The Role of Density in the Swarming Behavior of Soldier Crabs: Laboratory Experiments and Ecological Observations

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Abstract: Collective vigilance has commonly been considered as one of the possible hypotheses explaining swarming in (social) animals. According to this theory, by engaging in cooperative monitoring of the environment, groups of social animals can enhance threat detection and overall survival. At the same time, this enables them to spend more time foraging and engaging in social activities. In this study, we report a behavior observed in soldier crabs challenging some aspects of collective vigilance. Laboratory experiments were performed at three swarm density levels (low, medium, and high) to check whether crabs are able to collectively adapt their motion to the changing environment (a moving light). Results show that only medium densities allow dynamic realignment with the moving light, whereas no collective motion is shown at low densities, and changes do not occur at high density. Experimental results were qualitatively backed by ecological observations, in which we show that above a specific threshold of swarm sizes, individuals fail to detect external threats (such as a passing bus) and/or do not change behavior in response to this environmental stimulus. In general, our results hint at the fact that the ability of swarms to collectively adapt to external conditions depends on swarm density, with the relationship being non-linear regarding swarm density. Our study highlights the importance of considering complex systems from a closer microscopic perspective based on the ability of individuals to detect changes in the surrounding environment along with the interactions among them.

Keywords: Soldier crab, Swarming, Collective vigilance, Environmental stimulus, Swarm size

1. INTRODUCTION

Swarming is a commonly observed behavior in the animal kingdom [1]. Milling, for example, is observed in fish schools when a large number of individuals swim in a rotating structure [2]. Flocks of birds are observed in several species, resulting in thousands of birds moving in synchronized motion despite having no centralized coordinating mechanism [3]. Although air and water provide a three-dimensional medium to form these self-organized structures, swarms are also commonly seen on land. An example is sheep flocks; however, wolves also form packs, and desert locusts can also form large bands [4]. Ants are famous too for making highly organized trails. Lastly, humans are also known to form self-organized structures and assemble in crowds [5].

The reasons why animals form such large structures are not yet completely clear to researchers. Some hypotheses are widely accepted and would hold true for most species (in which collective organization is observed). However, other hypotheses are more specific to some species and/or are not widely accepted. In general, it is possible to identify a number of evolutionary advantages and disadvantages that can explain why animals move in swarms in some contexts and prefer individual motion in other situations.

† Claudio Feliciani is the presenter of this paper.

Collective vigilance is among the advantages linked with swarming. It is believed that if an individual spots a predator, even by chance, other individuals lying in the proximity can benefit from the information and take countermeasures (e.g., fleeing or hiding) [6]. Thus, individuals being part of a swarm can spend more time breeding, protected by the "many eyes" checking the surrounding environment. In addition, by gathering in large numbers, it is more difficult for a predator to target individuals, lowering the chances of successful attacks [7, 8]. Temperature regulation or other biological factors are also among the advantages of swarming, although, here, we want to focus on behavioral features. Among the disadvantages of swarming, we may list, for example, increasing competition among individuals, overcrowding, and risks related to the transmission of infectious diseases.

Although the factors explained above help to explain swarming in most social animals, there are always differences among species. Taking the specific case of collective vigilance, it has been reported that when swarm size increases, individuals become less vigilant, which is also called the "group size effect on vigilance" [9]. This behavior has been reported for several species of birds [10]. However, several studies failed to detect the group-size effects in primates [11], and the mechanism of collective vigilance has been challenged for some species of

Fig. 1 A small group of soldier crabs (*Mictyris guinotae*) in their natural habitat. This picture was taken in October when individuals tend to be larger and bluer compared to early times of the year.

birds too [12, 13]. This shows that collective vigilance is far from being a widely accepted phenomenon related to swarms, and despite being a valid explanation for some collective behavior, it is not universal among species.

In this study, we present an example of peculiar collective behavior and vigilance by reporting results from a laboratory experiment and an ecological observation on soldier crabs. We show that the ability of soldier crabs to respond to external stimuli depends on swarm density, and when density exceeds a specific threshold, threats or environmental changes may go unnoticed. This result can be interpreted as a non-linear behavior regarding swarm size, confirming that animal swarms are complex systems in which interactions among individuals result in emergent structures that are not a linear combination of all interactions.

2. TARGET ANIMAL SPECIES

Before discussing the details of the experiments and observations, a brief introduction is given to provide relevant information on the animal species considered in this work: the soldier crabs. This species of crab is known for its ability to form large swarms, called "armies." They are found on tropical shores such as those in Australia, Southeast Asia, and East Asia [14]. This study focuses on *Mictyris guinotae* from the Ryukyu Islands in Southwest Japan [15].

Grown adults typically have a carapace size of about 15 mm (see Fig. 1), with legs extending 5–10 mm. Soldier crabs live in tidal flats, and their behavior is governed by tidal cycles. They dig into the sand during high tide (as they cannot swim and would die after prolonged time in water) and emerge during low tide to feed near the water but avoid entering it. Their collective behavior is not limited to motion; for example, it has been shown that they are able to better predict low tides when in groups compared to isolated individuals [16]. In this study, we will also focus on collective behavior, considering both motion and threat detection. Laboratory experiments were performed at the Iriomote Station (Tropical Biosphere Research Center, The University of Ryukyus, Japan), which is not far from Funaura Bay on Iriomote Island where ecological observations were done.

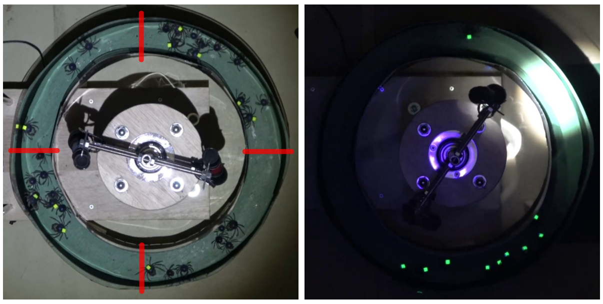

Fig. 2 The device used to test the collective organization of soldier crabs under the influence of an external stimulus is shown in the image. The left side of the image shows a fully lighted course with 30 individuals, while the right side depicts the rotating light used in an experiment with 10 crabs. The representation on the left side also shows the lines used to count individuals moving clockwise and counterclockwise in the initial and final minute of each experiment.

Given that soldier crabs' behavior is related to tidal cycles and they possess an internal clock informing them of tidal activity, experiments were performed during low tide when crabs are typically found wandering in large swarms. After each batch of experiments, individuals were returned to their natural habitat.

3. LABORATORY EXPERIMENT

3.1. Equipment

To study the ability of soldier crabs to respond to external stimuli and eventually self-organize under different swarm sizes, the experimental device illustrated in Fig. 2 was built.

The device consists of a circular course (with a circumference of 100 cm along the centerline) limiting the motion of crabs in the tangential direction. In other words, crabs can move either in the clockwise or counterclockwise direction, with radial motion being largely restricted (the course width is 5 cm, which is around 2–3 times the size of an individual). This geometry allows us to simplify the analysis of collective motion, as it is sufficient to determine whether there is a dominant direction of motion (e.g., all or most crabs moving clockwise or counterclockwise) or no dominant direction at all (i.e., random motion for each individual resulting in no collective rotation).

A rotating lamp lighting a portion of the course from above (see Fig. 2) was used as an "external stimulus" to influence crabs' motion. The light rotated at an angular speed of 7.3 rpm, resulting in a linear speed much higher than the crabs' moving speed. The light rotating speed was chosen based on previous studies that confirmed this setting would allow inducing behavioral changes in soldier crabs [17].

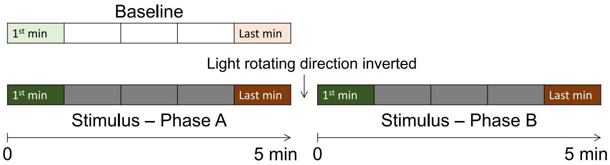

Fig. 3 Schematic of experiment timelines: light direction was inverted after 5 minutes, making each experiment 10 minutes long. Consequently, direct comparison between baseline and stimulus conditions is only possible in phase A. Data used for analysis were collected in the initial and final minutes.

3.2. Procedure

The goal of this experiment was to determine the extent to which it is possible to influence and steer collective organization through external stimuli and the role played by swarm size. More specifically, the experiment was designed in several steps, each having partially different roles but all linked to the same goal explained above. Fig. 3 schematically summarizes the outline of experiments, with details provided below.

1. **Baseline Condition** – *Collective organization under "normal conditions."* This condition aimed to determine if crabs self-organize more efficiently in large swarms. The course was fully illuminated, and swarm sizes of 3, 10, and 30 crabs were tested. Experiments lasted 5 minutes, comparing crab motion in the initial and final minute. The number of trials ranged from 10 (for swarms of 3 and 10 individuals) to 3 (for swarms of 30 individuals). A different batch of crabs was used in each trial. See the left panel of Fig. 2 for an example of the baseline condition.
2. **Stimulus Condition (Phase A)** – *Exploring the potential influence of an external stimulus on inducing self-organization.* The initial phase of this condition studied the possibility of externally inducing organized motion by rotating a light over the course to influence crabs to move in the same direction as the light (see the right panel of Fig. 2 for an example). Experiments also lasted 5 minutes, with assessment based on changes from beginning to end. Following this preliminary phase, Phase B was executed as listed below.
3. **Stimulus Condition (Phase B)** – *Assessing the swarm's ability to adapt to changing conditions.* This second part of the stimulus condition studied how different swarm sizes adapt to changing conditions by inverting the rotation direction of the light after Phase A. Videos were taken for another 5 minutes to observe if crabs could detect the change in external conditions and adjust their behavior accordingly to the inverted rotation of the light.

3.3. Data collection

Markers painted with ultraviolet paint were affixed to the crabs using a weak organic glue. This approach allows for the visualization of the crabs' positions in both bright and dark conditions (see Fig. 2). Initially, tracking was considered a viable technique for extracting information about the crabs' motion. However, the strong contrast created by the light and, in some cases, reflections of the markers on the course boundaries made tracking impractical and very time consuming. Since the overall direction of movement is the only information of interest in this study, the course was divided into 4 locations (see the red lines in Fig. 2), and the number of crabs moving clockwise or counterclockwise in the initial and final minute of each experiment was recorded. Based on the total number of transits and the proportion of those in the same direction, we can compute information such as average speed and the degree of self-organization, which will be presented along with the results below.

Table 1 Average speed based on swarm size and the presence (or absence) of an external stimulus. Speed calculations for the stimulus conditions combined phases A and B.

Swarm size	Baseline [cm/s]	Stimulus [cm/s]
3 (small)	2.15 ± 0.52	2.67 ± 0.65
10 (medium)	1.70 ± 0.33	2.11 ± 0.43
30 (large)	1.67 ± 0.52	1.65 ± 0.29

3.4. Results

As explained above, videos were analyzed to obtain counts related to the motion of crabs in the initial and final minute of each experiment over the four "transit lines." In presenting the results, we will start by considering the average moving speed of crabs for different swarm sizes in both tested conditions. The results are presented in Table 1 [1]. It can be noticed that the speed is higher in the stimulus condition (phases A and B were combined here), but only for small (3 crabs) and medium (10 crabs) swarm sizes. A one-way ANOVA test confirmed that there is a statistical difference (at a significance level of $p = 0.05$) between the baseline and stimulus conditions for 3 crabs ($F(59, 1) = 9.41$, $p = 0.003$) and 10 crabs ($F(59, 1) = 13.72$, $p < 0.001$), but the speed for 30 crabs is not significantly different among conditions ($F(17, 1) = 0.0087$, $p = 0.93$).

We can therefore conclude that the moving light makes crabs move faster. However, this effect is nullified for large swarm sizes where motion becomes physically difficult, and conflicts are commonly observed among individuals (see the right panel of Fig. 2). This result is not surprising because space is limited on the course, and even if self-organization is achieved, moving in large groups is difficult.

Next, we will consider the "degree of self-organization," a quantity defined to measure the degree of collective motion. The degree of self-organization can be defined as:

$$\frac{|n_{\text{clockwise}} - n_{\text{counterclockwise}}|}{n_{\text{clockwise}} + n_{\text{counterclockwise}}} \tag{1}$$

[1] In this table, phases A and B were combined because we can assume, as also confirmed by a statistical test, that only the presence of a rotating light will influence speed, not the direction of rotation.

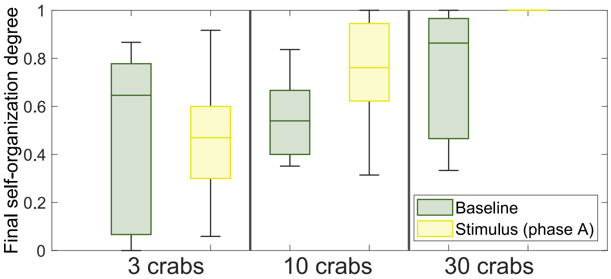

Fig. 4 Degree of self-organization in the final minute of the experiments. For the stimulus condition only phase A is considered to have a valid comparison with the baseline condition.

where $n_{\text{clockwise}}$ and $n_{\text{counterclockwise}}$ are the total number of transits (along the 4 transit lines) counted in the respective directions over one minute (either the initial or final one). According to our definition, when all crabs move in the same direction, degree of self-organization will be 1, and 0 corresponds to completely random motion (or something similar to it). It is important to note that in the stimulus condition, degree of self-organization is defined regardless of the light's rotating direction, so perfect self-organization may occur with crabs moving in the opposite direction of the light.

Self-organization degree in the final minute of the experiments is presented in Fig. 4. The results show that large swarms tend to be more self-organized, with most individuals moving in the same direction. In the stimulus condition, perfect self-organization (i.e., 1) was reached in all three trials with 30 crabs. A two-way ANOVA confirms that self-organization depends on swarm size ($F(45, 2) = 5.90$, $p = 0.006$), but not on the condition(i.e. baseline or stimulus; $F(45, 1) = 2.65$, $p = 0.11$). However, we are not simply interested in the final outcome; it is also important to study the mechanism of self-organization throughout the experiment. This additional analysis is needed to exclude the possibility that a good degree of self-organization is related to a swarm that was already self-organized when the experiments started, rather than emerging as a process *during* the experiments.

Therefore, to delve more deeply into the self-organization process, we need to compare its change from the beginning to the end of each experiment, with these results depicted in Fig. 5. In the stimulus condition, self-organization tends to improve more quickly in large swarms (changes are roughly symmetric around zero for 3 crabs and gradually increase to positive values for 10 and 30 crabs). Moreover, a one-tailed Wilcoxon signed-rank test shows that only swarms of 10 crabs exhibit increased self-organization (i.e., changes larger than zero) in both the baseline ($Z(54) = 2.65$, $p = 0.004$) and stimulus conditions ($Z(47) = 1.94$, $p = 0.026$). On the other hand, in the case of 3 crabs, self-organization increases, but it remains low at the end (see Fig. 4), whereas for 30 crabs, the change is not statistically significant, implying no change ($Z(5) = 0.80$, $p = 0.211$ in the baseline and $Z(6) = 1.34$, $p = 0.091$ in the stimulus condition). In short, from these results, we can conclude that the external stimulus aids in self-organization, and swarm size also plays a role.

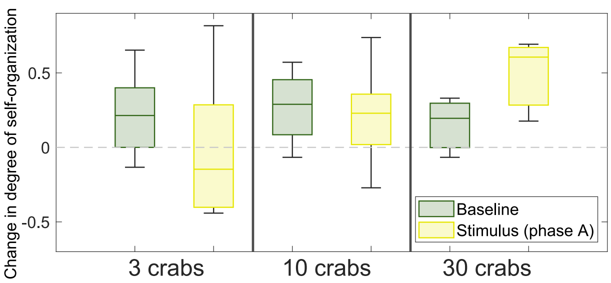

Fig. 5 Change in the degree of self-organization from the first to the last minute of the experiments. Values larger than 0 indicate an increase in the degree of self-organization.

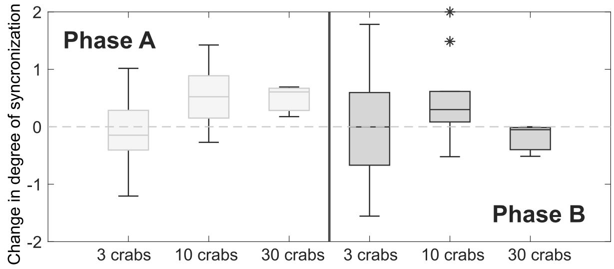

Fig. 6 Change in synchronization degree from the initial to the last minute of phases A and B. A synchronization change larger than zero implies that the swarm is better organized *and* the collective direction corresponds to that of the light. Values around zero imply no significant change, whereas negative values indicate better self-organization that is not synchronized with the light's rotating direction. Note that values larger than 1 or -1 are possible in this case.

However, in the results presented so far, the rotating direction of the light has not been considered. To address this, we can define a quantity called "degree of synchronization," which uses the same absolute value as self-organization degree but with the sign determined by the light's rotating direction. Hence, a self-organized swarm moving in the same direction as the light will have a positive synchronization degree, whereas one moving in the opposite direction will have a negative one.

We can now analyze the change in synchronization in both phases A and B of the stimulus condition. Since the light direction changes in phase B, crabs need to reverse their motion to have a positive change in synchronization degree. Results from Fig. 6 show that in the case of 3 crabs, degree of synchronization is quite symmetric around zero, indicating that crabs do not synchronize with the light. We can conclude that for 3 crabs, there is no collective motion in the first place, hence there will be no change either. For 30 crabs, synchronization is positive in phase A (median value is 0.606) but negative in phase B (median value is -0.051). This indicates that no inversion is observed; instead, motion is increasingly against the direction of the light, showing the inability of large swarms to adapt to changing conditions. Only 10 crabs show a positive increase in both phases A and B, which is confirmed by a one-tailed Wilcoxon signed-rank test: $Z(51) = 2.34$, $p = 0.010$ in phase A and $Z(45) = 1.73$, $p = 0.042$ in phase B. In short, the medium-sized swarm is able to change its motion based on external conditions: first aligning with the light in phase A and later inverting direction in phase B.

4. ECOLOGICAL OBSERVATION

The experiments presented above provide an overview of the collective behavior of soldier crabs. However, the conditions under which the experiments are performed are very artificial. As mentioned briefly, soldier crabs dig under the sand when a high tide is approaching. Additionally, they exhibit this behavior when they perceive an incoming threat. For example, when a person approaches them, crabs will quickly dig below the sand, making observations from a close distance difficult. On the other hand, crabs are completely nonreactive to flying drones, making aerial observation possible. In this section, we are reporting observations performed using DJI Mavic 2 drones in the Funaura Bay of Iriomote Island.

Aerial footage was taken in a sandy area close to a street (see Fig. 7), which is the natural habitat of thousands of soldier crabs. By chance, we observed that the behavior of crabs suddenly changes when buses pass over the street. Apparently, the appearance of a large object moving quickly prompts a simultaneous behavior, leading many crabs to dig below the sand and/or escape far away from the road. It is not yet clear whether the threat is perceived based on visual clues or other means (e.g., vibrations). However, crabs' reactions appear to be particularly strong for buses, nonexistent for cars (which are hard to see from the sand due to the vegetation hindering direct sight), and mild for trucks (which are heavy but smaller than buses). Hence, we may hypothesize visual detection. Regardless of the sensory means, we observed

Fig. 7 The location where observations were performed is the area indicated by round markers on the sandy beach. Large buses passing on the street induce a collective reaction in crabs, perceiving buses as a threat. This scenario allows us to make some considerations on collective vigilance in soldier crabs.

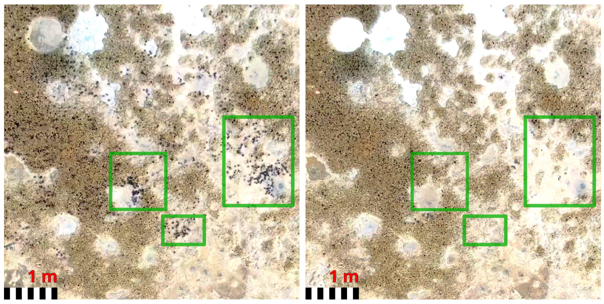

Fig. 8 Snapshots were taken 10 seconds before the bus transit (left) and 30 seconds after (right). Crabs are represented as black dots. While isolated individuals are recognizable before the bus transit, most of them quickly dig below the sand afterward. Green areas are highlighted to facilitate the before-after comparison. The images were modified in terms of contrast, lightness, etc., to enhance the identification of crabs.

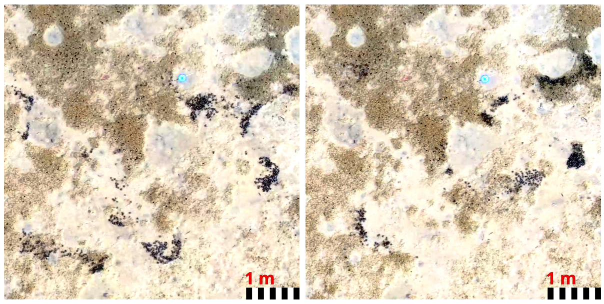

Fig. 9 Change in swarm structure and organization before (left) and after (right) the passage of a bus over the road close to the study area. The first snapshot is taken 10 seconds before the bus transit, and the second one is taken 30 seconds after. This image focuses on a region with large swarms. Parts were not highlighted here since the presence of crabs after the bus transit is rather clear and swarms tend to move rather quickly.

a density-dependent behavior, which will be described as follows.

In the case of sparse swarms with mostly isolated individuals, there is a tendency to dig below the sand as soon as a threat is detected, as shown in Fig. 8. This behavior is expected because a perceived threat should naturally lead to fleeing, or in the case of soldier crabs, digging.

However, the behavior is radically different in large swarms, which continue moving on the sand after a bus transit, only changing their shape and eventually splitting into smaller groups or merging into larger ones (see Fig. 9). This behavior is rather puzzling when considered from the perspective of collective vigilance. From that standpoint, we would expect that large swarms are more efficient in detecting threats and reacting accordingly, or at least should be as effective as smaller swarms.

Analysis of the videos reveals that especially mid-sized swarms do exhibit a fleeing behavior, but without digging. Very large swarms seem to barely notice the incoming threat. We can hypothesize that either large

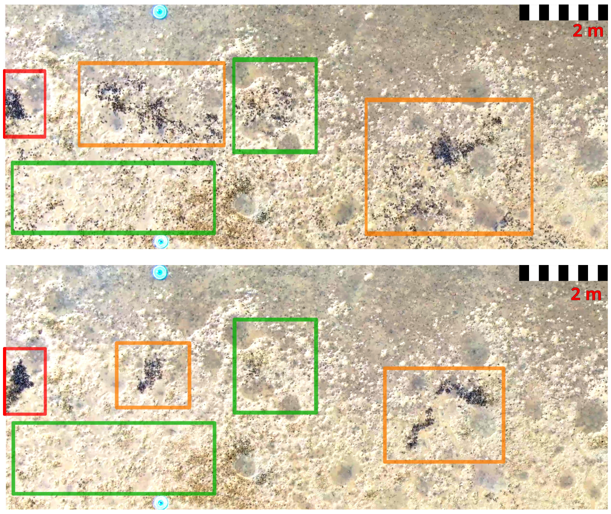

Fig. 10 Change in swarming patterns in an area with different swarm sizes. The top image refers to the situation 10 seconds before the bus transit, while the one below shows the scene 30 seconds after. The central part of the image mostly shows sparse individuals, the left side a large group, and the right side a mid-sized swarm. Unmodified swarms are highlighted in red, those changing spatial organization are depicted using orange squares, and low-density areas where most crabs dig are shown in green.

swarms fail to detect the threat, or individuals feel "protected" by the group and do not find it necessary to dig. It is also possible that in high-density conditions, digging is difficult due to limited space, thus preventing them from exhibiting such behavior. With all these hypotheses potentially valid, this behavior would deserve further investigation.

Fig. 10 illustrates a scenario where low-density swarms mix with high and medium-density ones. It is interesting to note that isolated crabs tend to dig after the passage of the bus, while large swarms maintain their structure relatively unchanged. However, when individual crabs are not too distant from each other, dense swarms tend to form in response to the perceived threat. This suggests that an inter-individual distance allowing for interactions prompts a reconfiguration of collective organization.

While the ecological observation lacks quantitative validation, qualitatively it aligns with the results from the earlier laboratory experiment. It confirms that low swarm densities do not foster collective behavior, with crabs behaving individually. On the other hand, large swarms exhibit collective motion but do not respond to external stimuli. Only medium-sized swarms show both self-organization and dynamic responses to environmental changes.

5. DISCUSSION

Collective vigilance posits that animals are consistently vigilant, with the level of vigilance varying according to swarm size. As a result, isolated individuals tend to allocate more time to scanning the surrounding environment, whereas those in large swarms rely on chance detections by their companions. However, some studies [13] have noted that even non-vigilant individuals can spot an incoming threat, leading to a reconsideration of antipredatory vigilance, especially in a collective context.

The ecological observation reported here confirms that individual soldier crabs are indeed vigilant, as evidenced by their fleeing behavior (digging) upon spotting a threat. The change in swarm configuration for mid-sized swarms could be linked to the search for protection from others, possibly to reduce the likelihood of successful predator attacks. However, the disappearance of fleeing behavior at high densities is puzzling, indicating a change in behavior after a certain swarm size threshold is reached.

These observations align with results from laboratory experiments, indicating that an overly interconnected swarm fails to adapt its behavior to changes in external conditions or does so slowly. Overall, we demonstrated that for soldier crabs, there is a transition in behavioral response from low to high swarm size, suggesting that a simple linear description based on swarm size is not sufficient. This highlights the complexity of collective behaviors, which emerge from intricate interactions and should be viewed as emergent phenomena.

6. CONCLUSIONS

In this study, we investigated the behavior of soldier crabs concerning changes in the external environment through both laboratory experiments and ecological observations. We found that under low swarm densities, individual behavior predominates, likely due to limited interactions among crabs. This manifested as random motion in laboratory experiments lacking coordination and immediate digging responses during bus passages in ecological aerial observations.

As swarm densities increased to medium levels, the proximity between individuals facilitated interactions, although the nature of these interactions, whether physical or cognitive, remains unclear. In laboratory settings, this translated into self-organized motion that was easily manipulable by altering external environmental conditions. In ecological contexts, we observed a shift in swarm organization, with the perception of a threat leading to the formation of dense swarms.

Interestingly, dense swarms exhibited reduced reactivity, possibly due to strong physical interactions hindering abrupt changes in collective motion. When considering the combined results of experiments and observations, soldier crabs appear to challenge the conventional notion that larger swarms are inherently more adept at detecting incoming threats. While this observation aligns with certain hypotheses related to swarming behavior, such as reducing predator success rates leading to the formation of large swarms, it raises questions about aspects of collective vigilance.

Future studies should focus on quantifying the qualitative findings presented here in ecological observations. For example, determining the thresholds at which behavioral changes occur, such as the distance at which digging is observed and the triggers for changes in swarm size in response to threats, would be valuable. In this context, the number of observations in the ecological setting should be increased. For example, one could drive a bus to target specific swarms observed at very specific moments. Additionally, further research is warranted to elucidate how crabs perceive incoming threats, whether through visual cues or other means, and to clarify whether large swarms fail to detect or simply ignore such threats.

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