Collective motion as a distinct behavioral state of the individual

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Collective motion is an important biological phenomenon, ubiquitous among different organisms. Locusts are a quintessential example of collective motion: while displaying a minimal level of cooperation between individuals, swarms of millions are highly robust and persistent. Using desert locusts in a series of carefully controlled laboratory experiments, we show that locust coordinated marching induces a distinct behavioral mode in the individual that we term a "collective-motion-state". Importantly, this state is not induced by aggregation or crowding per-se, but only following collective motion. It is manifested in specific walking behavior kinematics and has a lasting effect. Simulations confirm that the collective-motion-state provides an individual-based mechanism, which increases the robustness and stability of swarms in the presence of fluctuations. Overall, our findings suggest that collective-motion is more than an emergent property of the group, but a specific behavioral mode that is rooted in endogenous biological mechanisms of the individual.

Introduction

The ability to form groups that move collectively is a key behavioral feature of many species (Sumpter, 2006; Ward and Webster, 2016), that increases the survival of both individuals and groups (e.g. Be'er and Ariel, 2019; Yang and Schmickl, 2019). Collectively moving organisms, however, differ in the levels of peer-to-peer interactions, ranging from minimal cooperation to complex social behaviors (Attanasi et al., 2014; Cavagna et al., 2010). Analysis of both experiments and theoretical modeling of collective motion suggests a highly stochastic (or chaotic) movement pattern, which makes the trajectory of individuals difficult to predict in practice (Algar et al., 2019; Ariel and Ayali, 2015; Escaff et al., 2018). Furthermore, endogenous variability among individuals, heterogenic environments, and variability in the interactions between the individual and its direct environment, are all sources of randomness that may affect the coordinated behavior of the collective.

Accordingly, it is not clear how synchronized collective motion constitutes such a robust phenomenon, maintaining its form across various group sizes and densities, and under heterogeneous and unpredictable environmental conditions.

One of the most interesting, albeit disastrous, examples of collective motion is that of the marching of locusts. These insects swarm in groups of millions, migrating in mass across large distances, devastating crops and agriculture (Ayali, 2019; Cullen et al., 2017; Zhang et al., 2019). In the context of social interactions, locust swarming is characterized by a minimal level of cooperation between individuals: collectivity is mostly manifested in alignment among neighboring individuals and in maintaining the overall movement in the same general direction. Nonetheless, the locust swarming phenomenon is extremely robust, with huge swarms demonstrating moderate to high collectivity on huge scales (up to 6-7 orders of magnitudes), in terms of both the number of animals and their spatio-temporal distribution (Ellis and Ashall, 1957; Uvarov, 1977; and see further references in Ariel and Ayali, 2015). Thus, locusts exhibit a considerable disparity between little local cooperation and large-scale collectivity.

What is the key to this ability of locust swarms to maintain their integrity? Here, we show by a series of carefully controlled behavioral experiments that collective movement induces an internal switch in individual gregarious locusts, activating a behavioral mode we refer to as a “collective-motion-state”. In this state, the kinematic behavior of individuals notably differs from that during the non-collective state. It is important to emphasize that by “collective” and the “non-collective” states we are not referring to the well-known solitarious-gregarious phase transition in locusts (Ayali, 2019; Cullen et al., 2017).

How does the collective-motion-state affect the formation and robustness of the swarm? Interestingly, the switch into this state seems to occur rapidly, and in response to coordinated walking. In particular, our experiments indicate that aggregation alone is not sufficient. Switching out of the collective-motion-state occurs over a longer time scale – significantly longer than the typical time scale of fluctuations in the swarm dynamics. Hence, stochastic fluctuations are “smoothed-out”, leading to highly robust dynamics of the swarm collective behavior.

This ability to switch between socio-behavioral states appears to be beneficial for the swarm integrity. Using a simplified computer model, we simulated the swarming properties of locust-like agents with different kinematic parameters, representing the different

behavioral states. The results demonstrate that the ability to switch between the distinct behavioral states, as a consequence of both instantaneous and past stimuli, leads to swarms with tighter groups, compared for example to fixed or continuously changing dynamics, and without affecting the within-group alignment. Hence, we conclude that the collective-motion-state provides an individual-based mechanism that increases the stability of swarms in the presence of fluctuations, preventing the swarm from collapsing.

Results

The main objective of this report was to examine the behavior of individual animals upon joining or leaving a group of conspecifics. Here we studied gregarious locusts, reared in dense populations, one developmental stage before becoming adults and developing functional wings (i.e. fifth larval instar). The experiments comprised three consecutive stages, representing different conditions (Fig. 1 and Vid. S1): (1) Isolation stage: a single animal was taken from its highly dense rearing cage, tagged with a barcode, and introduced alone into a ring-shaped arena (outer and inner diameters: 60 cm and 30 cm, respectively); (2) Grouping stage: nine other individually tagged animals were added to the arena; and (3) Re-isolation stage: the nine added animals were removed from the arena, leaving the original animal alone. The duration of each stage was one hour, during which the animals' trajectories were fully reconstructed using a barcode tracking system. The middle 40 minutes of each stage were analyzed, as detailed in the Methods section. A range of kinematic statistics was collected in order to classify and compare the locusts' behavior in the different stages.

Swarm formation – validation of collective motion

In order to verify that our grouping conditions were indeed inducing collective motion (swarming), we calculated the synchronization in movement of the grouped animals (the order parameter, see Methods for definition). The median order parameter in the grouping stage was found to be significantly higher than that obtained for computationally randomized groups (as presented in our previous report, Knebel et al., 2019); medians: 0.348 and 0.239 respectively; Wilcoxon rank-sum test: $p < 0.01$). Consequently, we conclude that the groups in our experimental setup indeed demonstrate swarming and collective motion.

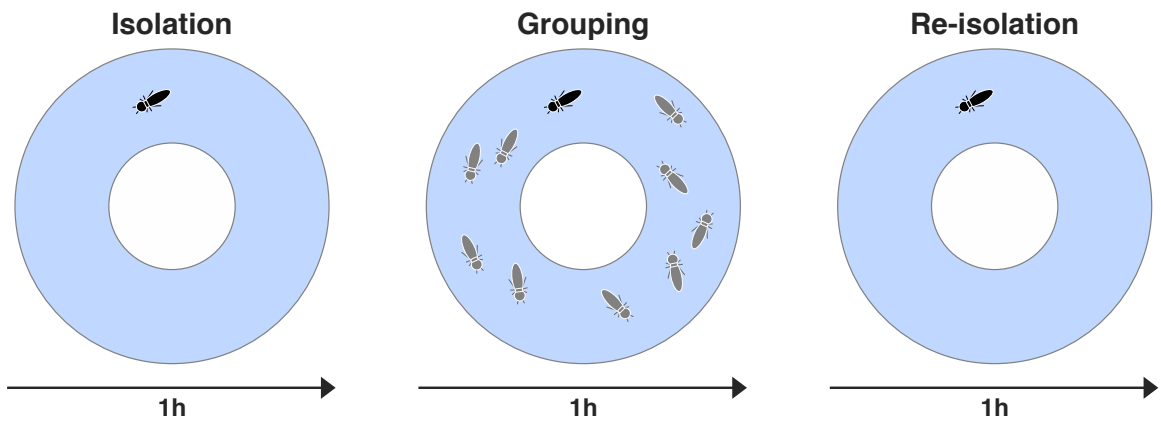

Figure 1. A schematic flow of the experimental procedure. Experiments comprised the following consecutive stages: (1) isolation for one hour in the arena; (2) grouping for one hour; and (3) re-isolation for one hour.

Kinematic differences among the isolation, grouping, and re-isolation stages

Locusts walk in an intermittent motion pattern (Ariel et al., 2014a; Bazazi et al., 2012), i.e., movement occurs in sequences of alternating walking bouts and pauses. To characterize individual locust kinematics, we measured four parameters: (1) the fraction of time an animal spends walking; (2) the average speed while walking; (3) the average walking bout duration; and (4) the average pause duration. Comparing these values across the three experimental stages, we found several statistically significant differences (Fig. 2). In the following, *p*-values correspond to a Friedman test followed by a multiple comparison test using the Bonferroni method.

We found that when comparing between isolation and grouping, the fraction of time spent walking and the pause durations differed significantly ($p<0.01$ and $p<0.001$, respectively), showing a larger fraction of time walking and shorter pauses while grouping. These findings are in accordance with previous reports (Knebel et al., 2019), and are consistent with the known propensity of locusts to walk more and rest for shorter times while in a swarm (Ariel et al., 2014a; Bazazi et al., 2012, 2008; Knebel et al., 2019). However, our experiments also revealed a new effect of swarming. Comparing the isolation and re-isolation stages, we found that all the studied parameters differed significantly. Specifically, the fraction of time walking, speed, and walking bout duration were all higher in the re-isolation stage, while the pause duration decreased ($p<0.001$, $p<0.001$, $p<0.05$ and $p<0.05$, respectively). Furthermore, comparing the grouping and re-isolation conditions revealed that the walking bout duration increased significantly following re-isolation ($p<0.01$). The data for

all other comparison combinations were found not to differ significantly. The increase in activity following re-isolation is surprising, and suggests that the marching behavior of locusts is not dictated by instantaneous or immediate interactions among individuals per-se. Rather, our findings indicate that the interactions with other marching locusts induce a switch to a new internal behavioral state, which outlasts the presence of the swarm. In accordance with our results, we term this internal state the “collective-motion-state”.

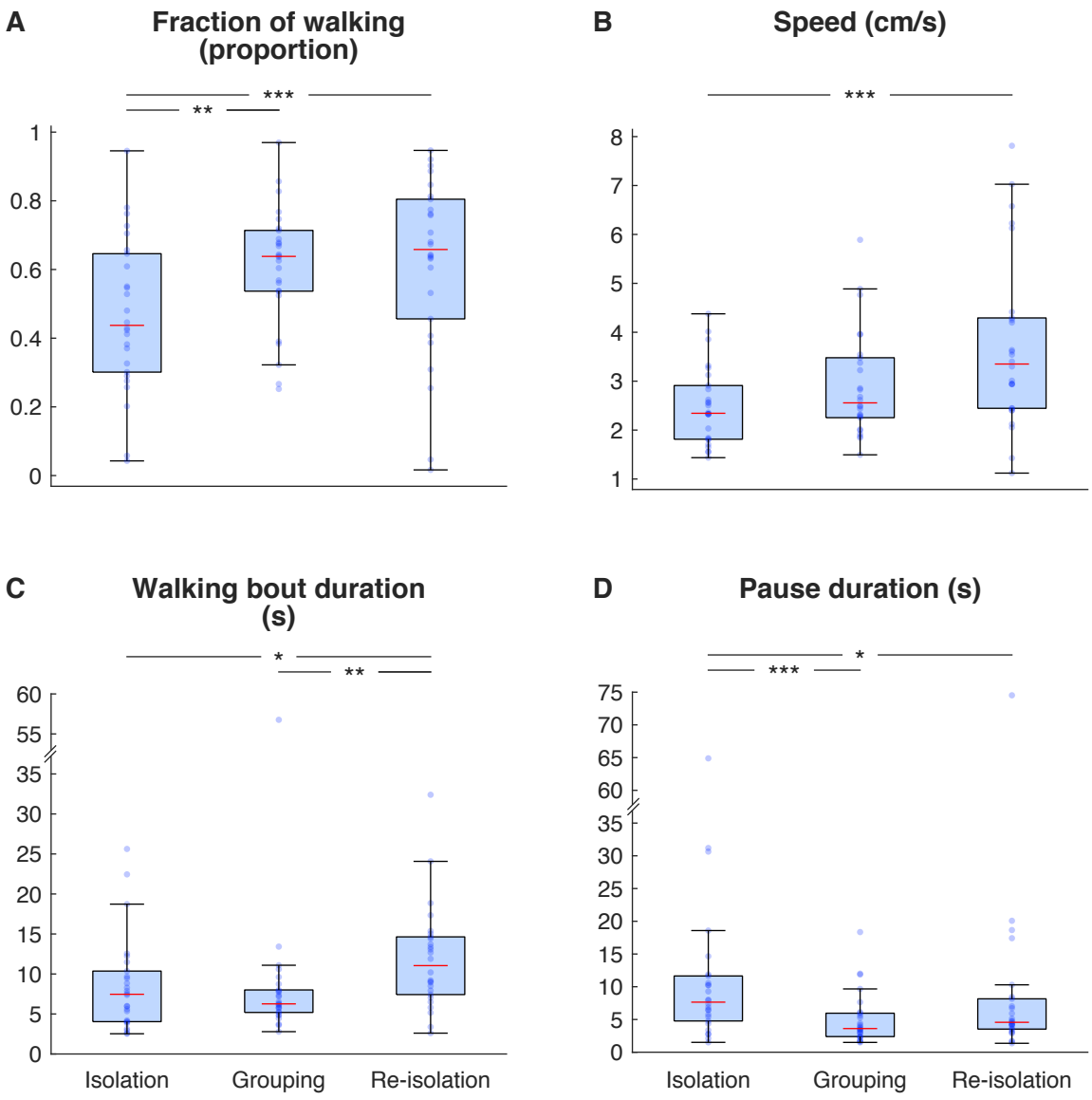

Figure 2. Kinematic changes throughout the three experimental conditions. (A) the fraction of walking, (B) the averaged walking speed, (C) the average duration of walking bouts, and (D) the average duration of pauses, of the traced animals in the isolation, grouping, and re-isolation stages. *p<0.05, **p<0.01, ***p<0.001.

In order to verify that the observed behavioral changes indeed represent a transient state, rather than a permanent behavioral modulation, a simple control experiment was performed. Following the re-isolation stage, the locusts were returned to their rearing cage (in high crowding conditions without collective motion), and tested the next day again alone in the arena (isolation condition). We found no significant behavioral difference between this latter isolation and the first isolation stage of the previous day (n = 6). Hence, the collective-motion state is transient. A second series of control experiments was performed in order to exclude potential time effects on the locusts' behavior due to the duration of the experiments. To this end, locusts were tested in isolation for three consecutive hours. The kinematic analysis procedure described above was then performed separately on three 40 min segments of the 3 hr tests and no significant differences were found (n = 6).

Consistency in individual behavioral tendencies

Despite the major differences in behavioral kinematics among the three experimental stages, we found that individual behavioral tendencies persisted. The fraction of walking, speed, and pause durations all showed high within-individual correlation across the three stages. The walking bout durations, however, were significantly correlated only between the isolation and grouped stages (see Table 1 for numerical details).

The increased values of this latter parameter upon re-isolation may reflect a mechanism that is activated when an animal finds itself away from the group, and overrides its prior behavioral tendencies. To test this hypothesis, and further explore the effects of the walking bout duration on the ability (and efficiency) of locusts to swarm, the effect of the different measured kinematic parameters was further studied using a simplified computer model.

Modeling and simulations

The experiments described above demonstrated that individual locusts introduced into a collectively moving swarm undergo a switch into a distinct internal socio-behavioral state. However, whether this change confers a benefit on the swarm formation and maintenance, and if so, of what kind, remained unanswered. To explore this aspect of the collective-motion-state, we developed a model that simulates locust swarms, in which individual kinematics and population size could be manipulated. We focused ,in particular, on

165 the walking bout duration, as this specific parameter seems instrumental in differentiating
166 the locust behavior after re-isolation (Table 1).
167

	p-Value	***rho*-Value**
Fraction of Walking		
Isolation - Grouping	0.000	0.706
Isolation - Re-isolation	0.001	0.679
Grouping - Re-isolation	0.002	0.638
Speed		
Isolation - Grouping	0.001	0.679
Isolation - Re-isolation	0.010	0.561
Grouping - Re-isolation	0.002	0.636
Walking bout duration		
Isolation - Grouping	*0.002*	0.628
Isolation - Re-isolation	*0.148*	0.391
Grouping - Re-isolation	*0.354*	0.314
Puase duration		
Isolation - Grouping	0.007	0.580
Isolation - Re-isolation	0.003	0.612
Grouping - Re-isolation	0.000	0.708

168
169 **Table 1. Correlation values between kinematic parameters throughout the three experimental conditions.** The
170 fraction of walking, the averaged walking speed, the average duration of walking bouts, and the average
171 duration of pauses were tested for correlation across the three experimental conditions: (1) isolation, (2)
172 grouping, and (3) re-isolation. The underlined values mark significant correlations.
173
174 To simulate swarms, we used a simplified agent-based model in a square domain with
175 periodic boundaries (size: 10 x 10). Agents were designed as rectangles with a circular
176 receptive field around their center. The agents' kinematics were programed to resemble that
177 of locusts, i.e. to move in an intermittent motion (pause-and-go) pattern: at every step of the

178 simulation, each agent made an individual decision whether to walk or stop, based on its
179 current state (walking or stopping) with predefined probabilities (p_W and p_S, respectively).
180 While moving, the speed was constant. The individual direction of movement was allowed to
181 change only when an agent changes its state from stopping to walking (Ariel et al., 2014a). An
182 agent's new direction was a weighted sum of its own direction (inertia), the direction of other
183 agents in its visual field, with a short memory (see Rimer and Ariel, 2017 for the importance
184 of memory in pause-and-go simulations), and noise. See Methods for details and Table S1 for
185 parameter values.

186 The spatial and temporal scales of the model were set as follows: 1 cm was considered
187 as a distance of 0.1 in the simulated arena, and 1 sec corresponded to 1 simulation step. Thus,
188 we fixed the model dimensions to correspond with real locusts' size and movement
189 parameters. The size of agents (0.1 x 0.4) maintains the proportions of 5th larval instar
190 locusts. Additionally, the visual range of 1 radius, ten times larger than the agent's rectangle
191 width, represents the proportional visual field of locusts (range just under 10 cm; Ariel et al.,
192 2014a). To adjust the temporal scale, an average stopping duration in the model was set to
193 be about 3 steps (by setting p_S to be 0.67; see Fig. S1), parallel to the median of 3 second
194 pause duration found in the grouping condition in the empirical experiment (Fig. 2D). The p_W
195 values were set to range between 0.6 and 0.92, making the walking bout durations
196 comparable with the empirical data (compare Fig. 2C and Fig. S1). Finally, the speed was set
197 to 0.25, corresponding to the typical swarming speed shown in Fig 2B.

198 In order to study the effect of individual bout duration on the swarm, we concentrate
199 on the effect of swarm size, N, and on p_W, describing the propensity of animals to keep
200 walking. We evaluated the effect of these parameters on four statistics that characterize
201 collective motion in the swarm:

202 1. The order parameter (the size of the average direction vector).
203 2. Spread (the average distance between all pairs).
204 3. The number of neighbors (within the field of view).
205 4. Regrouping time (the average number of steps it takes an agent that has lost all
206 other agents in its receptive field to re-obtain at least one neighbor).

207 Statistics were averaged over all agents and simulation steps. In order to allow comparison
208 with our experimental findings, we focus on relatively small swarms (up to 40 agents). Fig. 3
209 shows the median value over 40 independent repetitions for each parameter set. We found

that the order parameter increases both with p_W and with the number of agents, N (Fig. 3A). The spread shows a more complex dependence on p_W, depending on N (Fig. 3B). For small swarms, large p_W leads to a smaller spread, but the trend is reversed for large swarms, showing a smaller spread with small p_W. The number of neighbors (NN) is decreases with p_W but increases with N (Fig. 3C), and the slope is much larger for large swarms. For small swarms, the NN is small and practically independent of p_W. The regrouping time varies significantly with swarm size (increasing by a factor of up to 9) and is mostly independent of p_W for large groups (Fig. 3D). However, small groups (up to 20) reduce their time to regroup with higher p_W. This result makes sense assuming that isolated individuals perform a random search until they join a new cluster. Because agents only change direction when starting to move, the length of walking segments between rotations increases with p_W.

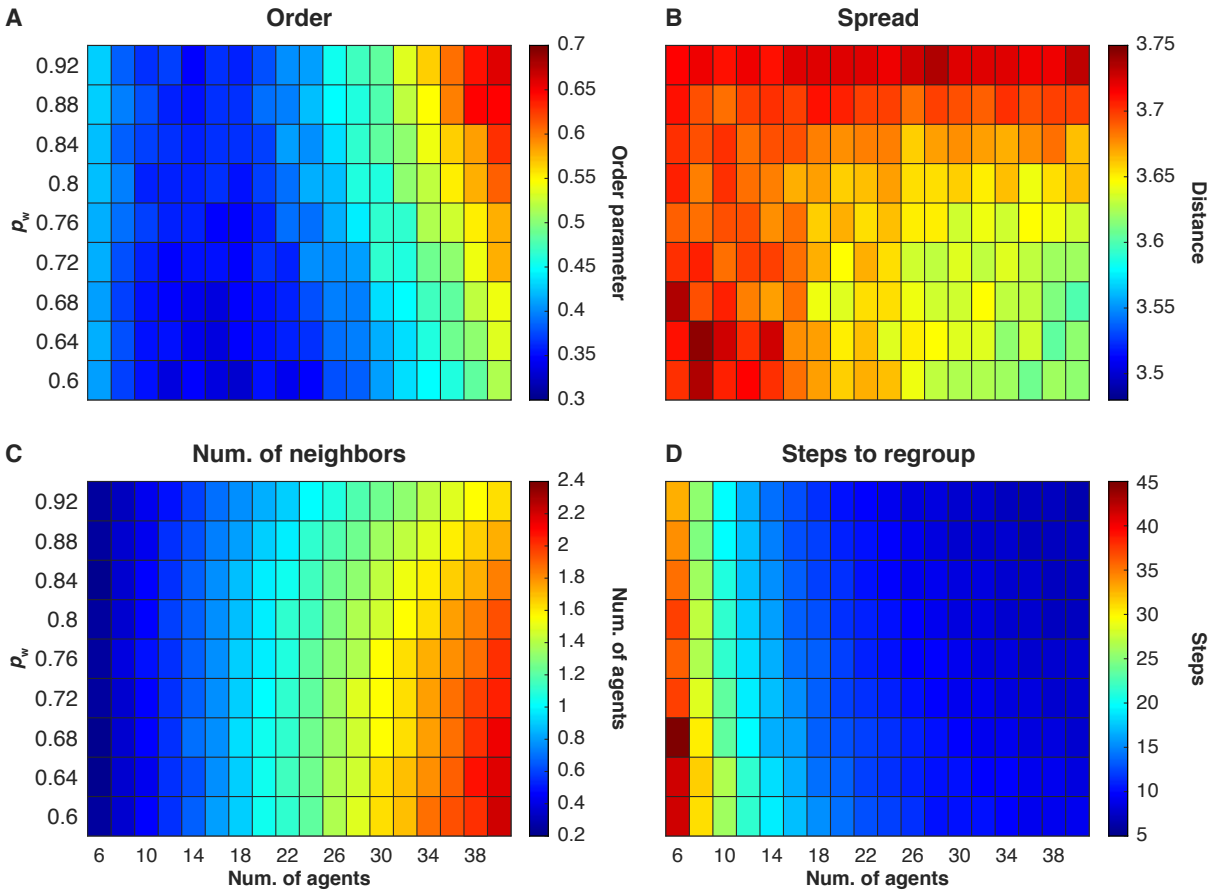

Figure 3. The influence of different p_W values on the collectivity parameters of simulated swarms. (A) The order parameters, (B) spread , (C) the average number of agents within each agent's visual field , and (D) the average number of steps to regroup, for different p_W values (rows), and different group sizes (columns). Each colored box represents the median of 40 simulations.

Fig. S2-S6 show a detailed sensitivity analysis, demonstrating the differences obtained when changing individual parameters. This analysis shows that, despite some quantitative differences, our qualitative observation that the propensity of animals to walk (modelled by the parameter p_W) has a different effect on small and large groups, holds in a wide range of parameters. However, some parameters do show a notable effect on the collective dynamics: increasing the noise level substantially (Fig. S3) may completely destroy collectivity, leading to a small order parameter. This observation is related to the well-known phase transition in Vicsek-like models (Vicsek and Zafeiris, 2012). In addition, several physical parameters, such as the visual range (Fig. S4), speed (Fig. S5), and the size of agents (Fig. S6) have a partial influence on some of the statistics. It is therefore important that such parameters are assigned realistic values, as measured from experiments.

Overall, these findings indicate that large p_W values, namely, longer walking bouts, increase the chances that low- density groups will stay together (smaller spreads, shorter time to regroup). However, for larger swarms, smaller p_W – shorter walking bouts – is favorable (more neighbors, smaller spread and a marginal cost in the order parameter and regrouping time). Therefore, if aggregation is essential to individuals, our results suggest that it might be beneficial for an agent to change its p_W as a function of the group size.

Sociality-dependent p_W

Several previous theoretical models of collective motion have found that adaptable interactions, i.e., interactions that can change according to the local environment, can improve the cohesiveness and performance of swarms (Gorbonos and Gov, 2017; Shaukat and Chitre, 2016; Shklarsh et al., 2011). Accordingly, in light of our experimental results, we sought to study the effect of the individual's ability to change its walking properties. To this end, we introduced an experience-dependent p_W to the simulated agents (Fig. 4). The p_W could change during a simulation as a result of the agent's receptive field of view in the last simulation steps. For simplicity, we assume linear dependence (Ariel et al., 2014b). Biologically, such a dependence may be due to the way locusts perceive their surrounding: many locusts walking in the same direction around one locust would affect it more than only a few. To be precise, denote by $\bar{n}_i(t)$ the average number of neighbors of a focal animal i in the previous k (memory length) steps before time t, the probability that animal i keeps walking, $p_W(i,t)$ was given by

$$p_w(i,t) = \begin{cases} 0.92 - \alpha\bar{n}_i(t), & 0.92 - \alpha\bar{n}_i(t) \geq 0.6 \\ 0.6, & 0.92 - \alpha\bar{n}_i(t) < 0.6 \end{cases}$$

where α is a constant determining the slope of the linear effect ($\alpha = 0.1$ in Fig. 4). As can be seen, p_W was ranged between 0.6 and 0.92, in order to avoid phlegmatic behavior or unnatural hyperactive of the agent (respectively). See Fig. S7 for the obtained p_W values and walking bout durations in those simulations.

This conditional individual behavior was found to minimize the spread and regrouping time, while maximizing the agent's number of neighbors for almost all swarm sizes (Compare Fig. 3 and 4). This conditional behavior, however, did not increase the order parameter above that in the fixed p_W case (Fig. 4A).

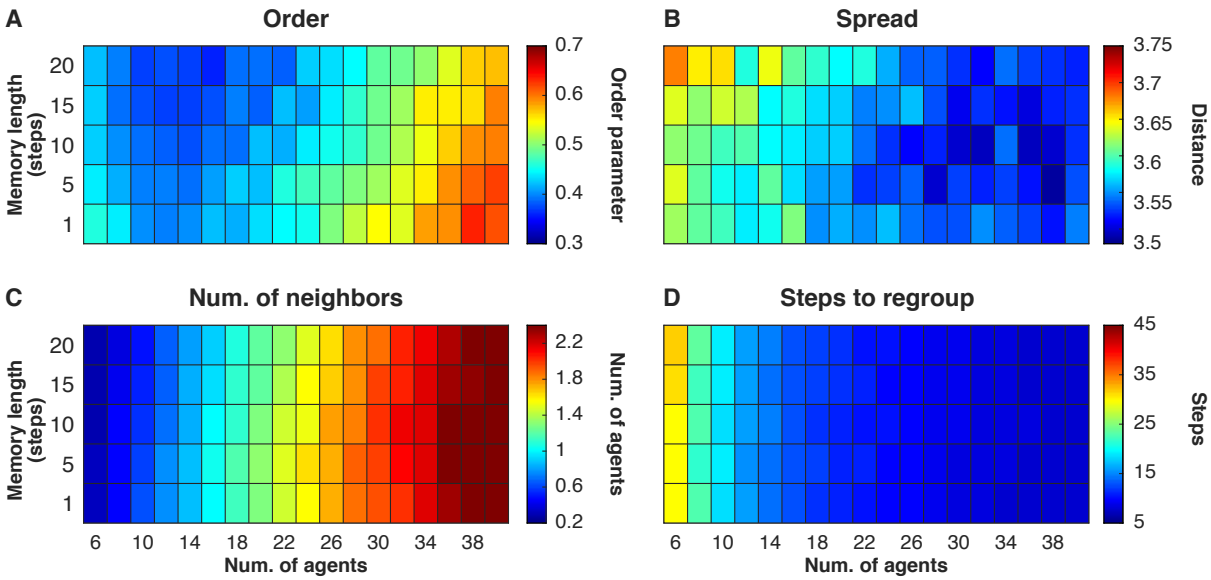

Figure 4. The influence of adaptive p_W values with different memory lengths on the collectivity parameters of simulated swarms. (A) The order parameters, (B) spread , (C) the average number of steps to regroup, and (D) the average number of agents within each agent's visual field, for adaptiveness memory (rows), and different group sizes (columns). Each colored box represents the median of 40 simulations.

We tested different memory lengths that affected the adaptive p_W. The average p_W did not change dramatically (Fig. S7B) but did result in higher variance across the simulation steps – the shorter the memory was, the higher the step-to-step p_W fluctuations were (Fig. S7C). This behavior is expected, as the sensitivity to the current situation of the agent decreased with memory length. Fig. 4 shows that while the order and spread favors short memory, the NN and steps to regroup were largely indifferent to it.

Overall, our simulations show that increasing the walking bout duration when an agent finds itself alone has a beneficial impact on its chances of meeting other agents and maintaining high group density. In regard to the empirical results, our simulations suggest an instrumental role for the increased bout duration in regrouping when an animal is isolated after swarming.

Discussion

Our findings reported here suggest that, in locusts, the sensory-motor act of collective motion is accompanied by an internal state of the individual locust – a collective-motion-state that is manifested in specific behavioral kinematics. This state is induced by the experience of synchronous, collective marching. In turn, it has an important role in maintaining the integrity and consistency of the swarm. Below we discuss several key aspects and implications of this finding.

The collective-motion-state

In a recent study (Knebel et al., 2019), we have introduced a comparison between the walking behavior kinematics of individual gregarious (crowded-reared) locusts in different social (density) contexts. Our reported findings are reconfirmed and further elucidated here by the results of the initial isolation and grouping stages in our experiments. The novel idea posited here is that these differences represent and are induced by not only the spatially and temporally immediate social environment, and the instantaneous local interactions among locusts, but also by the effects of an internal state induced by the general experience of collective motion. A fundamental aspect of the concept of the collective-motion-state arises from our findings related to its persistent effect in time: Upon re-isolation, the individual locust adopted behavioral kinematics that critically differed from that in the first experimental stage (initial isolation). We also showed that, as expected, the collective-motion-state is transient. If the locust does not experience collective motion for some time, and is then isolated once more, it loses the unique walking-related kinematics it previously adopted in response to the collective motion, i.e. the internal collective-motion-state.

A novel source of ecologically-relevant behavioral variability

The individual locusts in our experiments retained the variability observed among them (see also Knebel et al., 2019), while demonstrating a second layer of variability or plasticity upon experiencing collective motion, when entering the collective-motion-state. Considerable research has been devoted in recent years to understanding the effect of variability among individuals on the group's collective behavior, both experimentally—ranging from bacteria to primates (Benisty et al., 2015; Brown and Irving, 2014; Calovi et al., 2015; Crall et al., 2016; Dyer et al., 2009; Farine et al., 2017; Fürtbauer and Fry, 2018; Herbert-Read et al., 2013; Jolles et al., 2018; Planas-Sitjà et al., 2015)—and theoretically (Aplin et al., 2014; Ariel et al., 2014a; Copenhagen et al., 2016; Guisandez et al., 2017; Jolles et al., 2017; Menzel, 2012; Mishra et al., 2012; See Mar Delgado et al., 2018; Modlmeier et al., 2015; Webster and Ward, 2011 for recent reviews). The interactions between variability in specific aspects of the individuals' behavior and group-level processes were found to be complex and, moreover, bidirectional (e.g. Knebel et al., 2019). Variability among individual animals was found to have important consequences for the collective behavior of the group (e.g. O'shea-Wheller et al., 2017; Szorkovszky et al., 2018).

However, beyond the variability among the individuals composing a group, variability is also expected in the behavior of the individual animal over time, as it experiences changes in environmental and social conditions. The swarm (or flock, shoal, herd, etc.) is a heterogeneous entity, moving in a heterogeneous environment. The individual is bound on occasion to find itself in different locations within the swarm (leading edge, at the outskirts, trailing), and it may also find itself separated from the group by natural obstacles (vegetation, rocks and boulders). It is essential for the robustness and consistency of the swarm that throughout these changing conditions, the behavior of the individual will adapt accordingly, such as to be appropriate for the changing context. For example, if temporarily separated from the core of the swarm, a locust's walking kinematics should change to support rapid reunion with the group, as reported in both our experimental and simulation findings (e.g. increased fraction of walking and duration of walking bouts). If previously naïve to collective motion, that individual's kinematics would however be disadvantageous, or even hinder the formation of a swarm.

339 In Bazazi et al. (2012), the authors suggest that behavioral variability can be explained
340 by the existence of two internal states. Studying single locusts in isolation for eight
341 consecutive hours, they have observed changes in behavioral kinematics that were suggested
342 to result from "internal state behavioral modulation". The observed variations, however,
343 were merely attributed to changes in "starvation/satiation state", i.e. as the locust becomes
344 starved, it changes its walking behavior, searching more vigorously for food. Moreover, they
345 conclude that animals continually switch between the two states on a scale of minutes. The
346 collective-motion-state reported here is, of course, a very different type of internal behavioral
347 state, which is strongly involved with the locust past and current social environment.

348 It should be stressed once again that the current study focused on gregarious,
349 crowded-reared locusts only. The described behavioral states should not be confused,
350 therefore, with the well-known and much researched locust density-dependent phase
351 polyphenism (Ayali, 2019; Cullen et al., 2017). Collective motion is limited to the gregarious,
352 swarming and migrating phase. Accordingly, all our experimental animals were taken from
353 our gregarious breeding colony, maintained in crowded conditions for many consecutive
354 generations. In their breeding cages, mostly due to the physical constraints and abundance
355 of food, despite experiencing high density the locusts very rarely, if at all, demonstrate
356 collective motion. Thus, they adopted the collective-motion-state only upon experiencing and
357 taking part in collective marching within the experimental arena.

358 The reported collective-motion-state is also in accord with the overall daily behavioral
359 changes of marching locust swarms. The swarm will spend the night (as well as times of low
360 temperature or other unfavorable climatic conditions) roosting among the vegetation. Upon
361 suitable conditions, after a period of feeding, the locusts will initiate marching – highly
362 synchronized, collective motion. Frequently, when temperature becomes too high around
363 noon, or when dusk arrives, the swarm will again switch to feeding and roosting. These daily
364 patterns call for corresponding changes in the internal behavioral states of the individual
365 locusts and mostly a dedicated collective-motion-state.

366 **Physiological basis of the collective-motion-state**

367 In the current work we are cautious in talking about *behavioral* states. Although this
368 is beyond the scope of this study, it is clear that these behavioral states represent
369 physiological states. With some confidence, we can speculate about the nature or the

370 physiological mechanisms involved in the demonstrated behavioral states. Behavioral
371 plasticity in locust behavior has been attributed to various second messengers or
372 neuromodulators, or to the balance among them. Most notable are the biogenic amines (e.g.
373 Serotonin, a prominent bio-amine, was recently reported to inhibit walking behavior in
374 *Drosophila*; Howard et al., 2019). Hence, it may well be that the (spatial and temporal)
375 immediate social environment affects biogenic amine levels, and these in turn modulate the
376 walking-related behavioral kinematics manifested in the different behavioral states.

377 Another candidate that may be involved in the collective-motion-state is the locust
378 adipokinetic hormone (AKH). AKH is a metabolic neuropeptide principally known for its
379 mobilization of energy substrates, notably lipid and trehalose, during energy-requiring
380 activities such as flight and locomotion, but also during stress (e.g. Perić-Mataruga et al.,
381 2006). It is well accepted that the metabolic state affects the level of general activity of an
382 organism, and AKHs are reported to stimulate locomotor activity, either directly by way of
383 their activity within the central nervous system (e.g. Wicher, 2007), or via octopamine – a
384 biogenic amine with ample behavioral effects (Verlinden et al., 2010; Yang et al., 2015).

385 Furthermore, as noted, we have demonstrated here an extended effect of the
386 experience of collective motion. Hence, learning and memory-related mechanisms would also
387 seem to be involved. Again, previous work may suggest some candidate molecules and
388 pathways, including cGMP-dependent protein kinase (PKG), and Protein Kinase A (Geva et al.,
389 2010; Lucas et al., 2010; Ott et al., 2012).

390 Last, as noted, solitarious phase locusts lack the capacity to demonstrate collective
391 motion, and thus also the collective-motion-state. Accordingly, they differ from gregarious
392 locusts in all the above physiological pathways (bioamines: e.g. Alessi et al., 2014; Cullen et
393 al., 2017; Ma et al., 2015; AKH: Ayali and Pener, 1992; Pener et al., 1997; PKG: Lucas et al.,
394 2010; PKA: Ott et al., 2012). An in-depth investigation of the development of gregarious-like
395 states in solitary locusts should prove to be very enlightening.

396 **Concluding remarks**

397 A central question is whether a collective (herd, flock, or swarm) is merely a sum of its
398 parts, or a new entity. Most related studies have perceived collectivity as a self-emergent
399 phenomenon, suggesting that new dynamics and behavior are the result of intricate, multi-

body, typically non-linear interactions (e.g. Cucker and Smale, 2007; Vicsek and Zafeiris, 2012). One hidden assumption underlying this perception, is that individuals remains inherently unchanged when isolated or in a crowd. Even studies of heterogeneous swarms, in which conspecifics may differ from each other, still assume consistency in the properties of the individual over time. This is essentially a physical point of view, in the sense that agents/individuals possess certain properties that determine their behavior across a range of situations. Thus, the collective motion is an emergent property that builds up in particular contexts, such as a sufficiently high local density of animals. This point of view allows, among others, extrapolation from experiments with one, two, or a few animals to large swarms (e.g. Calovi et al., 2015).

Our findings reported here suggest a fundamentally different point of view. We perceive the sensory-motor act of collective motion as accompanied by an internal state – a collective-motion-state that is manifested in specific behavioral kinematics. This state is induced by the experience of synchronous, collective motion. Most importantly, it is *not* induced by spatial aggregation alone. Collectivity, therefore, is not just self-emerging. Rather, the collective-motion-state has an important role in maintaining the integrity and consistency of the swarm. The robustness of the swarm is also a major challenge and requirement in swarming robotics, making the current novel insights applicable and even important also to this emerging field.

In the case of locusts, our far from complete understanding to date of this phenomenon is also proving crucial for human well-being and even survival, as evident from the current devastating locust situation in large parts of Africa and Asia (FAO, 2020). Much scientific attention has been dedicated to the perception, decision-making, and individual kinematics of locusts in a swarm. These efforts have led to various models that attempt to explain the collective behavior on the basis of local interactions among the individual locusts (review in Ariel and Ayali, 2015). The current study is, to the best of our knowledge, the first to provide a more in-depth focus, by including the internal state of the individual locust as an important factor in dictating its behavior, and in turn affecting the maintenance and the properties of the swarm.

Methods

Animals

The empirical experiments were conducted on gregarious desert locusts, *Schistocerca gregaria* (Forsskål), which are bred at Tel Aviv University, School of Zoology. The animals are kept at high density: over 100 animals in cages of 60 l, under a 12 h:12 h light/dark regime, a temperature of 30°C, and 30-65 % humidity. Animals are fed daily with wheat seedlings and dry oats. All experimental locusts were the offspring of many generations of gregarious locusts reared in these conditions.

Experimental setup

The ring-shaped arena comprised blue plastic walls (60 cm diameter and 55 cm high) with an inner central cone dome (30 cm diameter). The bottom of the structure was covered with a thin layer of Fluon (Whitford Plastics Ltd., Runcorn, UK), in order to prevent locusts from climbing. A white paper covered the floor of the arena and was changed before each experiment. Light sources around the arena lit its floor evenly. A video camera (Sony FDR-AXP35: 4K Ultra HD) was positioned above the arena and filmed the locusts throughout the experiment.

Monitoring the locust movements

Prior to the experiments, each of the experimented locusts was tagged with a unique barcode glued to the dorsal side of its prothorax using a drop of Epoxy glue. Using the video footage at 25/3 frames per second, the trajectory of each animal was reconstructed offline using BugTag software (Robiotec Ltd., Israel). To this we added a custom-designed multiple-target tracking and a trajectory-smoothing method (for details: Ariel et al., 2014b). briefly, segments in which tags were not identified (less than 5 cm or 25 s) by the system positions were interpolated. We thus obtained the positions of the tags' center of mass relative to the arena center, at a final resolution of 2-3 pixels (ca. 0.5 mm), for about 99% of the video frames. In order to reach 100% recognition, we completed the analysis manually for the remaining frames. In three out of the 26 experiment the tracking system failed to recognise 1-2 animals in the grouping stage. Therefore, the order parameter was calculated based on the recognized animals only. These miss-identifications, which only slightly affect the order

459 parameter calculated in the grouping stage, have no influence on any of the kinematic
460 statistics in any of the stages (that only describe the focal animal).

461 **Experimental procedure**

462 In the morning of each experiment day, 10 locusts were taken from their cage and
463 individually tagged. Thereafter, one locust was randomly chosen and placed in the arena
464 alone for one hour. The other 9 locusts were then added for an additional hour; after which
465 they were removed. The remaining locust was then filmed for another hour.

466 **Analyzed parameters**

467 Following the recognition process, we analyzed the middle 40 min of each of the 3 hours
468 of the experiment using MATLAB (MathWorks, Natick, MA, USA). The following parameters
469 were calculated:

470 1. Order parameter – the absolute value of the average direction of movement of the
471 walking animals (clockwise denoted as -1 and anticlockwise as +1), averaged for all the
472 frames.
473 2. Fraction of walking – the number of frames an animal walked divided by the total
474 number of analyzed frames, averaged over all experimental animals.
475 3. Detection of walking bouts – a walking period is defined as walking at a speed above
476 0.25 cm/sec for more than one third of a second.
477 4. Speed – averaged for all experimental animals and analyzed frames when the animal
478 walked and the speed differed from zero.
479 5. Walking bout duration – the time an animal moved continuously between one pause
480 to the next, averaged for all walking bouts and experimental animals.
481 6. Pause duration – the time an animal did not walk between one walking bout and the
482 next, averaged for all pauses and experimental animals.

483 **Statistical analysis**

484 All statistical tests were conducted with MATLAB. To compare the order parameters,
485 Wilcoxon rank-sum test was used. To compare among the three stages, Friedman Test was
486 used. Since all comparisons were significant according to the latter test, Bonferroni multiple
487 comparison post-hoc test accompanied each Friedman Test, in order to reveal the

significantly different groups. The p values noted are of the Bonferroni multiple comparison post-hoc test. Correlations were conducted using Spearman's Rank Correlation test.

Modeling

We employed a two dimensional model comprising N agents moving at a fixed speed v in a square domain of linear size L and periodic boundaries. Position and heading (direction) of each rectangle center are denoted by $x_i(t)$ and $\hat{v}_i(t)$, respectively, where $x_i(t) \in [0, L]^2$ and $\|\hat{v}_i(t)\| = 1$. In addition, $w_i(t)$ is a Boolean variable that denotes whether at time t, agent i is moving ($w_i(t) = 1$) or pausing ($w_i(t) = 0$). In order to take into account the physical size of animals, we assume that each agent is a rectangle with sides $a_1 \times a_2$.

In each simulation step, the position of moving agents changes by amount v in the direction $\hat{v}_i(t)$,

$$x_i(t+1) = x_i(t) + v w_i(t) \hat{v}_i(t) \quad (mod\ L).$$

The new velocity of agent i depends on three terms: i. Inertia (its own direction); ii. the direction of other agents in its receptive field (see below), possibly with a memory; and iii. a random vector with unit norm $\xi_i(t)$. The receptive field view is a circle around $x_i(t)$. Unlike previous models, we assume that an agent sees all other agents whose rectangle is within a distance r from $x_i(t)$, and not merely the center of the rectangle. Denoting the four corners of the rectangle describing agent j as indexes $c_i^1(t), \dots, c_i^4(t)$, we define the set of observable neighbors of agent i at time t as

$$I_i(t) \coloneqq \{j: \left\|x_i(t) - c_j^k(t)\right\| \leq r \text{ for some } k = 1 \dots 4\},$$

the average direction in the receptive field at time t, is $\hat{u}_i(t) = u_i(t)/\|u_i(t)\|$, where

$$u_i(t) = \left(\frac{1}{n_i(t)} \sum_{j \in I_i(t)} \sin(\hat{v}_j), \frac{1}{n_i(t)} \sum_{j \in I_i(t)} \cos(\hat{v}_j)\right).$$

Here, $n_i(t)$ is the number of elements in $I_i(t)$.

Overall, the new heading $\hat{v}_i(t+1)$ is the weighted average of four terms: inertia, direction of intersecting rectangles at time t, the average heading of intersecting rectangles at time $[t-5 \dots t-1]$, and independent random vector with unit norm $\xi_i(t)$. Let the set of the weights be $[q_1 \dots q_4]$.The updated weighted averaged direction, is, therefore, $\hat{v}_i(t) = v_i(t)/\|v_i(t)\|$, where

$$v_i(t+1) = q_1\hat{v}_i(t) + q_2\hat{u}_i(t) + q_3\frac{1}{5}\sum_{s=1}^{5}\hat{u}(t-s) + q_4\xi_i(t)$$

In Fig. 3 and 4, the weights were set to $Q = [0.2, 0.3, 0.2, 0.3]$.

Switching between walking and pausing is determined as follows. Assuming exponential distributions of moving and pausing durations, the probability to proceed moving is given by a single parameter, p_w, describing the probability per-step of an agent to continue walking, $p_w = P(w_i(t+1) = 1 | w_i(t) = 1)$. Similarly, $p_s = P(w_i(t+1) = 0 | w_i(t) = 0)$ is the probability per-step that a stopping agent will continue stopping.

In the simulations which introduce adaptive p_w, the latter was updated each time "walking" started, and ranged between 0.4 and 0.8, as a linear function of the average number of neighbors , $\bar{n}_i(t)$ in the last k. steps.

The following parameters were calculated over 200-1000 stimulation steps. Brackets denote averaging over all analyzed frames.

1. Order: $\theta(t) = \frac{1}{N}\langle\|\sum_{i=1}^{N}\hat{v}_i\|\rangle$.
2. Spread: $S(t) = \frac{1}{N(N-1)}\langle\sum_{i=1}^{N}\sum_{j\neq i}|x_i(t) - x_j(t)|\rangle$
3. Number of neighbors: $n_i(t) = \frac{1}{N}\langle\sum_{i=1}^{N} I_i(t)\rangle$
4. Steps to regroup: the number of steps that passed from the first time an agent is alone $(n_i(t) = 0)$ until it has a first neighbor $(n_i(t+s) > 0)$.

Author contributions

D.K., G.A., and A.A. designed the study. D.K. and C.S. performed the experiments. D.K. and C.S. analyzed the data. D.K. N.A. and G.A constructed the model. D.K. wrote the code, performed simulations and analyzed the data. D.K., G.A., and A.A. wrote the manuscript. All authors reviewed and approved the paper.

Competing interests

The authors declare that they have no competing interests.

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708

709 Supplementary information

710 Figures

Varibale		Value
Simulation parameters	Num. of agents (N)	6 - 40
	Num. of steps	1000
	Arena size (periodic bounderies; *L*)	10 x 10
Agents dimensions	Size of agents (*a1* x *a2*)	0.1 x 0.4
	Visual range radius (*r*)	1
Movement parameters	Probability to stop (p_s)	0.67
	Probability to walk (p_w)	0.6 - 0.92
	Speed (*v*)	0.25
Direction parameters	Inertia weight (*q*1)	0.2
	Current surrounding weight (*q*2)	0.3
	Memory surrounding weight (*q*3)	0.2
	Memory length (of surronding memory)	5
	Random vector weight (*q*4)	0.3

711
712 **Table S1. Model parameters.**

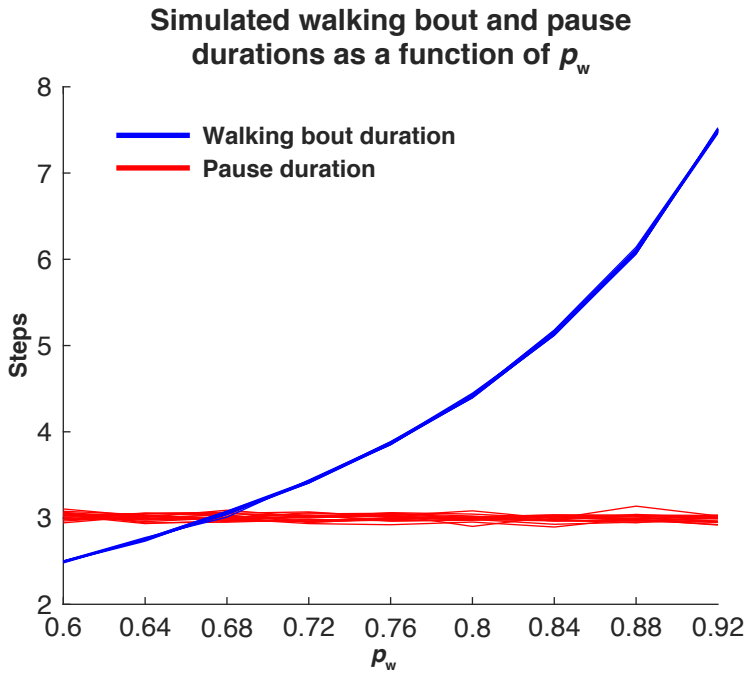

Figure S1. Walking and pause durations for different p_W values. The median bout and pause durations for each row in Fig. 3 presented by each line in the graph, as a function of p_W.

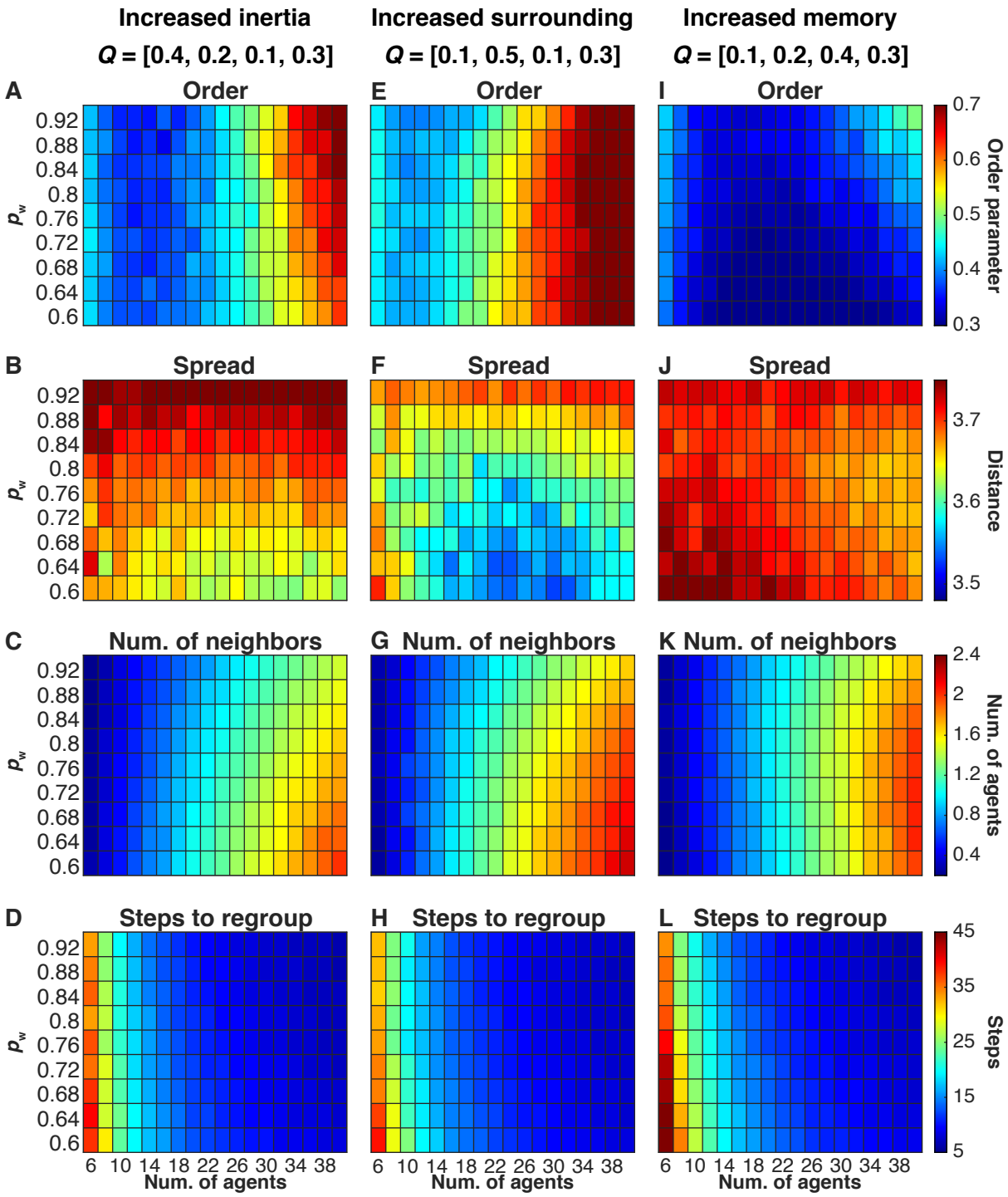

Figure S2. Collectivity parameters for differently weighted influences on the walking direction of the simulated agents. Despite some quantitative differences, our qualitative observation that the propensity of animals to walk, modelled by the parameter p_{W}, has a different effect on small and large groups. The same analysis conducted in Fig. 3, but with different weight vector Q in deciding an agent a new direction $\hat{v}_i(t+1)$. Each colored box represents the median of 40 simulations. (A-D) The order, spread, average number of agents within each agent's visual field and the average number of steps to regroup (respectively), for increased weight of inertia ($q1$): $v_i(t+1) = 0.4\hat{v}_i(t) + 0.2\hat{u}_i(t) + 0.1\frac{1}{5}\sum_{s=1}^{5}\hat{u}(t-s) + 0.3\xi_i(t)$. (E-H) The same as (A-D), but for increased weight of the direction of intersecting rectangles at time t ($q2$): $v_i(t+1) = 0.1\hat{v}_i(t) + 0.5(t) +$

$0.1\frac{1}{5}\sum_{s=1}^{5}\hat{u}(t-s)+0.3\xi_i(t)$. (I-L) The same as (A-D), but for increased weight of the average heading of intersecting rectangles at time $[t-5\ldots t-1]$ ($q3$): $v_i(t+1)=0.1\hat{v}_i(t)+\ 0.2\hat{u}_i(t)+0.4\frac{1}{5}\sum_{s=1}^{5}\hat{u}(t-s)+0.3\xi_i(t)$. As can be seen, the order parameter becomes almost independent of p_W when $q2$ is increased. The spread dependency on p_W increases when $q1$ is increased, but maintains approximately the same trend, despite the different weights, as in Fig. 3. The number of neighbors shows the greatest dependency on p_W when $q1$ is increased and the smallest one when $q3$ is increased. The steps to regroup parameter maintains low dependency on p_W for the different Q's in large groups, but is critical for small groups, corresponding with the results showed in Fig. 3. Therefore, Qualitatively, little differences are found for different Q values. Without empirical evidence regarding those values, we chose mid values, but the obtained results can be generalized to a wider range of Q values.

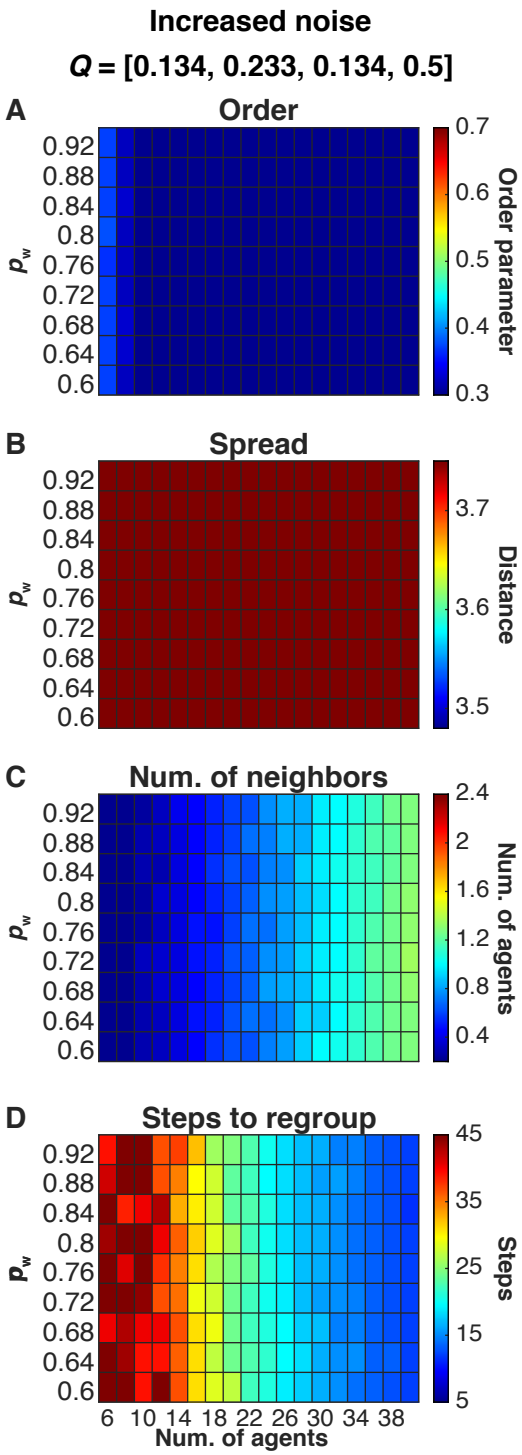

Figure S3. Collectivity parameters with increased noise. The same analysis conducted in Fig. 3 and S2, but when the choice of an agent to of a new direction $\hat{v}_i(t+1)$ was calculated as $(q4)$: $v_i(t+1) = 0.134\hat{v}_i(t) + 0.233\hat{u}_i(t) + 0.134\frac{1}{5}\sum_{s=1}^{5}\hat{u}(t-s) + 0.5\xi_i(t)$. Each colored box represents the median of 40 simulations. The order, spread, average number of agents within each agent's visual field and the average number of steps to regroup (A-D, respectively). As can be seen, changing the weight of the error abolish most of the collectivity of the simulated swarm. Therefore, in Fig. 3 we chose a weight that will not destroy the swarm, yet big enough to maintain randomness in the system.

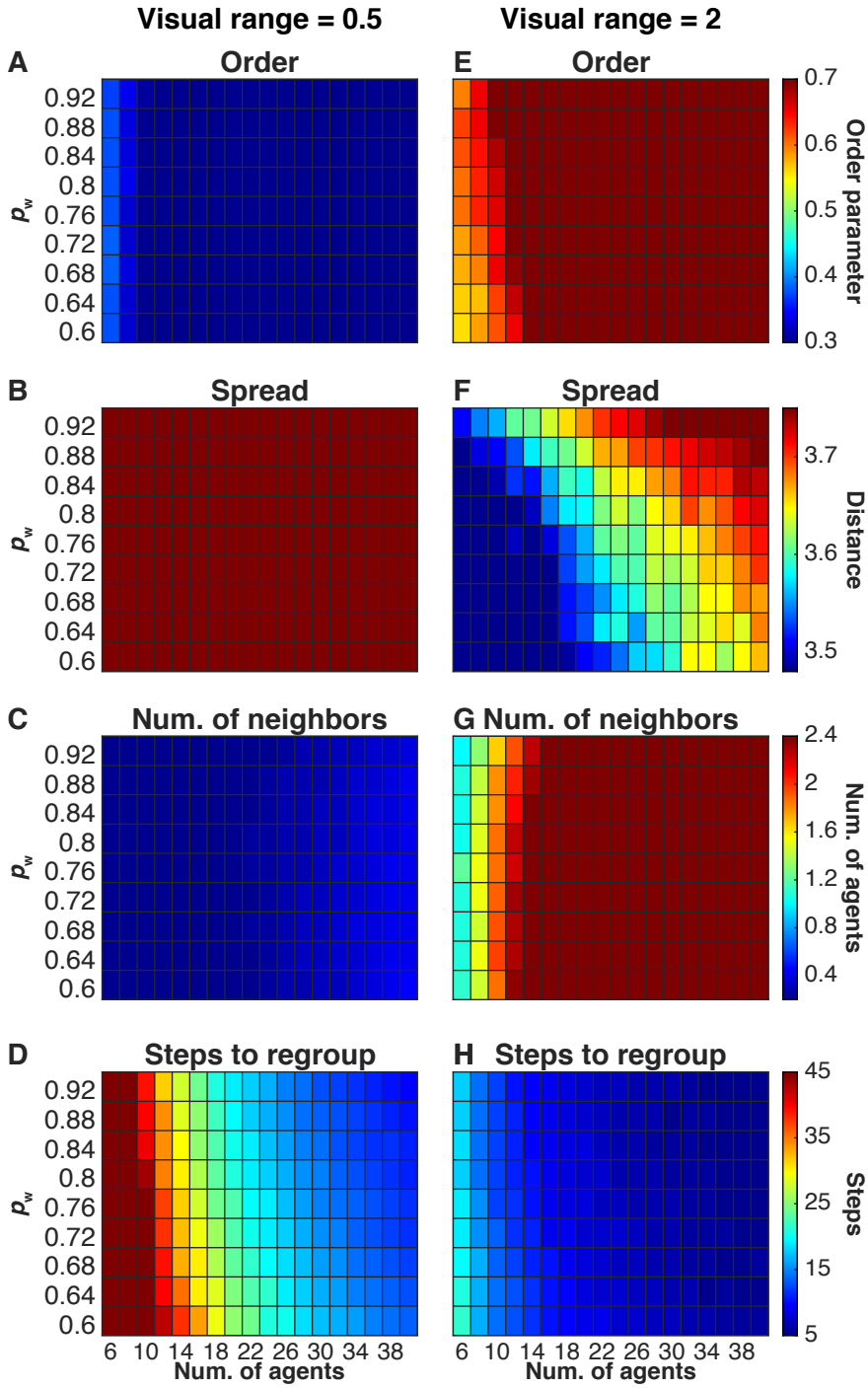

Figure S4. Collectivity parameters for a different visual range radius of the simulated agents. The same analysis conducted in Fig. 3 and S2, but when the visual range of agents was either halved or doubled. Each colored box represents the median of 40 simulations. (A-D) The order, spread, average number of agents within each agent's visual field and the average number of steps to regroup (respectively), for $r = 0.5$. (E-H) The same as (A-D), but for $r = 2$. As can be seen all parameters changed drastically with the different visual ranges. That values used to generate Fig. 3 and 4 were chosen in accordance with the empirical visual range inferred from experiments.

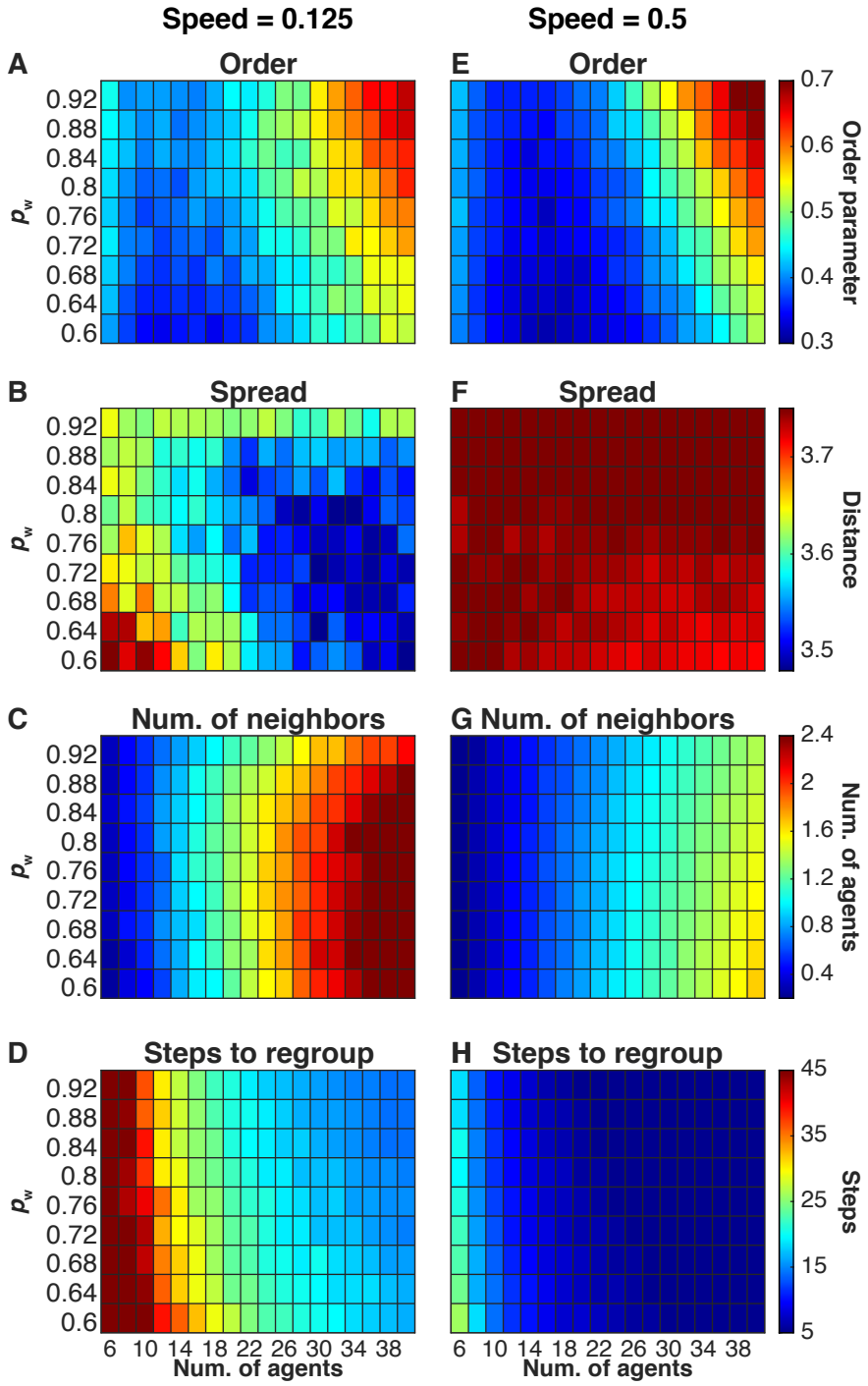

Figure S5. Collectivity parameters for a different speed of the simulated agents. The same analysis conducted in Fig. 3 and S2, but when the speed of the agents was either divided or multiplied by 2. (A-D) The order, spread, average number of agents within each agent's visual field and the average number of steps to regroup (respectively), for $v = 0.125$. (E-H) The same as (A-D), but for $v = 0.5$. As can be seen all parameters maintain the same trends found in Fig. 3, but with different numerical values (excluding the order parameter that maintained the same range of values). The speed chosen for Fig. 3 was calibrated according to the median speed of locusts, as found in experiments. However, as can be seen here, the results are consistent at a wider range of speeds.

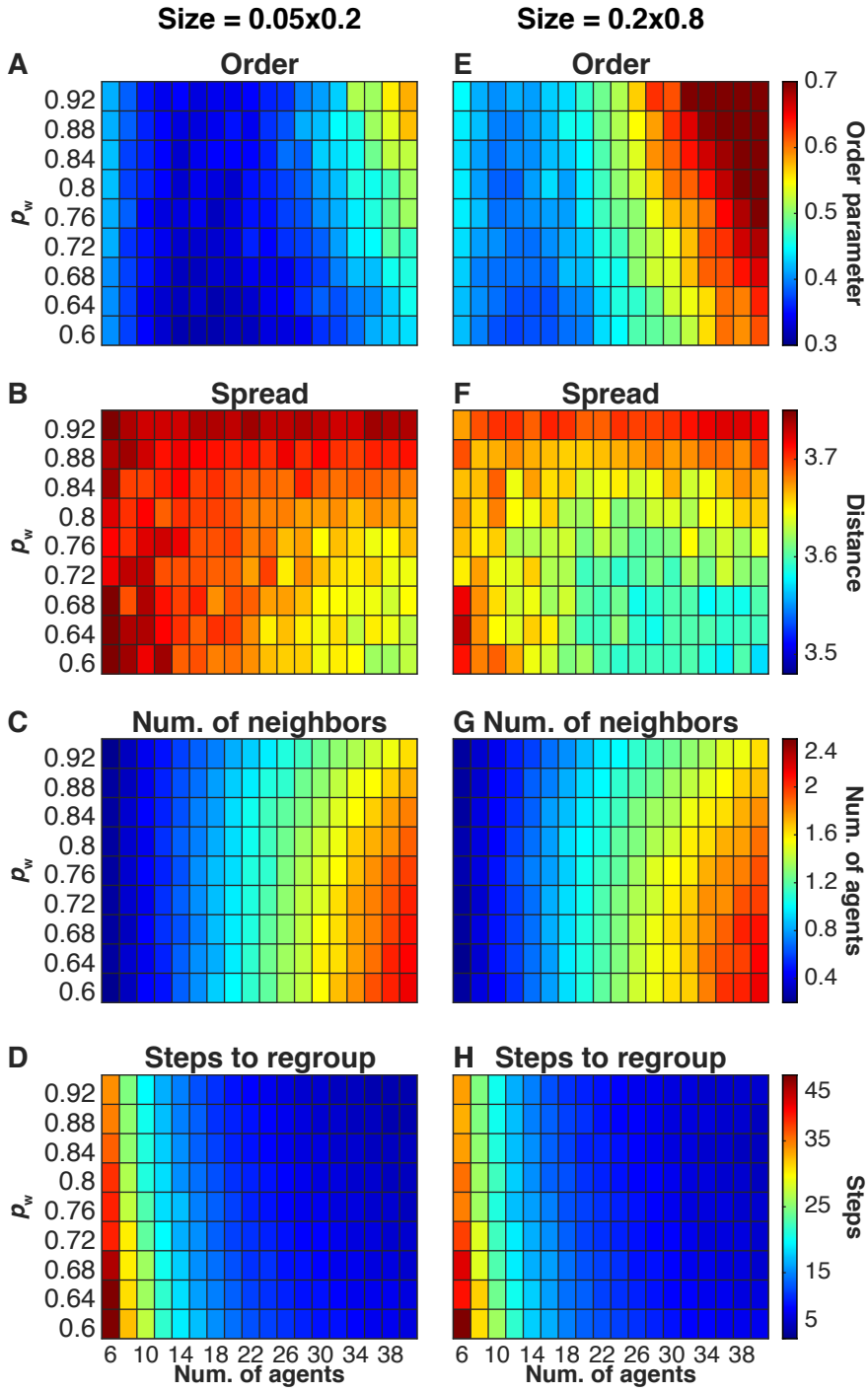

Figure S6. Collectivity parameters for different rectangle sizes of the simulated agents. The same analysis conducted in Fig. 3 and S2, but when the speed of the rectangle dimensions of the agents were either halved or doubled. (A-D) The order, spread, average number of agents within each agent's visual field and the average number of steps to regroup (respectively), for rectangle dimensions of 0.05×0.2. (E-H) The same as (A-D), but for rectangle dimensions of 0.2×0.8. As can be seen all parameters maintain the same trends found in Fig. 3. The agent's size chosen for Fig. 3 aimed at reflecting the spatial scales of real locusts' dimensions. However, as can be see here, the results are coherent at a wide range of sizes.

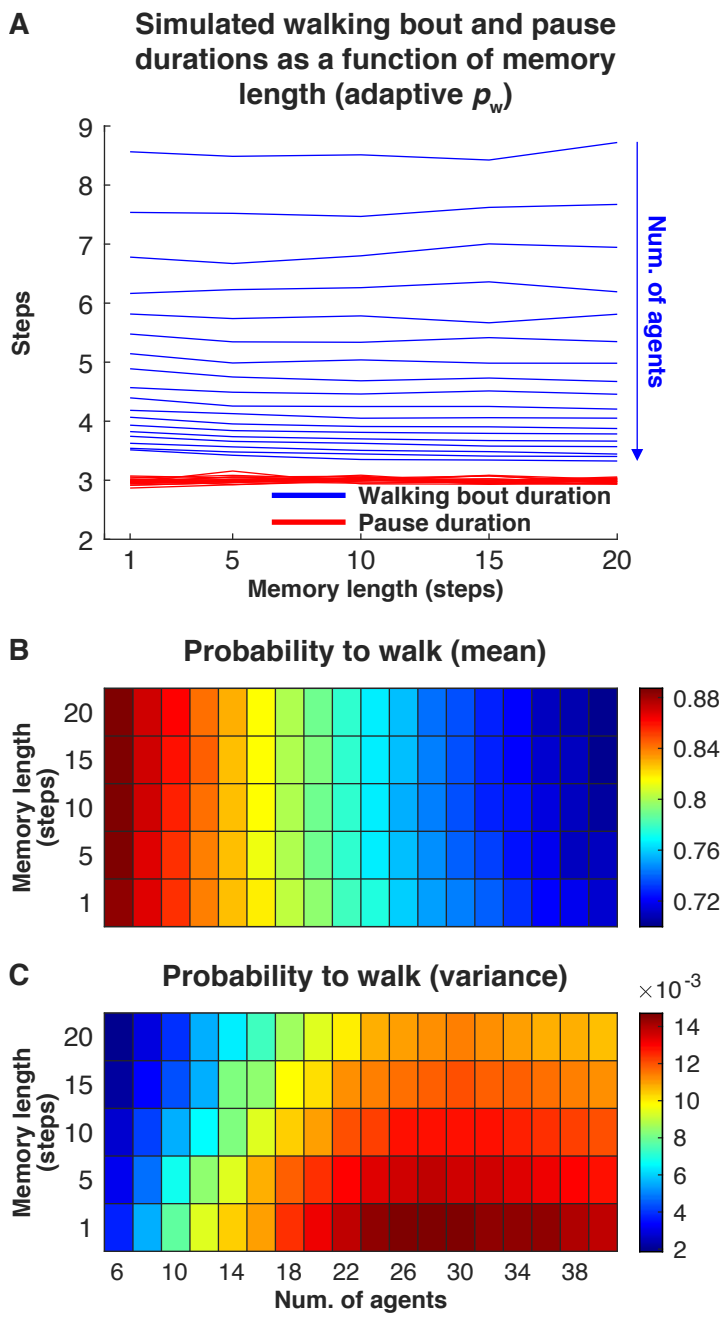

Figure S7. Walking bout durations and statistics of p_W values in the sociality-dependent model. (A) The median bout and pause durations for each row in Fig. 4, presented by each line in the graph, as a function of memory length. The arrow on the right indicates that each blue line represents simulations with different number of agents, ranging from 6 (up) to 40 (down). This is different from Fig. S1, in which the number of agents did not affect the walking bout duration (which was solely dependent on a predefined p_W). (B) The average p_W values obtained by the different agents in different simulations in each category of memory length and number of agents. Each colored box represents the median of 40 simulations. (B) The variance of p_W values obtained by the different agents in different simulations in each category of memory length and number of agents. Each colored box represents the median of 40 simulations. As can be seen, while the average value of p_W only slightly changes across the different memory lengths, the variance is changing drastically. Therefore, the fluctuations in p_W (that

depend on the social context), rather than the average, are the main source of the differences between the lines in Fig. 4.