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James G. Puckett,[1] Rui Ni,[2] and Nicholas T. Ouellette[2, *]

[1]*Department of Physics, Gettysburg College, Gettysburg, Pennsylvania 17325, USA*
[2]*Department of Mechanical Engineering & Materials Science,*
Yale University, New Haven, Connecticut 06520, USA
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The macroscopic emergent behavior of social animal groups is a classic example of dynamical self-organization, and is thought to arise from the local interactions between individuals. Determining these interactions from empirical data sets of real animal groups, however, is challenging. Using multi-camera imaging and tracking, we studied the motion of individual flying midges in laboratory mating swarms. By performing a time-frequency analysis of the midge trajectories, we show that the midge behavior can be segmented into two distinct modes: one that is independent and composed of low-frequency maneuvers, and one that consists of higher-frequency nearly harmonic oscillations conducted in synchrony with another midge. We characterize these pairwise interactions, and make a hypothesis as to their biological function.

Social animals across the biological size spectrum routinely form groups, and the collective dynamics of the aggregation are often qualitatively different from the behavior of isolated individuals [1]. Collective behavior is ubiquitous because it can impart many advantages to both the group and individuals, such as enhanced environmental sensing [2], reduced individual risk of predation [1], energetically efficient group movement [3], or the ability to navigate complex terrain [4]. It is generally thought that the collective states of animal groups arise spontaneously from local, low-level interactions between individuals, much as thermodynamic states emerge from the interactions of molecules. Indeed, computational models of animal groups based on identical self-propelled particles that interact via simple rules or effective social "forces" can produce self-organized states that qualitatively resemble real animal groups [5, 6]. Such models have been shown to reproduce the mean motion observed in traveling aggregations such as bird flocks, fish schools, and migrating locusts [7–10] or the shape and mean-field features of collective systems with no net motion such as insect mating swarms [11].

Such simple models, however, are typically not sufficient to describe many of the *details* of collective animal behavior, such as the turning of bird flocks [12] or the long-range collision anticipation exhibited in human crowds [13]. To capture such features accurately and develop models that can predict more than mean-field behavior, we need to characterize the inter-individual interactions more completely.

In this Letter, we seek to pick out and characterize such interactions by measuring individual flight trajectories in a laboratory colony of swarming midges. Previously, it has been shown that the ensemble-averaged statistics of swarms show little structure [14–16]. Here, therefore, instead of considering, for example, acceleration statistics as a proxy for force-like interactions [9, 10, 16], we

make the ansatz that the spatiotemporal structure of the midge trajectories contains information about their social behavior. Then, using time-frequency analysis, we show that the midges follow slowly evolving flight paths that are punctuated by bursts of high-frequency activity. These events are typically shared between two nearby individuals, and thus are indicative of pairwise interactions.

We used a multi-camera stereoimaging and tracking setup [15, 17] to measure the trajectories of each individual insect in 307 swarming events in a laboratory colony of the non-biting midge *Chironomus riparius*. Details of our insect husbandry protocols and measurement techniques are given elsewhere [15, 16]. Briefly, our midge colony is maintained in a cubical enclosure measuring 91 cm on a side that is exposed to overhead light on a circadian cycle with 16 hours of light and 8 hours of darkness per day. Twice daily, at "dawn" and "dusk", male midges spontaneously form swarms, with sizes ranging from just a few individuals up to about 100 [15, 18]. To promote swarm nucleation, we place a black felt swarm marker measuring 30×30 cm^2 in the center of the enclosure. We image the swarms with three hardware-synchronized Point Grey Flea3 cameras at a rate of 100 frames per second, fast enough to resolve even the acceleration of the midges [15]. The cameras lie in a horizontal plane about 1 m from the center of the swarm with an angular separation of approximately 45°. Prior to recording data, the camera system is calibrated using Tsai's model [19]; subsequently, the two-dimensional coordinates of each midge on each camera (found by simple image segmentation and intensity-weighted averaging) can be combined to find the midge positions in three-dimensional space. The sequences of time-resolved positions are then linked into trajectories using a fully automated multi-frame predictive tracking algorithm [17]. Since individual trajectories may sometimes be broken, in

a post-processing step we link trajectory fragments using Xu's method of re-tracking in a six-dimensional position-velocity space [20], greatly increasing the mean trajectory lengths. After trajectory construction, we compute accurate time derivatives by convolving the tracks with a smoothing and differentiating kernel [15].

To search for distinct behavioral modes in these trajectories, we performed a time-frequency analysis using the continuous wavelet transform (CWT) with Morlet wavelets [21, 22]. This approach allows us to characterize the frequency structure of the trajectories locally in time, and therefore to find intervals when the structure of the trajectories qualitatively changes.

To apply the CWT to the midges, we must first choose a signal to analyze. In addition to the raw position along each trajectory, we also extract the three components of velocity and acceleration; thus, our data present us with a number of possibilities. But since we are primarily interested in extracting interactions between individuals, we choose to use a pairwise quantity rather than a single-midge measurement; and since we are using a time-frequency analysis, we choose to limit the number of derivatives we take, since differentiation acts as a high-pass filter and can artificially enhance the high-frequency content of a signal. Thus, we consider here the relative distance $r_{ij}(t) = |\mathbf{X}_i(t) - \mathbf{X}_j(t)|$ between pairs of midges, where $\mathbf{X}_i(t)$ is the time-resolved position of midge i.

If two midges are not interacting and are simply exploring the swarm volume, their position signals should be uncorrelated. The typical speed of a midge in our swarms is roughly 100 mm/s and the typical swarm diameter is roughly 200 mm; typical fluctuations in these quantities are about 50% of the mean value for the speed and 10% for the swarm size. Thus, if a midge were to move ballistically until it hits the swarm edge (as they do, statistically [15]), it would traverse the swarm at a rate no faster than 0.5 Hz. The relative distance between a pair of such independent midges must then evolve at a rate less than 1 Hz, since switching to the relative distance effectively rectifies the signal. One arrives at the same estimate by supposing that independent midges execute simple harmonic motion as they traverse the swarm, a reasonable ansatz given that the swarm acts at the mean-field level as a harmonic potential well for the midges [11, 15], and measurements of the power spectra of the ensemble of all midges confirm this estimate. These simple arguments suggest that if the relative distance r_{ij} is dominated by higher-frequency modes, the two individuals may be interacting.

In Fig. 1(a), we show $r_{ij}(t)$ along with its CWT for a pair chosen at random. For this pair, the CWT spectrum contains most of its power in a band centered at about 0.4 Hz. For most pairs, we find similar behavior. Sometimes, however, we find pairs whose relative position signal contains power not in this low-frequency band but rather at higher frequencies. An example is shown
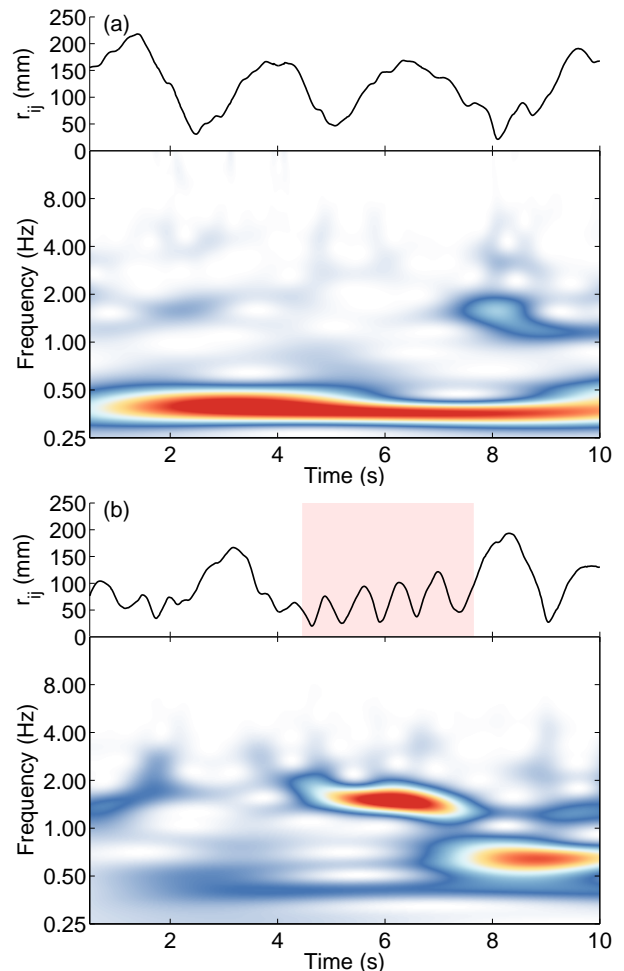

FIG. 1. (color online) Time-frequency analysis of the relative distance $r_{ij}(t)$ between midge pairs. (a) Time series of r_{ij} for a randomly chosen insect pair as well as its continuous wavelet transform (CWT). Nearly all of the power in the signal for this non-interacting pair is at low frequencies. (b) Time series of r_{ij} and CWT for an interacting pair. In the shaded region, r_{ij} oscillates nearly harmonically with power at higher frequencies.

in Fig. 1(b). For nearly 4 seconds, the relative distance between this pair of midges displayed nearly harmonic oscillations with a frequency of about 1.5 Hz. This kind of behavior is visually apparent when watching swarms, and is reminiscent of observations by Okubo and Chiang, who noted qualitatively that the trajectories of some individuals in swarms of *Anarete pritchardi* (a different species of midge) resembled harmonic oscillators [14].

To analyze this behavior quantitatively, we considered all midge pairs and isolated segments of the trajectories where the CWT of $r_{ij}(t)$ had significant power P at high frequencies (above ~ 1 Hz) and not at low frequencies (below ~ 1 Hz), where the threshold of 1 Hz comes from the estimate given above. To make this cutoff more robust and avoid some false positives and
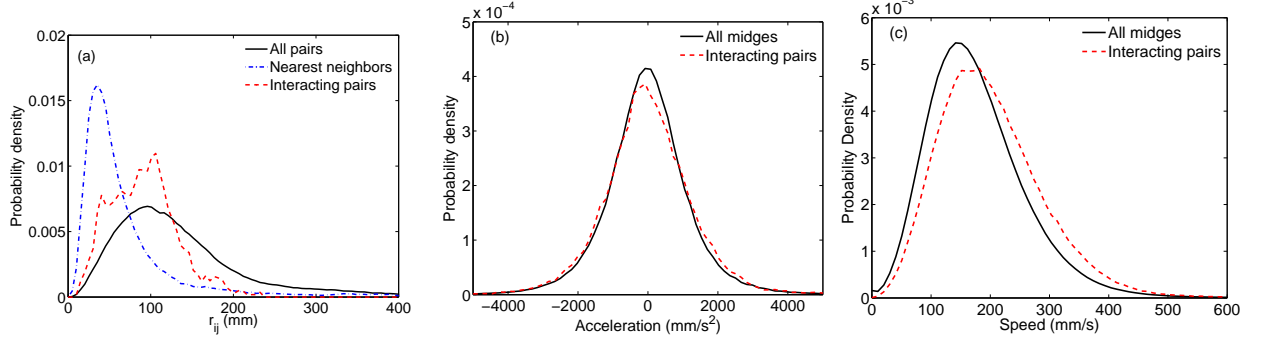
FIG. 2. (color online) (a) Probability density functions (PDFs) of the separation between insects for all pairs, nearest neighbors, and interacting pairs. Interactions do not in general occur between nearest neighbors. (b) PDF of acceleration for all insects and those engaged in interactions. Interactions do not show distinct signatures in the acceleration statistics, and are thus not representable by a simple mean-field force-like model. (c) PDF of speed (that is, the modulus of the velocity) for all insects and those engaged in interactions. The distribution is shifted to slightly faster speeds for interacting midges.
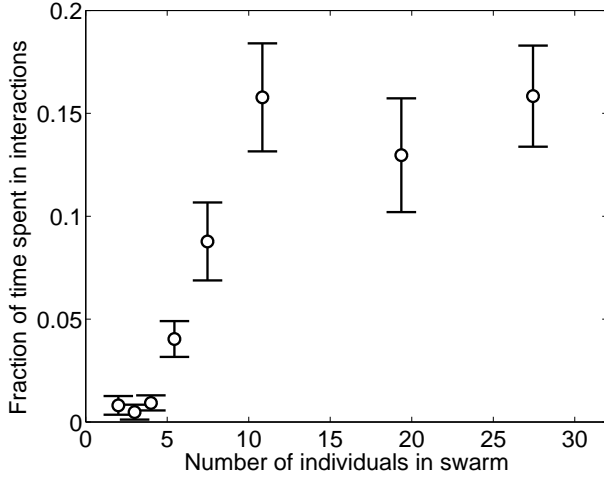

FIG. 3. Fraction of flight time spent engaged in interactions as a function of the number of individuals in the swarm. Interactions are rare in small swarms, but occur about 15% of the time for larger swarms.

false negatives, since wavelets are somewhat imprecise in frequency, we specifically looked for times t where $P(f < 0.95 \text{ Hz}, t) < P_0$ and $P(f > 1.25 \text{ Hz}, t) > P_0$ for a threshold power P_0. We estimated $P_0 = |\bar{a}/(2\pi f_0)^2|^2$, where $\bar{a}$ is the mean midge acceleration, and choose $f_0 = 2$ Hz (twice the frequency above which we expect to find interacting midges). To reduce the chance of spurious detection, we also required that P satisfy these conditions for at least 1 s, so that we could see a full period of oscillation at the lower bound of the "high frequency" band. The segmentation of the trajectories we obtained following this method was not significantly changed by by varying f_0 over a reasonable range. We note that this segmentation procedure is distinct from looking for rare events or outliers in the ensemble statistics of the midges, and is more analogous to pattern-recognition schemes.

The events we find in this way appear to be clear interactions between pairs of midges. Intriguingly, however, these interactions do not typically occur between midges that are nearest neighbors (defined as those that are instantaneously closest in a metric-distance sense). As we show in Fig. 2(a), the distribution of separation distances between interacting midges is distinct from the distribution of nearest-neighbor distances, and its mean value is larger (95 mm, as compared with a mean nearest-neighbor separation of 70 mm). These interactions are also not readily placed into an effective-force framework; the individual acceleration statistics, for example, of ensemble of interacting midges are indistinguishable from those of the entire ensemble of insects (Fig. 2(b)). We do observe a shift in the velocity statistics for interacting midges (Fig. 2(c)), though it is small. But even though their mean-field statistical weight is small, characterizing these interactions is necessary for fully understanding the swarm dynamics, since they are not particularly rare events; aside from very small swarms, which may exhibit different behavior [18], we find that midges spend about 15% of their time engaged in these pairwise interactions (Fig. 3).

To gain more insight into these interaction events, we consider the *individual* velocity statistics of midges both engaged in interactions and flying freely through the swarms. In Fig. 4(a) and (b), we plot the velocity projected in the direction of the interaction partner (that is, $\mathbf{v}_i \cdot \mathbf{r}_{ij}/r_{ij}$ for midge i and $\mathbf{v}_j \cdot \mathbf{r}_{ji}/r_{ji}$ for midge j) for the same two pairs as in Fig. 1. Although these projected velocities are not independent of the original relative velocity signal we analyzed, we are not using them to identify interactions. Rather, we use them to study the nature of these already-identified events. For the non-interacting pair (Fig. 4(a)), the two velocity signals are uncorrelated. But for the interacting midges (Fig. 4(b)), the two velocity signals are highly correlated, and oscillate nearly in phase with one another. To check the statis-
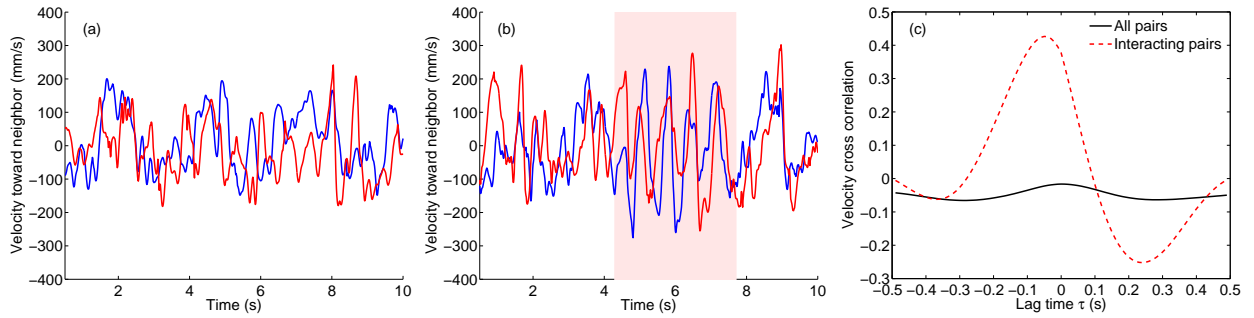
FIG. 4. (color online) (a,b) Velocity projected in the direction of the other individual for the two pairs shown in Fig. 1. Velocities are typically uncorrelated. But during an interaction, such as the shaded region in (b), the velocity signals for the two midges oscillate in phase. (c) Velocity cross-correlation functions for all midge pairs and for those engaged in interactions. During interactions, velocities are much more strongly correlated than they are for the population in general. The positive peak indicates anti-parallel velocity vectors.

tical robustness of this result, we calculated the velocity cross-correlation function for all pairs and for those pairs engaged in interactions (Fig. 4(c)). Non-interacting pairs show no correlation, while interacting pairs are strongly correlated. Given our definition of the projected velocities, the positive peak of the correlation function reveals that in general the velocities of the two midges are anti-parallel. When combined with the nearly harmonic signature in the frequency structure of the relative position, our results suggest that interacting midges behave as if they are connected by a linear spring. The net correlation we observe also shows that on average the interactions are mutual: both insects are engaged in similar behavior at the same time, rather than one midge flying freely an another oscillating near it. Relatedly, these correlations also indicate that these interactions are not the result of one midge chasing another.

So far, we have shown that these interactions involve pairs of highly correlated individuals moving with anti-parallel velocities. But what is the behavioral function of these interactions? To address this question, we consider the biological goals of the midges in the swarm. Chironomids swarm as part of their mating ritual [23, 24], and the swarms are composed exclusively of males. Females, who spend most of their time outside the swarms, are attracted to the aggregated males and occasionally fly through the swarm; once inside, they are chased and caught by males, and copulation occurs. Thus, each swarming male has two primary goals: to explore the volume of the swarm, both to be aware of potential predators and to search for females, and to keep track of the identity of the other individuals in the swarm, to identify whether they are male or female. We hypothesize that the low-frequency, independent behavior we observe (namely, periods that are not identified as interactions and during which the midges behave statistically like particles in an ideal gas [16]) is associated with exploration, while the high-frequency interactions are used for ascertaining the gender of other individuals. Moving in a
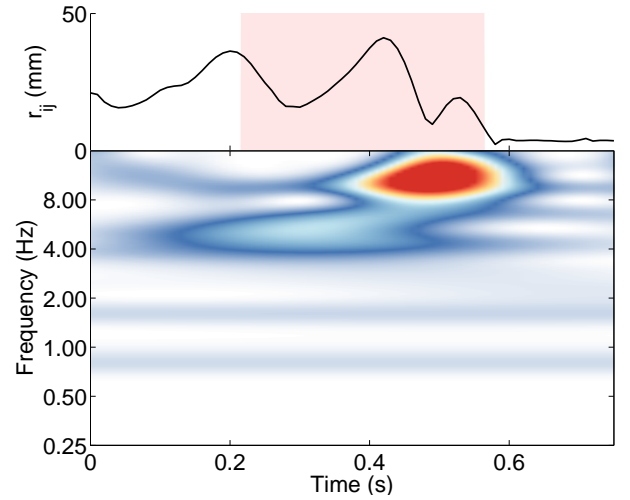

FIG. 5. Time-frequency analysis of a single male midge and a virtual female. When the male detects the female wingbeat sound, as played back by a small speaker, it executes very high frequency motion (shaded region) before flying toward the speaker and landing on it.

controlled, oscillatory fashion relative to another midge may be a way for an individual to isolate the sound of the target from the background hum of the rest of the swarm [11]. This hypothesis suggests that the post-interaction behavior of a male midge should be different depending on whether its interaction partner is male or female: the interaction should simply end (as it does in the example shown in Fig. 1b) if the other individual is male, but should result in chasing if the other individual is female.

Testing this hypothesis in detail is difficult, since our imaging resolution is not sufficient to distinguish females optically and their entrance into the swarms is rare. We can, however, provide some indirect evidence that it is reasonable. It is known that midges can distinguish gender by listening to wingbeat sounds, which are different for males and females [25, 26]. Thus, we measured the

response of individual males to the sound produced by a female. We recorded the sound of a freely flying female, and played it back to a swarm of males via a small speaker suspended inside the swarm; we then performed the same time-frequency analysis on the relative distance between the swarming males and the speaker. Males near the speaker moved rapidly toward it once the female sound was played, typically landing on the speaker and remaining there. But before flying to the speaker, males performed the same kind of harmonic oscillations as in the male-male interactions, although typically at a higher frequency. An example is shown in Fig. 5.

We have demonstrated that a time-frequency analysis of the trajectories of swarming midges reveals two distinguishable behavioral modes. We hypothesize that these modes can be associated with the biological goals of the individuals, who must balance exploring the swarm volume and registering the identities of their neighbors. In future work, we hope to confirm or reject this hypothesis more directly. In the meantime, however, our results suggest that models based on biological goals and not only on a large-scale tendency to order may be fruitful for studying collective animal behavior.

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* nicholas.ouellette@yale.edu

[1] J. K. Parrish and L. Edelstein-Keshet, Science **284**, 99 (1999).
[2] A. Berdahl, C. J. Torney, C. C. Ioannou, J. J. Faria, and I. D. Couzin, Science **339**, 574 (2013).
[3] S. J. Portugal, T. Y. Hubel, J. Fritz, S. Heese, D. Trobe, B. Voelkl, S. Hailes, A. M. Wilson, and J. R. Usherwood, Nature **505**, 399 (2014).
[4] N. J. Mlot, C. A. Tovey, and D. L. Hu, Proc. Natl. Acad. Sci. USA **108**, 7669 (2011).
[5] T. Vicsek, A. Czirók, E. Ben-Jacob, I. Cohen, and O. Shochet, Phys. Rev. Lett. **75**, 1226 (1995).
[6] I. D. Couzin, J. Krause, R. James, G. D. Ruxton, and N. R. Franks, J. Theor. Biol. **218**, 1 (2002).
[7] J. Buhl, D. J. T. Sumpter, I. D. Couzin, J. J. Hale, E. Despland, E. R. Miller, and S. J. Simpson, Science **312**, 1402 (2006).
[8] R. Lukeman, Y.-X. Li, and L. Edelstein-Keshet, Proc. Natl. Acad. Sci. USA **107**, 12576 (2010).
[9] Y. Katz, K. Tunstrom, C. C. Ioannou, C. Huepe, and I. D. Couzin, Proc. Natl. Acad. Sci. USA **108**, 18720 (2011).
[10] J. E. Herbert-Read, A. Perna, R. P. Mann, T. M. Schaerf, D. J. T. Sumpter, and A. J. W. Ward, Proc. Natl. Acad. Sci. USA **108**, 18726 (2011).
[11] D. Gorbonos, R. Ianconescu, J. G. Puckett, R. Ni, N. T. Ouellette, and N. S. Gov, submitted (2014).
[12] A. Cavagna *et al.*, arXiv:1403.1202 (2014).
[13] S. J. Guy, S. Curtis, M. C. Lin, and D. Manocha, Phys. Rev. E **85**, 016110 (2012).
[14] A. Okubo and H. C. Chiang, Res. Popul. Ecol. **16**, 1 (1974).
[15] D. H. Kelley and N. T. Ouellette, Sci. Rep. **3**, 1073 (2013).
[16] J. G. Puckett, D. H. Kelley, and N. T. Ouellette, Sci. Rep. **4**, 4766 (2014).
[17] N. T. Ouellette, H. Xu, and E. Bodenschatz, Exp. Fluids **40**, 301 (2006).
[18] J. G. Puckett and N. T. Ouellette, J. R. Soc. Interface **11**, 20140710 (2014).
[19] R. Y. Tsai, IEEE J. Robotic. Autom. **RA-3**, 323 (1987).
[20] H. Xu, Meas. Sci. Technol. **19**, 075105 (2008).
[21] C. Torrence and G. P. Compo, Bull. Am. Meteorol. Soc. **79**, 61 (1998).
[22] G. J. Berman, D. M. Choi, W. Bialek, and J. W. Shaevitz, J. R. Soc. Interface **11**, 20140672 (2014).
[23] J. A. Downes, Annu. Rev. Entomol. **14**, 271 (1969).
[24] R. M. Neems, J. Lazarus, and A. J. Mclachlan, Behav. Ecol. **3**, 285 (1992).
[25] M. V. Federova and R. D. Zhantiev, Entomol. Rev. **89**, 896 (2009).
[26] L. J. Cator, B. J. Arthur, L. C. Harringtona, and R. R. Hoy, Science **323**, 1077 (2009).