Title

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Journal

Journal of Animal Ecology, 90(3)

ISSN

0021-8790

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Publication Date

2021-03-01

DOI

10.1111/1365-2656.13390

Peer reviewed

Received: 21 April 2020 | Accepted: 6 November 2020

DOI: 10.1111/1365-2656.13390

Journal of Animal Ecology | BRITISH ECOLOGICAL SOCIETY

RESEARCH ARTICLE

Visual contagion in prey defence signals can enhance honest defence

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Funding information
Chinese Academy of Sciences President's International Fellowship Initiative, Grant/Award Number: 2016VBA035; National Natural Science Foundation of China, Grant/Award Number: 31770420; China Postdoctoral Science Foundation, Grant/Award Number: 2019M653514 and BX20180354; CAS 135 Program, Grant/Award Number: 2017XTBG-T01

Handling Editor: Spencer Behmer

Abstract

1. The co-evolutionary arms race between predators and their prey has led to complex signalling, especially in groups that benefit from the social transmission of alarm signals. In particular, pursuit deterrence signals can allow individuals and groups to indicate, at relatively low cost, that a predator's further approach is futile.
2. Pursuit deterrence signals are usually more effective if amplified, for example, by becoming contagious and rapidly spreading among prey without requiring individual prey to confirm predator presence. However, this can also lead to runaway false signalling.
3. We provide the first evidence of a contagious pursuit deterrence signal in social insects. The Asian honey bee *Apis cerana*, performs an I See You (ISY) signal that deters attacking hornets.
4. We show that these signals enhance defensive signalling by also attracting guard bees and that the visual movements of appropriate stimuli alone (hornets and ISY signalling bees, but not harmless butterflies) provide sufficient stimuli. Olfaction and other potential cues are not necessary. The ISY signal is visually contagious and is buffered from runaway false signals because it is specifically triggered and by likely selection for honesty within the highly cooperative bee colony.
5. These results expand our understanding of contagious signals and how they can be honestly maintained in highly cooperative collectives.

KEYWORDS

alarm signals, deimatic signals, honey bee, hornet, pursuit deterrence

1 | INTRODUCTION

Pursuit deterrence signals have independently evolved in multiple vertebrate taxa such as birds (Murphy, 2006), chipmunks (Clark, 2005), lizards (Cooper, 2001) and fish (Brown et al., 1999) and are used to inform predators that they have been detected by prey, and that attempts to capture the prey are therefore likely to be unsuccessful (Caro, 1995; Hasson, 1991). For example, when attacked, phrynosomatid lizards can elevate and waggle their tails, revealing a bold pattern of black and white bars that signals to predators that they have been detected (Dial, 1986), In social animals, such signals could benefit from being contagious, meaning that the signal alone can trigger another signaller to transmit the signal without detecting or checking for the actual presence of danger (Oliveira & Faustino, 2017). Such signalling is self-replicating and auto-propagating even in the absence of its original trigger and has advantages for rapidly alerting the group and creating an amplified deterrence signal that signals to the predator that it has been detected. However, contagious signals need to be constrained by honesty because they lose their value if they are

unreliable (Laidre & Johnstone, 2013). A signal in which receivers blindly accept threat presence is susceptible to runaway false signalling that reduces the efficacy of alarm signalling. Different strategies have therefore evolved to increase accurate signalling from prey to other prey (Hamel & Cocroft, 2012).

Here we focus on signals between prey that are highly informative and can incur strong fitness costs by reliably eliciting costly actions (Bradbury & Vehrencamp, 2011). We distinguish our definition of contagious signals from prior work on social contagion, which considers the propagation of affective states (Videan et al., 2005) or contagion which is non-signalling (such as the simple transmission of an excitatory state (Broly & Deneubourg, 2015). Likewise, pursuit deterrence signals differ from aposematic signals because the prey is not simply advertising its toxicity, but providing more complex information about its active ability to escape, counter-attack, or both (Caro, 1995). Pursuit deterrence signals also differ from deimatic displays, which cover a much broader range of behaviours designed to startle, confuse, shock or frighten a predator, of which only some are signals (Umbers & Mappes, 2016).

In highly social insects such as honey bees, the problem of false runaway signalling should be curbed by the shared interest of individuals that are typically closely related within a colony. In fact, honey bees are all highly social and are the only social insects in which pursuit-deterrent signals have been identified. Termites (Kirchner et al., 1994) and *Camponotus* ants (Fuchs, 1976) produce alarm drumming signals in response to disturbances, but it is not clear if these signals deter predators or are contagious. Shimmering has been observed in *Apis cerana*, *Apis florea* and *Apis dorsata* (Breed et al., 2004), and is best described in *A. dorsata* in which hundreds of bees flip their abdomens upwards in a highly coordinated manner to generate rippling waves that rapidly spread over the colony and confuse and repel hornets (Kastberger et al., 2008). Such shimmering likely propagates via contagion because the coordinated wave-like motions depend upon the behaviour of nearby bees (Kastberger et al., 2014). However, to date, no experiments have excluded the predator to test for contagious pursuit deterrence signalling in any social insect. Without such exclusion, it is unclear if signallers are responding to each other or simply to the predator.

The I See You (ISY) signal of *A. cerana* may be a contagious pursuit deterrence signal. When a hornet is detected near the nest, guards produce the ISY signal by synchronously shaking their abdomens laterally (Tan et al., 2012). This signal is specific, increases with threat intensity and can deter predators. Guards barely respond to a non-threatening butterfly, their ISY signalling becomes more intense when a hornet gets closer, and hornets are repelled when a sufficient number of guards perform this signal (Tan et al., 2012). Moreover, if a hornet lands near the bee hive entrance, guard bees move towards the hornet and tend to aggregate together against the hornet intruders. Hornets that are not dissuaded can be enveloped in a ball of bees that generate deadly heat and carbon dioxide (Sugahara & Sakamoto, 2009). The number of bees performing the ISY is therefore an honest reflection of the colony's ability to muster sufficient attackers for an effective and dangerous heat ball (Ono et al., 1995). This heat ball is somewhat costly to the colony because workers die (Tan et al., 2016), and thus the ISY signal provides a way to deter attacks before deadly escalation is necessary.

If the ISY signal demonstrates a colony's ability to defend itself, then it should fulfil two predictions that we tested: it should draw guard bees towards to the signaller and be contagious, causing them to also perform the ISY signal even in the absence of a true threat. We therefore conducted experiments with six *A. cerana* colonies in Kunming, China, where they are naturally preyed upon by the hornet, *Vespa velutina*. We determined the proximate causes of ISY signalling and focused on bee-to-bee transmission of this signal. We tested signal synchronization with video playbacks, and investigated the attractiveness and contagiousness of these signals with real bees and hornets and with video playbacks.

2 | MATERIALS AND METHODS

2.1 | Colonies

We studied six *A. cerana cerana* colonies at the apiary of the Eastern Bee Research Institute in Kunming from August-September 2018, a season in which hornets are plentiful and hornet colonies are at their peak populations. All bee colonies were healthy and queen-right, and each had four combs.

2.2 | Experiment 1: Does the visual presence of the hornet elicit the ISY signal?

We filmed three types of visual stimuli. We recorded a tethered (1) *V. velutina* hornet (predator) or (2) butterfly (*Parantica sita* Kollar, 1844, a non-predator control stimulus) for 5 min against a background of leaves away from any bees with a digital video camera (Sony™ HDR-PJ790) at 30 fps. We also recorded (3) a single guard honey bee performing the ISY signal on its nest entrance in the absence of any other bees in the video frame.

For the playbacks, we used an Apple iPad (2017 model MPGW2CH/A, iOS 12). The screen of the iPad was a 9.7-inch (diagonal) LED-backlit IPS LCD, 16 M color, 1536 × 2048 pixels (264 ppi), maximum brightness of 514 lux (average brightness of 485.4 lux, 88% brightness distribution, 1117:1 contrast ratio (black corresponding to 0.46 lux), 97.4% sRGB (Calman 2D) and 2.22 gamma correction (60 Hz refresh rate and black to white response time of 26 ms).

We used CorePlayer Mobile v1.3.6 video software, which allowed us to pause or playback the video at half, normal or double speed. We played back all videos with the subject (hornet, butterfly or bee) at life size and maximum brightness (see above). During playbacks, the nest and trees were in full shade. Playbacks had no sound and consisted of the following treatments: motionless control (still hornet), moving controls (moving butterfly at half, normal or double

speeds), moving hornet (at half, normal or double speed) and ISY signalling guard bee (at half, normal or double speed).

During the 5-min playback trial, we placed the camera directly in front of and parallel with the nest entrance, separated by 10 cm (Figure S1). We conducted playbacks from 10:00 to 15:00. Ac guards group their production of ISY signals, likely to enhance their visual conspicuousness, such that multiple bees appear to synchronously shake their bodies and wings to perform the signal (one bout), followed by a brief pause and then repeats of the signal (subsequent bouts; Tan et al., 2012). Since signalling is usually a group behaviour, we scored the number of signal bouts elicited by each playback type. We used six colonies and conducted three trials per colony, running only one trial per day (18 different days spread over 1 month). On average, we observed 221.2 ± 96.1 (mean ± 1 *SD*) ISY signals per trial.

2.3 | Signal synchronization

To determine if ISY signals are synchronized, we analysed videos of guard bees producing ISY signals in response to a live, tethered hornet. For standardization, we only chose groups of six guard bees and measured the start and stop times of the first four ISY signals produced (one bout). Each ISY signal began with lateral abdominal shaking and ended when this shaking ceased. After a brief pause, the next signal would then begin with abdominal shaking. We used three colonies (four signals per bout from six different bees per colony). Each bout came from a different trial conducted on a separate day (18 different bees from 18 days spread over 1 month).

2.4 | Experiment 2: Bee attraction to a real ISY signalling guard bee

The ISY signal appeared to attract guards. To test this attraction and measure the attraction distance, we placed an opaque paper screen (20 high × 29 wide, clamped to a laboratory stand) separated by a 1-cm gap from the nest to allow bees on the nest entrance to view and sense each other, but to block the visual stimulus provided by a hornet on one side of the nest (Figure S1). We captured a *V. velutina* hornet with a hand net and tethered it to a 1-m long wood rod by wrapping wire around its petiole and the end of the rod. We waited until one only guard bee was on the designated test side of the nest (randomly chosen as right or left) and held this hornet at the corner and 10 cm in front of the chosen nest side. At this distance, Ac workers do not heat-ball hornets (Dong et al., 2018), but will perform the ISY signal after detecting the hornet. Within a few seconds, the guard bee usually began to ISY signal, and the 5 min trial began. In all cases, we filmed the bees with a video camera placed 1 m away from and centred in front of the nest. From this video, we measured the detection distance, defined as the distance at which a bee from the opposite side of the nest would shift its orientation and walk over to the bee performing the ISY signal (Exp 2A). We used a total 60 bees from six colonies (10 bees per colony, half tested as right side and half as left side). A trial consisted of testing five bees from one colony. We ran one trial per day and conducted these tests over 12 days within a 3-week period.

In some cases, the guard bee *did not perform the ISY signal*, allowing us to test an alternative hypothesis that hornet odour or non-visual hornet attributes (such as the potential electromagnetic field generated by the hornet) could have attracted the guard bees. This lack of ISY signalling happened at different times throughout the day and did not appear to be correlated with weather. Because the number of guard bees varied over the day, we could select occurrences in which only one guard bee was on each side of the nest entrance. When this occurred, we conducted the *single guard attraction trials* (*Exp. 2B*), and presented the focal guard with a tethered hornet (left or right side, randomly chosen but with an equal number of trials conducted on each side). After each trial, we captured and removed the focal guard bee to avoid reusing it. In total, we used six colonies (four trials per colony, 144 bees total). We ran one trial per day (consisting of four treatments of equal numbers of ISY signalling and non-ISY signalling guard bees on both sides with one colony) and conducted these tests over 36 days within a 6-week period (1.8 ± 0.4 guards crossed over per trial).

In the *multiple guard attraction trials* (*Exp. 2C*), we followed the same design, but used cases in which there were multiple guards on both sides of the colony. We counted the number of guards that crossed over when (1) there was no hornet, (2) the focal bee performed the ISY signal, or (3) the focal bee did not perform the ISY signal. We then calculated the net movement to each side. We conducted these trials on separate days from the two-guard experiment, and captured and eliminated the focal guard at the end of each trial to avoid reusing this bee. The three treatments tested (left side hornet, right side hornet and no hornet) constituted one trial, and we ran three trials per colony with six colonies, running only one trial per day (a total of 18 days over 1 month: 10.1 ± 5.1 guards moving per trial).

2.5 | Experiment 3: Testing if video playbacks of a guard bee performing the ISY are sufficient to attract guards

In experiment 1, we tested the kinds of video playbacks that could elicit ISY signalling from bees. In experiment 3, we tested if the video playback of an ISY signal could attract guards from the opposite end of the nest. In this way, we focused on the visual signal produced by the guards, eliminating all other potential guard cues and all hornet cues in experiment 4. We waited until a group of approximately 20 guards was located on one side of the nest entrance (randomly selected left or right) and placed the playback screen on the opposite side. We then played back the ISY signal for 5 min and counted the number of guards that crossed over to the ISY signal playback (1× playback speed) as compared to the control (motionless image of the

ISY playback). With each of our six colonies we ran a trial consisting of two treatments per day (control and playback). We replicated these tests three times with each colony and therefore tested bees for 18 days over 1 month (0.32 ± 0.08 is the mean proportion of guards moving towards both playback treatments).

2.6 | Experiment 4: Do guard bees producing the ISY signal also produce an olfactory signal?

We used a pump to sample the air (1 ml/s intake velocity) from six guard bees that were either performing the ISY signal or were not. Each sample came from a separate group of guard bees. The pump drew in air from a clean PFTE tube (1.5 mm diameter) that was placed approximately 3 mm from guard bees (not in contact). Inside the PFTE tube, we placed a 65-mm PDMS/DVB solid-phase microextraction (SPME) fibre (Supelco). To elicit ISY signals from guard bees, we placed a living and moving hornet swaying at 5 cm from the centre of the colony entrance. The control consisted of guard bees that did not produce ISY signals but were still exposed to a living hornet (with its wings removed because we found that hornet wing movement is key to eliciting ISY signals) and placed 5 cm in front of the colony entrance. Each treatment lasted 30 min and was run in the absence of other hornets near the colony entrances.

For comparison, we also collected the volatiles of one Ac guard bee sting gland per colony. We froze each guard bee (−18°C), and then used forceps to dissect out its sting gland, which was placed in a 1.5-ml glass vial whose lid we penetrated with a clean SPME fibre for 30 min. For our chemical analyses, we used a gas chromatography-flame ionization detector (GC-FID) with a HP 7890B (Agilent) gas chromatograph, and a HP-5 column (30 m × 320 mm × 0.25 mm; Agilent) through which helium carrier gas flowed at 37 cm/s. The oven ramp temperature was 50°C for 2 min, then was increased to 10°C/min for 23 min. Each SPME fibre was desorbed into the injector port (heated at 250°C) for 1 min. With each of three different colonies we tested one trial per day that consisted of three treatments (bees producing ISY signals, bees not producing ISY signals, and sting gland extract). We replicated these tests four times with each colony and thus conducted these measurements over 12 days within a 3-week period.

2.7 | Quantification and statistical analyses

We used JMP Pro v14.2.0 (SAS Institute, Inc.). To analyse the effects of video playbacks to guard bees (experiment 1 and 4), we used a Univariate Repeated-Measures Analysis with colony as a repeated measure. We then made all pairwise using comparisons with post hoc Tukey Honestly Significant Difference (HSD) tests. To analyse guard attraction to the ISY signal, we used 2-tailed Fisher's exact texts (https://www.graphpad.com/quickcalcs/contingency1/). To analyse signal synchronization, we used a Univariate Repeated-Measures Analysis with bee identity as the repeated measure and examined the relationship between signal number (within a sequence of four signals) and signal start time or signal stop time. We report mean ± 1 *SD*.

3 | RESULTS

3.1 | Video playbacks show that the ISY signal is visually triggered by specific stimuli, contagious and synchronized

By using a video screen, we found that video playbacks of predators and, separately, of guard bees performing the ISY signal significantly increased ISY signalling by receiver bees (treatment effect $F_{9,165} = 28.2$, $p < 0.0001$). An image of a moving hornet at normal or double speed and a bee performing the ISY signal at normal speed significantly elevated ISY signalling (Tukey HSD test, $p < 0.05$; Figure 1), and the hornet moving at normal speed (1× playback) and higher speed (2×) elicited significantly more signals than any other type of playback. However, ISY signalling was not elicited by the harmless butterfly control at any playback speed (Tukey HSD test, $p < 0.05$, Figure 1).

Guard bees synchronized their ISY signals. The start times ($F_{11,43} = 6{,}978.09$, $p < 0.0001$) and stop times ($F_{11,43} = 9{,}940.42$, $p < 0.0001$) of ISY signals are correlated (Figure 2). ISY signals were 0.39 ± 0.07 s in duration with an inter-signal interval of 0.56 ± 0.15 s.

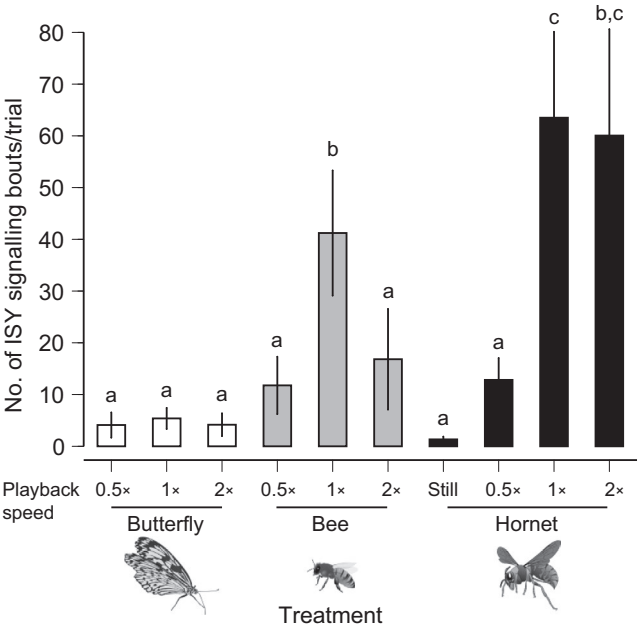

FIGURE 1 Effect of different video playback treatments on honey bee ISY signalling. Means and 95% confidence intervals are shown. Different letters indicate significant differences (Tukey HSD tests, $p < 0.05$). The butterfly treatment demonstrates that bees did not respond non-predators. Likewise, the still treatment shows that the appearance and motion of the hornet are important. Bees performed the ISY signal in response to other bees, but only at the correct playback speed

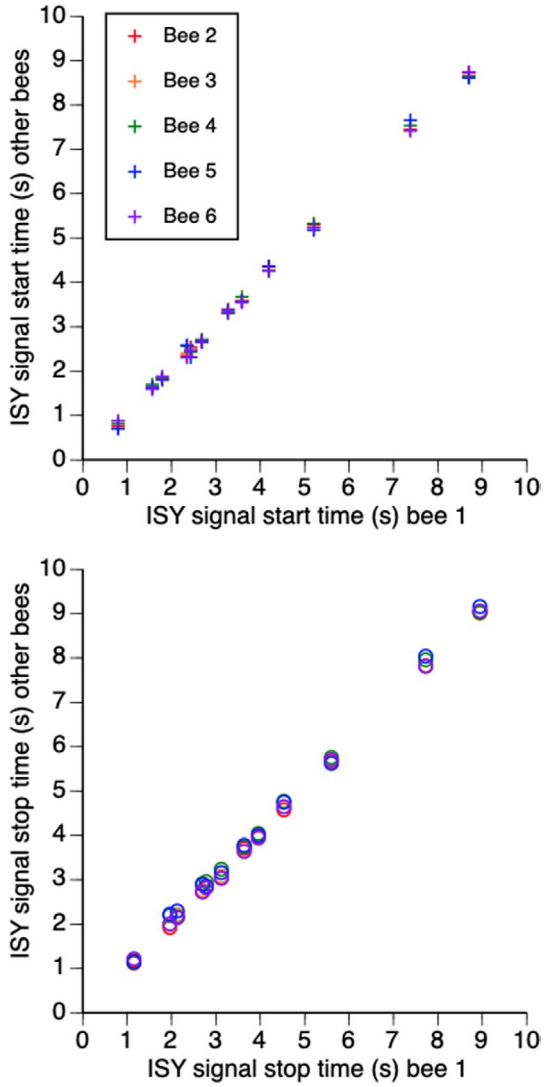

FIGURE 2 ISY signals are synchronized. The start and stop times of ISY signals in groups of guard bees (four signals per bout produced by six bees per group from three colonies) from video analyses are shown. For these plots, bee 1 is randomly chosen within each group and all other signals within a sequence are compared with it

3.2 | The ISY signal attracted guards (single guard attraction)

Increasing the number of bees joining in ISY signalling is known to enhance predator deterrence. We found that guard bees could be attracted to focal guard bees performing the ISY signal, not to potential cues produced by the hornet. In this experiment, only the focal guards could see the hornet, which was hidden behind a screen (Figure S1). The attracted guard would initially shift its orientation and approach from 10.1 ± 0.6 cm away ($N = 60$). Because we used a live hornet, the attracted guard could have been drawn to hornet cues such as its odour and electrostatic signature. However, such cues were also present in cases when guard bees did not perform the

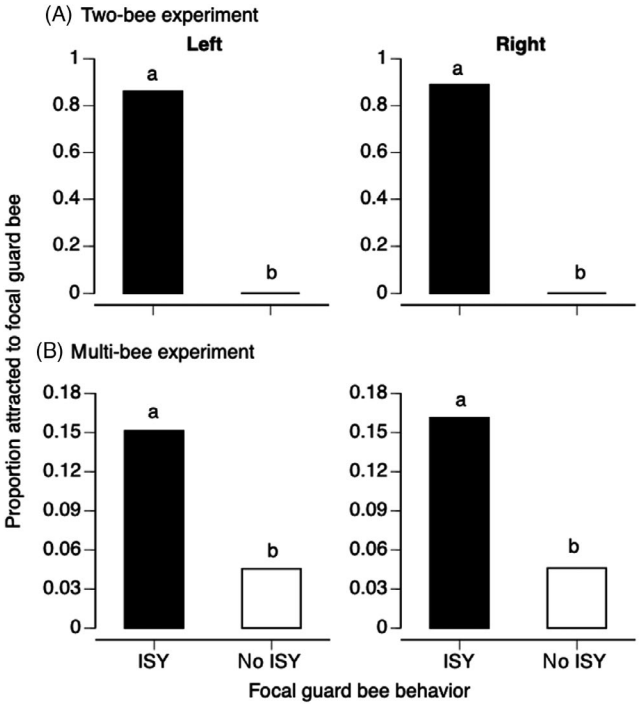

FIGURE 3 Attraction of guard bees that cannot see the hornet to a visible guard bee performing the ISY signal. The plots show attraction when the focal bee was on the left or right side of the colony. Different letters indicate significant differences (Fisher's exact tests, $p \leq 0.002$). (A) The two-bee experiment ($N_{left} = 72$, $N_{right} = 72$ bees) and (B) the multi-bee experiment ($N_{left} = 434$, $N_{right} = 435$ bees) are shown

ISY signal (Figure 3A). Overall, 0% of guards were attracted when the focal guards did not perform the ISY signal (two-tailed Fisher's exact tests, $p < 0.0001$), but 86% (left side presentation) to 89% (right side) of guards were attracted when the focal guards performed the ISY signal (two-tailed Fisher's exact tests, $p < 0.0001$).

3.3 | The ISY signal attracted guards (multi-guard attraction)

The single guard attraction experiment provided a more standardized and controlled way of testing guard attraction. However, a more natural scenario involves multiple guards distributed on both sides of the colony. Similarly, groups of guards were attracted to multiple guards performing the ISY signal. When there was no hornet, 11 net bees moved to the right and 11 net bees moved to left (Figure 3B). This data provided a baseline for guard movements in the absence of hornets. When guard bees signalled from the left, 83 net bees moved to the left and there was no net movement to the right (4.6 ± 2.7 bees per trial, Fisher's Exact test, $p < 0.0001$). When guard bees signalled from the right, 77 net bees moved to the right and there was no net movement to the left (4.3 ± 3.0 bees per trial, Fisher's Exact test, $p < 0.0001$, Figure 3B).

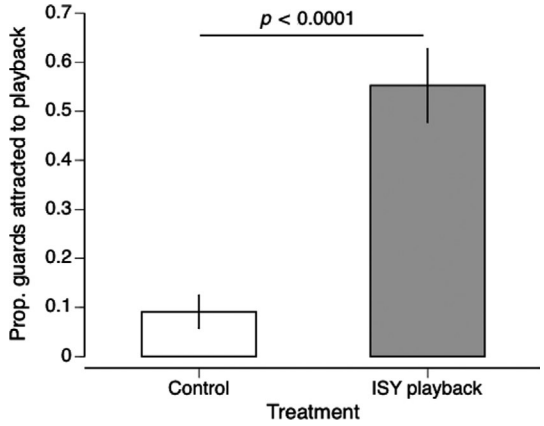

FIGURE 4 Attraction of guard bees to a video playback of single guard bee performing the ISY signal versus a still image (control) of the same guard bee. The mean proportion of attracted guard bees per trial is shown along with the 95% confidence intervals: $N_{trials} = 36$, $N_{colonies} = 6$, $N_{guard\ bees\ total} = 721$, $N_{guard\ bees\ per\ trial} = 20.0 \pm 3.7$ (mean $\pm$ 1 *SD*). The results of the Univariate Repeated Measures *F*-test are shown

3.4 | Guards were attracted to video playbacks of the ISY signal

The visual stimulus of a guard bee performing the moving ISY signal was enough to attract guard bees. Video playback of a guard performing an ISY signal caused a significantly higher 6.1-fold greater proportion of guard bees to move towards the playback as compared to a still image of the same guard (treatment effect, $F_{1,29} = 151.14$, $p < 0.0001$, Figure 4).

3.5 | Guards that performed the ISY signal did not produce detectable alarm pheromone volatiles

We did not observe guard bees extending their stings when detecting a hornet and performing the ISY signal. Solid Phase Micro Extraction (SPME) Gas Chromatography detected no alarm pheromone volatiles from guard bees that produced ISY signals or from guards that were presented with the hornet and did not perform ISY signals. However, all sting glands, as expected, had alarm pheromone compounds (significantly greater than the guard bees, L-R $\chi^2 = 45.83$, 2 *df*, $p < 0.0001$, Figure S2).

4 | DISCUSSION

In the arms race between prey and predator, sophisticated counter strategies evolve, such as signals that reduce the risks to predator and prey by deterring before lethal action is necessary. For example, the ISY signal communicates to an attacking hornet that a colony can defend itself and form a deadly heat ball (Ken et al., 2005). We show that the ISY signal is also attractive to other nestmates (drawing in defenders) and contagious (spreading simply when one guard sees another guard performing this signal). The ISY signal thereby serves two functions that are logically connected because the signal's predator deterrence efficacy is linked to the number of bees that produce the signal, a reliable indicator of a colony's ability to defend itself.

This attraction was not due to the production of alarm pheromone (which we did not detect in SPME assays) or other odours because video playbacks of bees producing the ISY signal were sufficient to attract guards. Guards may produce attractive odours that we did not detect, but we previously used the same SPME technique and found that guards that extended their stingers produced clearly detectable alarm pheromone compounds (Dong et al., 2018). Moreover, the presence of a predator was not necessary since guards were attracted to the video playbacks of an ISY signaller but not its still image. These video playbacks also excluded electrosensory information provided by living hornets or bees. Our video playback device did produce electrical fields, but ones that should be quite different from those generated by living hornets and bees. Moreover, any device-created electric fields should largely be similar regardless of whether the image was moving (experimental) or still (control).

Moving images of the correct type, video playbacks of a hornet or a guard bee performing the ISY signal (but not a harmless butterfly), were sufficient proximate stimuli to elicit ISY signals. Motion was essential because still images of a guard bee or a hornet did not elicit ISY signals. The required degree of motion depended upon its source and demonstrated selectivity. Bees most effectively elicited other ISY signals when they signalled at a normal rate (1×), not at lower (0.5×) or higher (2.0×) speeds. This selectivity may be adaptive given that the ISY signal is contagious and bees should therefore be quite choosy in distinguishing a true ISY signal before producing it and passing it on. In contrast, the ISY signal was easily triggered by hornet videos played back at 1× and 2× speed, a broader range of acceptable motion that may be linked to natural variation in hornet flight speeds but also likely reflects the greater reliability of this information, the visual appearance and motion of a real predator, for indicating threat. Bees were not indiscriminate about large flying objects. Video of hornets elicited ISY signals, but video playbacks of a naturally encountered harmless stimulus, a sympatric moving butterfly, did not.

Other factors may help to maintain honesty in ISY signal contagion. Like decisions such as which workers will attack colony predators (Breed et al., 2004) or, in a reproductive context, which workers will participate in swarming (Rangel et al., 2009), ISY collective decisions should be made for the overall benefit of the colony because selection should disfavour colonies with guards that 'cry wolf' and perform inappropriate ISY signals. These false signals would not benefit colony fitness. The exact cost is unclear, but *A. cerana* colonies that detect hornets change their behaviour: foragers move approximately twofold more rapidly to and from the nest to avoid hawking hornets (Tan et al., 2007). In addition, since ISY signals are attractive, false signals could inappropriately

draw guards away from general monitoring. Given the likely fitness costs, we predict that guards drawn to the purported location of a predator by false ISY signals will likely stop producing ISY signals if they detect no predator. Signalling cessation could occur via habituation. In the contagion experiment, we played back the video ISY signal over 5 min in the absence of any hornet predator and found no reduction in ISY response signalling over this fairly short period. However, in preliminary experiments in which we played back the ISY signal at seasons when hornets were not present or occurred at very low numbers, we found a reduced ISY signalling response. Guards or the colony may be informed of the seasonal likelihood of hornet attack, and frequent daily attacks during hornet season likely sensitize the colony to hornet presence. Such informed responses should place an additional curb on runaway false signalling.

The ability to coordinate such group defenses against predators has repeatedly evolved in social insects as a necessary counterbalance to a major detriment of sociality—the tempting concentration of resources provided by a colony. The heat-balling defence of honey bees against their formidable sympatric hornet predators is a classic example that illustrates two types of honest communication from different receiver perspectives. First, the size and efficacy of the heat ball defence depends upon bee colony size and is therefore linked to the number of ISY signallers, which honestly demonstrates the colony's defensive ability to the hornet (Ken et al., 2005; Tan et al., 2012). Second, the experiments reported here show that the ISY signal is contagious among bees and safeguarded from runaway false signalling because, proximally, contagion only occurs for correctly produced signals and, ultimately, because the close genetic relatedness of nestmates and status of the colony as the primary reproductive unit promotes honesty among nestmates. We predict the existence of similar safeguards in other contagious pursuit deterrence signals. In the case of large social insect colonies in which individual recognition of signaller identity and therefore individual reliability assessment is unlikely, emergent properties may have evolved to protect contagious signalling, an intriguing aspect of social signalling that is poorly understood.

ACKNOWLEDGEMENTS

We wish to thank the editor and two anonymous reviewers whose comments and suggestions have significantly improved the quality of our manuscript.

AUTHORS' CONTRIBUTIONS

S.H.D., K.T. and J.C.N. conceived of experiments, designed them and wrote the paper; S.H.D. collected the data; and J.C.N. performed the analyses.

DATA AVAILABILITY STATEMENT

All data used for our statistical analyses and figures are freely available via Zenodo.org at https://doi.org/10.5281/zenodo.4026397 (Dong et al., 2020).

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SUPPORTING INFORMATION

Additional supporting information may be found online in the Supporting Information section.

How to cite this article: Dong S, Tan K, Nieh JC. Visual contagion in prey defence signals can enhance honest defence. *J Anim Ecol*. 2020;00:1–8. https://doi.org/10.1111/1365-2656.13390