles, and this is a previously undescribed strategy for dampening collective behavior in animals.

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Appendix 1. Supplementary data: **Umbonia crassicornis** *familial responses to flying and walking predators*

Table 1. Comparison of maternal and offspring signaling rates (mean ± SD) to repeated attacks from flying predators (wasps) in the field and from introduced walking predators (pentatomids) in the laboratory.

	context	flying predator*	walking predator**
mother	baseline	3.3 ± 3.5	5.1 ± 12.3
	during	5.6 ± 4.7	17.1 ± 14.4
	after	49.3 ± 33.3	33.0 ± 39.1
offspring	baseline	0.2 ± 0.4	0.4 ± 0.5
	during	22.3 ± 5.2	9.2 ± 5.3
	after	7.4 ± 7.5	5.4 ± 5.6

* Data from Cocroft (1999b).
** Data from Chapter 1.

Appendix 2. Supplementary data: predator introductions with **Platycotis vittata**

In September 2007 I conducted a preliminary study to investigate the responses of *P. vittata* families to pentatomid predators *(Podisus maculiventris)*. Whereas other experiments in this dissertation with *P. vittata* were conducted with a population in Putnam Co., Florida, this study was conducted in the Alum Creek Experimental Forest (Saline Co., Arkansas).

I located *P. vittata* mothers with first and second instar nymphs by scanning branch ends of two oak species (*Quercus alba* and *Q. rubra*). I detected maternal and offspring vibrational signals with an accelerometer (PCB Piezotronics, NY, USA; Model 352A24, weight 0.8 g, frequency range: 0.8 Hz to 10 kHz ± 10%) attached ≤ 10 cm from each family using mounting wax and powered by a PCB Model 480E09 ICP Sensor Signal Conditioner. I recorded both offspring and maternal signaling responses on a Marantz PMD670 digital audio recorder at a sampling rate of 44100 Hz. I recorded family behavior using a digital video recorder (Sony Handycam Model HDR-HC7). For each family, I first set up signal detection and video equipment and allowed the family 1 h to acclimate.

I manipulated predation risk by introducing invertebrate predators (juvenile *Podisus maculiventris*) to seven *P. vittata* families on oak tree branches. I allowed a predator to walk up a thin string tied to the treehopper family branch, ≥ 1 cm from the edge of the offspring group. Each family also received a control treatment, where I mimicked my movements as in an introduction but did not introduce a predator and then recorded family responses for 1 h. I alternated treatment order and used each predator only once. I scored family responses (i.e., maternal signals, offspring group signals) for the duration of the predator encounter and for 15 min after the encounter ended. For control treatments, I scored family responses for the same timeframe as during the predator introduction treatment. I scored predator encounters as beginning when a pentatomid made physical contact with one or more *P. vittata* 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.

I obtained pentatomid predators (*Podisus maculiventris* nymphs) from the USDA-ARS Biological Control of Insects Research Laboratory (Columbia, MO) and transported them to Alum Creek Experimental Forest. I maintained a laboratory colony of *P. maculiventris* at ~25°C on a 14:10 h light:dark cycle. Pentatomid nymphs and adults were fed a combination of coddled fourth instars of *Trichoplusia ni* (Hübner) and a zoophytogenous artificial diet (Coudron *et al*. 2002) and were provided with water via moist dental wicks (Richmond Dental) in small plastic weigh boats (Fisher Scientific). I housed adults of each sex in half-pint paper containers; when females produced eggs, eggs were collected in a new container in which nymphs developed.

Results

Offspring group signaling rates differed by predator encounter context (Quade test: N = 7 aggregations, Quade F =15.697, df = 2/12, $p = 0.0004$) (Figure 1). Group signaling rate was greater during and after predator encounters than during control treatments (control vs. during predation, Wilcoxon $W = 0$, $p = 0.016$, $p_{\mathrm{FDR}} = 0.031$; control vs. post-predation, Wilcoxon $W = 1$, $p = 0.016$, $p_{\mathrm{FDR}} = 0.031$). Offspring signaling rates while predators were in contact with families did not differ statistically from those after predators left families (predation vs. post-predation, Wilcoxon $W = 5$, $p = 0.156$, $p_{\mathrm{FDR}} = 0.156$).

Like offspring group signaling rates, the proportion of time mothers signaled differed among predator encounter contexts (Quade $F = 5.006$, df = 2/12, $p = 0.026$). Post-hoc comparisons here were not significant after controlling for FDR (control vs. during predation, Wilcoxon $W = 4$, $p = 0.219$, $p_{\mathrm{FDR}} = 0.219$; control vs. post-predation, Wilcoxon $W = 0$, $p = 0.031$, $p_{\mathrm{FDR}} = 0.094$; predation vs. post-predation, Wilcoxon $W = 5$, $p = 0.156$, $p_{\mathrm{FDR}} = 0.219$). However, mothers tended to signal for a greater proportion of time after predator encounters than during controls.

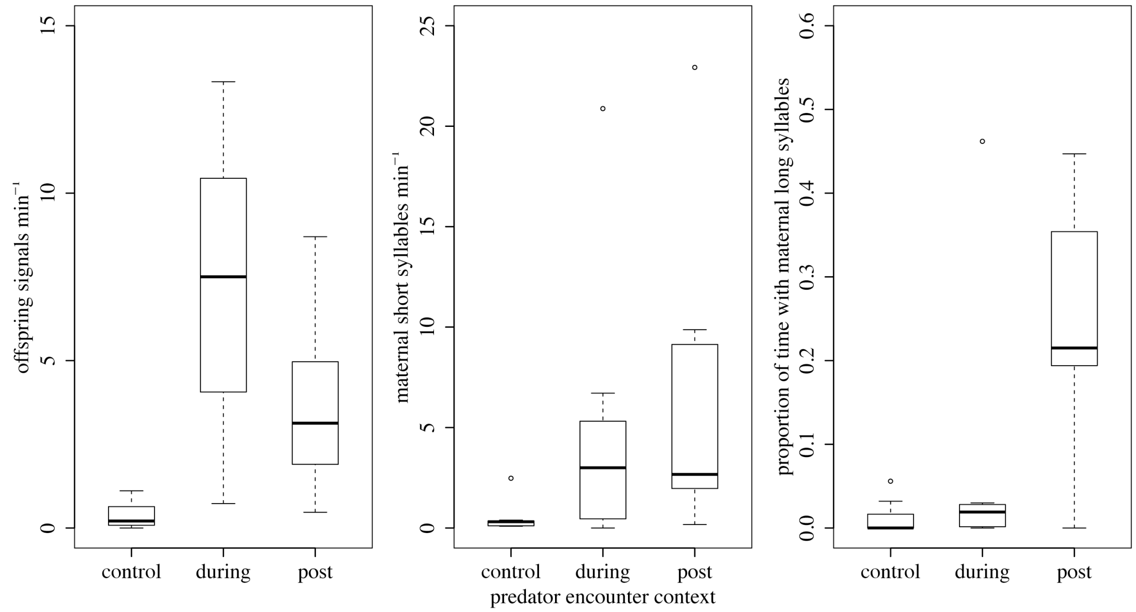

Figure 1. Signaling responses of *Platycotis vittata* families to introduced predators. Box plots show distributions of (*left*) offspring group signaling rate, (*center*) maternal short syllable rate, and *(right)* the proportion of time with maternal long syllables (minimum, first quartile, median, third quartile, maximum; open circles represent outliers).

Appendix 3. Supplementary data: playback of maternal signals to **Platycotis vittata** *offspring, Spring 2009*

In March 2009 I investigated the influence of *P. vittata* maternal signals on 10 aggregations of signaling *P. vittata* offspring.

Based on observations from the predator introductions in Chapter 2 (Experiment 1), and from a preliminary study with a separate *P. vittata* population (Appendix 2, Figure 1), I hypothesized that *P. vittata* maternal signals reduce offspring signaling after predator attacks. To test this hypothesis, my experimental approach was to remove the mother from a family; cause the offspring to begin signaling by simulating predation; and then play back the mother's signals, wind vibrations or silence.

To conduct this experiment, I first obtained a recording of each mother's signals. To record the mother's vibrational signals, I simulated predation with each family one day before the playback experiment. I presented a crushed nymph from a different *P. vittata* family on a 1/8" diameter wooden dowel ~1 cm under the center of the aggregation. A chemical cue from a crushed nymph acts as a predator cue (Nault *et al.* 1974; Cocroft 1999b) and reliably elicits collective signaling from offspring. Nymphs were frozen before being crushed and presented to offspring, and each dowel was used once. When offspring began signaling, mothers patrolled the family, signaled, and searched for the source of disturbance. I allowed mothers to find the dowel with the crushed nymph, which they kicked as they would a predator. As soon as a mother kicked the dowel, I withdrew it from the aggregation, simulating a predator eviction. At this point, mothers walked back to their resting position and produced steady bouts of signals.

I recorded maternal signals from the start of the simulated attack until after each mother located and evicted the simulated predator.

I returned to each family the day after recording maternal signals, removed the mother, and again simulated predator encounters (as described above) to elicit offspring signaling. I elicited 10 group signals from each offspring group and then simultaneously withdrew the crushed nymph and began playing maternal vibrational signals, wind vibrations, or silence (generated in Audacity v.1.3.12) for 14 min. Each family received all three playback treatments. Each playback was a loop comprised of 30 s of stimulus followed by 30 s of silence; I included silent intervals for scoring of offspring signaling response, in case the presence of playback signals on the audio track interfered with scoring. However, because offspring group signals contain energy at higher frequencies than do the maternal signals or wind vibrations, I was easily able to score all group signals, including those produced during vibrational stimuli.

To play vibrational stimuli to the *P. vittata* offspring, I glued the magnet to the branch at the trunk end of the aggregation, the mother’s typical position at rest. I played vibrational stimuli using an electromagnet as described in Chapter 3, Experiments 2 and 3. I controlled for possible effects of treatment order by randomly assigning each family to a pre-determined treatment sequence, and by waiting 1 h between treatments.

I used XBAT (Harold Figueroa, Ithaca, NY) to score offspring group signaling rates for each family in response to each playback treatment. I compared signaling responses among treatments in both experiments using the Quade test (Quade 1979), a non-parametric analog of repeated-measures ANOVA. Statistical tests were conducted with R statistical software, version 2.13.0.

Results

Maternal vibrational signals did not reduce offspring group signaling after simulated predator attacks. Offspring group signaling rate did not differ by vibrational playback stimulus (Quade $F = 1.519$, df = 2 / 18, $p = 0.25$) (Figure 1).

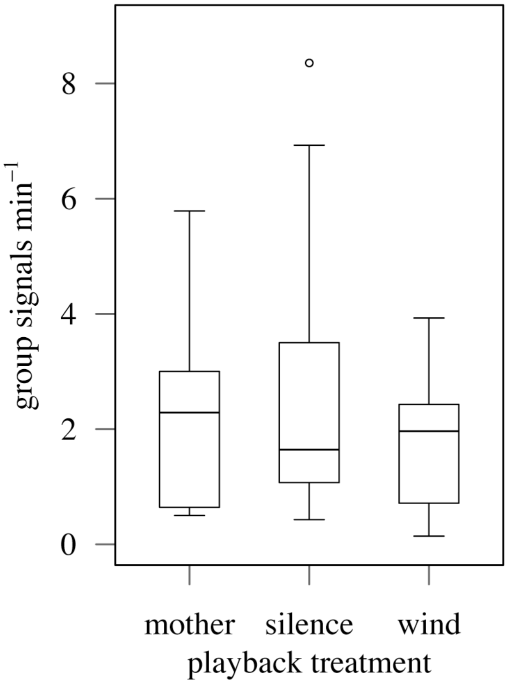

Figure 1. Signaling responses of *Platycotis vittata* offspring aggregations to playback of maternal signals, silence, or wind vibrations *after* simulated predator attacks. Box plots show distributions of offspring group signaling rate (minimum, first quartile, median, third quartile, maximum; open circles represent outliers). $N = 10$ families.

Appendix 4. Supplementary information for Chapter 3, Experiment 3.

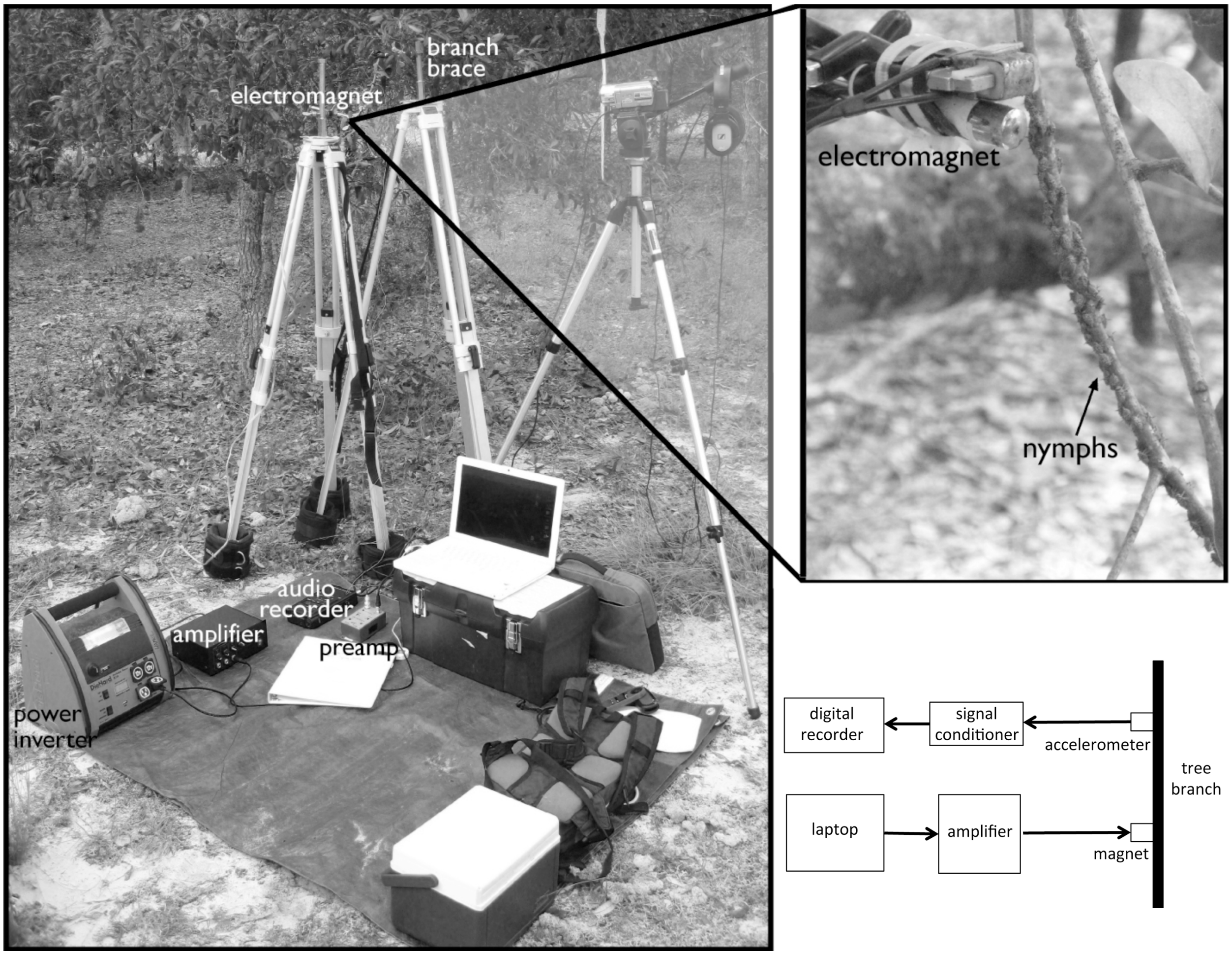

Figure 1. Field apparatus for vibrational playbacks to tree branches.

Table 1. Generalized linear mixed model assessing the effects of maternal signals on offspring signaling rate.

Fixed effect	Percent variation explained	Coefficient	SE	*p*
Full model	68.02			
Temperature	21.70	0.8009	0.2412	0.0009 ***
Playback treatment	13.23			
early encounter signals		-0.2673	0.1767	0.1304
post search signals		-0.6085	0.1945	0.0018 **
Carryover	4.89			
silence		0.08	0.2856	0.7688
early encounter signals		-0.4674	0.2902	0.1073
post search signals		-0.2387	0.2899	0.4103
Treatment sequence	2.14			
post search - silence - early enc.		-0.2345	0.2992	0.4332
post search - early enc. - silence		0.2356	0.3652	0.5188
silence - post search - early enc.		-0.0752	0.3929	0.8483
silence - early enc. - post search		-0.2720	0.2478	0.2723
early enc. - silence - post search		0.5450	0.2312	0.0184 *
Total wind energy	0.30	-0.0627	0.0810	0.4389
All temperature interactions	11.53			
Playback treatment : temperature	2.67			
early encounter signals : temperature		-0.0452	0.2405	0.8507
post search signals : temperature		1.0496	0.2365	9.1e-06 **
Carryover : temperature	6.28			
silence : temperature		-1.7731	0.3325	9.6e-08 ***
post search signals : temperature		-0.2832	0.2772	0.3068
early encounter signals : temperature		-0.5234	0.3544	0.1397

Random effect	Estimate	SE
sequence(family)		
intercept	1.3691e-06	0.0002
post search - early enc. - silence	6.2568e-06	0.0008
silence - post search - early enc.	0.3881	0.3325
silence - early enc. - post search	0.3394	0.3237
early enc. - post search - silence	7.0507e-06	0.0009
early enc. - silence - post search	3.2647e-06	0.0004

Regression coefficients are shown for fixed effects; variance estimates are shown for random effects. Raw data for temperature and total wind energy were standardized for analysis. Significance codes: '***' 0.001, '**' 0.01, '*' 0.05

VITA

Jennifer Anne Hamel, née Theresa Coyle, was born in New York, New York on May 19th, 1973 and adopted by Mr. Robert William Hamel and Mrs. Maureen Anne Hamel of Cortlandt, New York. She graduated from John F. Kennedy Catholic High School in Somers, New York. She studied art and Russian language at Carnegie Mellon University. After completing three years at Carnegie Mellon, she left her studies to play traditional Irish, Scottish and Breton music with a folk ensemble. She performed with the ensemble from 1994 to 2002 and toured through the U.S., parts of Canada, and Brittany.

In 2002, she returned to academia to pursue studies in Biology. From 2002 to 2005, she took coursework in Biology and Chemistry at the University of North Carolina at Asheville (UNCA), and also completed her degree in Art and Russian Studies at Carnegie Mellon. At UNCA, she discovered a love for animal behavior, ecology, research, and teaching. She assisted with amphibian population monitoring as part of Dr. Jim Petranka's Tulula wetland project, and with Dr. Tim Forrest's study of a cryptic species complex of phaneropterine katydids in the Blue Ridge Mountains. She also conducted a short study on female response to advertisement calls with Dr. Tim Forrest.

In 2005, she moved to Columbia, Missouri and entered the Ph.D. program at the University of Missouri under the advisement of Dr. Reginald Cocroft. After 6.5 years, Jennifer earned her doctoral degree. Jennifer is now a postdoctoral researcher at the University of Florida and works with Dr. Christine Miller. She is studying the influence of environmental heterogeneity and community composition on sexual selection.