

Spaces between insects in laboratory swarms move like insects in natural swarms

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Abstract Sparse swarms of flying insects show a high degree of spatial cohesion and are a form of collective animal behaviour; albeit one different from flocks and schools as they do not display ordered collective movements and under quiescent (laboratory) conditions long-range correlations are also absent. A better understanding of these outliers of collective behaviour may help to answer a long-standing open question in collective behaviour studies, namely 'What is the signature that a group is 'collective'? Even though dilute swarms of flying insects are mostly empty space no studies have reported on the dynamics of the spaces between swarming insects. Here I show that the spaces between insects (i.e., the centroids of empty tetrahedra formed by individuals and their 3 nearest neighbours) in laboratory swarms exhibit long range (maximal) correlations and novel dynamic scaling in common with insects in natural swarms. Spaces within laboratory swarms therefore move like insects in natural swarms. I thereby unify seemingly disparate behaviours as long range correlations between individuals are absent in laboratory swarms but present in natural swarms. With the aid of stochastic trajectory models of non-interacting insects I show that long range (maximal) correlations and the novel dynamic scaling arise generally and are not indicative of fine tuning. These results call for a re-evaluation of the importance of correlations and scaling in collective behaviours.

25 **Keywords:** Collective behaviours, swarms, correlations, dynamic scaling, criticality.

Sparse swarms of flying midges show a high degree of spatial cohesion and are a form of collective animal behaviour; albeit one different from flocks and schools as they do not display ordered collective movements [Okubo 1986, Kelley and Ouellette 2013, Attanasi et al. 2014a, Puckett et al. 2014]. The occurrence of these swarms makes it clear that group order and morphology are not sufficient to accurately describe animal aggregations. This has prompted the suggestion that correlation, rather than order, is the true hallmark of collective behaviour in biological systems [Attanasi et al. 2014a]. However, results in the literature have reported contradictory results as to the presence of long-range correlation in insect swarms, with swarms in the wild displaying correlation but those in a controlled laboratory environment not [Puckett et al. 2014, Ni and Ouellette 2015, Reynolds 2021a]. Under controlled laboratory conditions individuals 'appear somewhat paradoxically to be tightly bound to the swarm while at the same time weakly coupled inside it' [Puckett et al. 2014]. They behave on the average as if they are trapped in an elastic potential well that keeps them bound to the swarm [Kelley and Ouellette 2013]. van der Vaart et al. [2020] resolved these apparently incompatible results for laboratory and natural swarms by showing that external perturbations generically induce the emergence of correlations. Here I show that correlations of the kind identified in natural swarms (mating swarms of the non-biting midge *Chironomidae* and the biting midge *Ceratopogonidae* typically containing hundreds even thousands of individuals) which seemingly lie within a novel dynamical class [Cavagna et al. 2017] are present in unperturbed in much smaller laboratory swarms (mating swarms of the non-biting midge *Chironomus riparius* containing tens of individuals) and characterise the movements of the spaces between insects. I thereby unify two seemingly disparate outliers of collective behaviour by establishing a duality between natural and laboratory insect swarms. This is significant because a long-standing open question in collective behaviour studies is 'What is the signature that a group is 'collective'? [Ouellette 2022]. A comprehensive answer to which must encompass insect swarms.

Long-range correlations between insects are absent in laboratory swarms [Puckett et al. 2014, Ni and Ouellette 2015, Reynolds 2021a]. The centroids of tetrahedra formed by individuals and their 3 nearest neighbours will, however, be correlated because each individual can belong to more than one tetrahedron (Fig. 1). Such centroids are necessarily positioned between insects and are used here to define the 'spaces' between insects, i.e., the most empty regions of space in the vicinity of the insects. Note that tetrahedra are the minimum configuration capable of describing the 3-dimensional movements of adjacent individuals (since 3 individuals will always lie in a plane). The statistical and dynamical properties of these tetrahedra are documented in Reynolds [2021a]. Spaces could be defined differently, being situated, for example, at the centres of Voronoi cells or at the centres of circumspheres of the

65 tetrahedra. These possibilities are not considered here because such centres can be located outside of the swarm and even infinitely distant from the swarm making their interpretation in terms of spaces problematic. Moreover, such centres can move exceedingly fast.

The spaces can be linked together in various ways to form trajectories. Here, in the first instance, this is done by linking together spaces associated with individuals, i.e., the spaces
70 in the vicinity of the n^{th} insect at successive positional fixes of that insect form the trajectory of the n^{th} space.

Here following Attanasi et al. [2014a] the dynamics of the spaces between insects in the laboratory swarms was quantified by the ‘connected correlation function’ which measures the
75 extent to which the behaviour of individual i is correlated to that of individual j , at a distance r . The connected correlation function is given by

$$C(r) = \frac{\sum_{i \neq j}^N \delta v_i \cdot \delta v_j \delta(r - r_{ij})}{\sum_{i \neq j}^N \delta(r - r_{ij})} \quad (1)$$

where δv_i is the velocity of individual i relative to the swarm centre and where $\delta(r - r_{ij}) = 1$ if
 $r < r_{ij} < r + dr$ and zero otherwise, and dr is the space binning factor. And following Cavagna
80 et al. [2017] I tested for ‘dynamic scaling’ by computing the spatio-temporal correlation functions of velocity fluctuations in Fourier space

$$C(k, t) = \left\langle \frac{1}{N} \sum_{ij} \frac{\sin(kr_{ij}(t_0, t))}{kr_{ij}(t_0, t)} \mathbf{v}_i(\mathbf{t}_0) \cdot \mathbf{v}_j(\mathbf{t}_0 + \mathbf{t}) \right\rangle \quad (2)$$

where $r_{ij}(t_0, t) = |r_i(t_0) - r_j(t_0 + t)|$ is the distance between insects i and j at different times.
Cavagna et al. [2017] evaluated $C(k, t)$ at $k = 1/\xi$ where ξ is the correlation length. Here the
85 root-mean-square swarm size (averaging over both time and individuals) was used as a proxy for the correlation length.

Over distances of about $1/2$ the root-mean-square swarm size there is a positive correlation, indicating that spaces between insects in the laboratory swarms have common velocity
90 fluctuations (Fig. 2a). Such correlations are entirely absent between the individual insects (Fig. 2a) but are present between individuals within natural swarms [Attanasi et al. 2014a]. Moreover, in common with individuals within natural swarms, the spaces between insects in

the laboratory swarm **may** exhibit dynamic scaling. In accordance with the analysis of Cavagna et al. [2017] for insects in natural swarms, spatio-temporal correlation functions tend to collapse onto the same curve when presented as functions of $k^z t$ where the dynamical critical exponent $z=1$ (Fig. 2b,c). This suggests that the natural swarms reported on by Cavagna et al. [2017] and the spaces within the laboratory swarms belong to the same dynamic universality class; a seemingly novel dynamic universality class [Cavagna et al. 2017]. It is not conclusive **because there is only partial collapse of the data under rescaling** and because the laboratory swarm root-mean-square sizes only range between about 188 mm and 230 mm and. **Partial rather than complete collapse of the data may be due to the relative scarcity of long trajectories in the dataset, making the correlation functions noisy at long times [Sinhuber et al. 2019].** Nonetheless, the conjecture finds support in the results of numerical simulations using stochastic model for the trajectories on **non-interacting** swarming insects [Reynolds et al. 2017]. Individuals in these simulated swarms **have in accordance with observations [Kelley and Ouellette 2013] Gaussian position and velocity statistics** and behave on the average as if they are trapped in an elastic potential well that keeps them bound to the swarm. **In these Langevin-like models the position and velocity of an insect are jointly Markovian.** The models are in close agreement with all available observations of laboratory swarms accounting for example for: the emergence of tensile strength; collective viscoelastic response to applied oscillatory visual perturbations; environmental perturbations induce correlations; the coexistence in equilibrium of core ‘condensed’ phases surrounded by dilute ‘vapour’ phases that maintain their macroscopic properties even though individual insect pass freely between them [Reynolds et al. 2017, Reynolds 2018a, Reynolds 2019a,b, van der Vaart et al. 2019, 2020]. Spatio-temporal correlation functions characterizing spaces within simulated laboratory swarms collapse onto the same curve when presented as functions of $k^z t$ when $z=1$ (Fig. 3a,b); mirroring the dynamic scaling behaviour of insects in natural swarms [Cavagna et al. 2017]. Moreover, associated characteristic timescales for the spaces, τ_k , as determined by

$$\int_0^{\infty} \frac{dt}{t} \sin(t/\tau_k) \mathcal{C}(k,t) = \pi/4, \text{ scale like } \tau_k \sim k^{-z} \text{ (Fig. 3c), as do the characteristic timescales}$$

for insects in natural swarms [Cavagna et al. 2017].

Cavagna et al. [2017] noted that the dynamical exponential exponent $z=1$ is novel, setting natural swarms apart from other dynamical systems: the swarm (disordered) phase of the 3-dimensional Vicsek model [Vicsek et al. 1995], for example, exhibits dynamical scaling but is characterized by $z=2$ [Cavagna et al. 2017]. Further evidence for something qualitatively new in the dynamics of natural swarms comes from the non-exponential shape of the spatio-

temporal correlation functions for times $t < \tau_k$ [Cavagna et al. 2017]. This holds true for the spatio-temporal correlation functions characterizing the spaces within laboratory swarms (Fig. 4).

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The duality between spaces in laboratory swarms and insects in natural swarms does not depend sensitivity on how spaces are stitched together. Long-ranged correlations and $z \approx 1$ dynamic scaling are evident to the same degree when, for example, spaces are not tied to particular individuals as in the above approach (Figs. 5 and 6). Data shown in Figs. 5 and 6 were obtained as follows. First the positions, $x_n(t)$, and velocities, $u_n(t)$ of the spaces at time t were used to estimate the positions, $\hat{x}_n(t + \Delta t)$, of the spaces at the next time step, i.e., $\hat{x}_n(t + \Delta t) = x_n(t) + u_n(t)\Delta t$ where the subscript denotes the n^{th} space; the positions, $x_n(t + \Delta t)$, of the centroids at time $t + \Delta t$ were then calculated, as above, using the locations of individual insects and their 3 nearest neighbours at time $t + \Delta t$; finally the actual position of a space at time $t + \Delta t$ was taken be the position of the centroid that was closest to the estimated position of that space. To make the mapping one-to-one, once a centroid has been assigned to the trajectory of a space it is removed from the remainder of the assignment process.

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145 Discussion

In studies of collective behaviour attention is naturally drawn to the patterns traced out by individuals. Here it was shown that additional insights can be gained by studying how the spaces between individuals move. In the case of insect swarms, examined here, such analyses were shown to unify disparate behaviours seen in the laboratory under quiescent conditions and in the wild where individuals must contend with environmental perturbations. Long range correlations between insects are absent in quiescent laboratory swarms [Puckett et al. 2014, Ni and Ouellette 2015, Reynolds 2021a] but are a hallmark of natural swarms [Attanasi et al. 2014a,b, Cavagna et al. 2017]. Previously it was shown how perturbations can induce correlations between individuals, thereby reconciling seemingly conflicting results [van der Vaart et al. 2020]. Moreover, the results of numerical simulations indicate that perturbations result in novel dynamic scaling of the kind seen in natural swarms [van der Vaart et al. 2020]. Here it was shown that long-range correlations and novel dynamic scaling of the kind seen in natural swarms are, in fact, present in quiescent laboratory swarms, characterizing the movements of the spaces between individuals. This was found to be case for two differing definitions of a 'space' (Figs. 2, 3, 5 & 6).

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Neighbouring spaces (defined in terms of the surrounding individuals) are necessarily correlated because some individuals will be associated with two or more spaces. But this does not account for the presence of long-range correlations and the novel dynamical scaling (Fig. 2). These characteristic features of the correlations may be partly a consequence of individuals being trapped with harmonic potentials; a facet of swarming that is also evident in bird flocks [Kelley and Ouellette 2013, Reynolds et al. 2022].

The long-range correlations and the dynamical scaling identified in natural swarms have been interpreted as evidence that wild swarms are nearly critical and tune themselves to be close to a phase transition from disorder to order (though always remaining on the disordered side) [Attanasi et al. 2014b]. The findings obtained here for much smaller laboratory swarms suggest instead that even when the intrinsic dynamics are always disordered with no hint of criticality, long range correlations and scaling can be hiding in plain sight. This has wide significance because scaling is one of the most powerful concepts in statistical physics but one limited in scope to strongly correlated systems and seemingly not applicable to weakly correlated systems like laboratory swarms. Nonetheless, fine tuning and proximity to a phase transition are not required to obtain dynamic scaling and maximal correlations (correlations that grow with swarm size) as these are evident in the simulation data obtained with arbitrarily chosen model parameters, and so like near critical damping [Reynolds 2021a] and tensile strength arise freely [Reynolds 2019a]. They are not indicative of selection for potentially advantageous behaviours, although they could be accidentally advantageous allowing for maximal information transmission and dynamic range [Bialek et al. 2014]. The findings reported here also demonstrate the surprising utility of stochastic models for simulating the trajectories of independent, unperturbed non-interacting insects in laboratory swarms to describe accurately the flight patterns of strongly interacting insects in wild swarms. This is significant because accounting directly for correlations in 3-dimensional stochastic models remains a formidable challenge [Reynolds et al. 2017, Reynolds et al. 2022]. Nonetheless, future work could be directed at devising better ways to the define spaces and their trajectories as there are shortcomings with the tetrahedral methods. In the first tetrahedral method, large displacements can arise whenever there is a change in the make-up of the tetrahedral because the centroid can then shift abruptly (there is no positional matching); in the second tetrahedral method, large accelerations can arise whenever there is a change in the make-up of the tetrahedral because there is no velocity matching. Neither method is consistent with the observed functional forms of the connected correlation functions which have positive primary

lobes and negative secondary lobes [Attanasi et al. 2014a]. This is a not fundamental problem because $z=1$ dynamic scaling together with negative second lobes can be obtained with somewhat contrived definitions of spaces (results not shown).

200 The duality established here between laboratory and natural swarms bolsters the approach to collective behaviour championed by Ouellette [2019, 2022] who recognized that the properties of animal aggregates cannot be determined by passive observation alone; instead one must interact with them, by for example applying controlled perturbations. This approach allows for the extraction of emergent group properties that are not directly linked to the characteristics of
205 the individuals [Ni and Ouellette 2016, Sinhuber et al. 2021]. The identification and understanding of these emergent macroscopic properties of insect swarms holds promise of a unified ‘thermodynamic’ theory of insect swarms, where one seeks to describe their mechanical-like properties in a way that does not directly reference individual behaviours [Ouellette 2017, Sinhuber et al. 2021]. The duality established here suggests that many of the
210 emergent mechanical/thermodynamic properties of laboratory swarms will be present in some form in wild swarms [Ni and Ouellette 2016, van der Vaart et al. 2019, Sinhuber et al. 2021]. Moreover it suggests that theoretical insights into laboratory swarms (which are relatively easy to obtain because long-range interactions are absent [Puckett et al. 2014, Ni and Ouellette 2015, Reynolds 2021a]) can be carried over to natural swarms which are strongly correlated
215 [Reynolds 2018a,b, Reynolds 2019a,b, 2021a,b].

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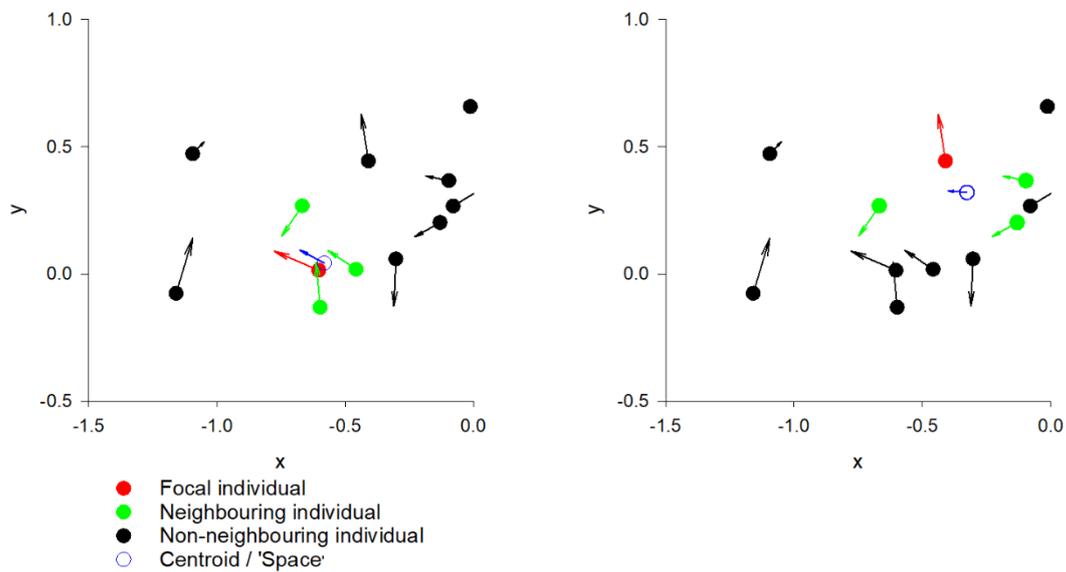
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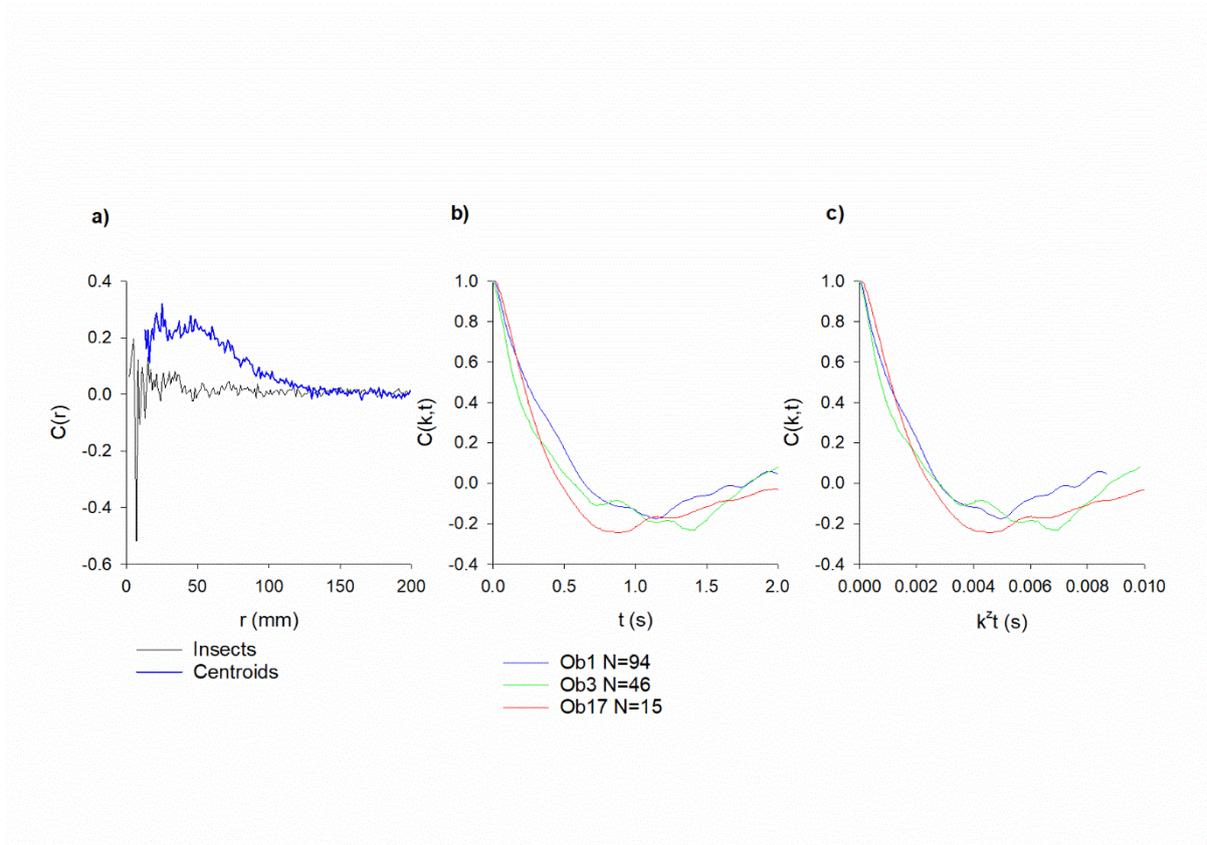
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300 **Figure 1. Examples of tetrahedra formed by individuals and their 3 nearest neighbours, their centroids and their correlations.** A snap shot of simulation data is shown illustrating two focal individuals (●), their 3 nearest neighbours (●), the centroids of the tetrahedra formed by the focal individuals and their 3 nearest neighbours (●), i.e., the locations of the 'spaces' in the vicinity of the focal individuals. Some other individuals are also shown (●). The vectors indicate velocities. The two focal individuals share a common nearest neighbour. The movements of the two spaces are therefore correlated. Data were obtained using a two-
 305 dimensional version of the stochastic model of Reynolds et al. [2017].



310 **Figure 2. Spaces within laboratory swarms move like insects in wild swarms. a)** The connected correlation function, $C(r)$ and the cumulative correlation for insects and spaces within a laboratory swarm Ob1 containing on average 94 individuals and with root-mean-square size 230 mm. **b)** Normalized time correlation functions for spaces, $C(k, t)$, were evaluated at $k = 1/\xi$ where $\xi = \sigma_r$ is the root mean square size of the swarm. **c)** $C(k, t)$ as a
 315 function of the scaling variable $k^z t$ for the same cases as shown in panel b). Data are taken from Sinhuber et al. [2019]. Ob1 is the latest swarm in the dataset. Ob17 is the smallest dusk time swarm with root-mean-square size 188 mm. **The partial collapse of the data under the rescaling is here quantified with $\Delta = \frac{1}{N} \sum_{t, i \neq j} (C(k, t)_i - C(k, t)_j)^2 = 0.028$ and $\hat{\Delta} = \frac{1}{N} \sum_{k^z t, i \neq j} (C(k, k^z t)_i - C(k, k^z t)_j)^2 = 0.008$ where i and j refer to the swarms Ob1, Ob3 and
 320 Ob17 and where N is the number of positional fixes.**

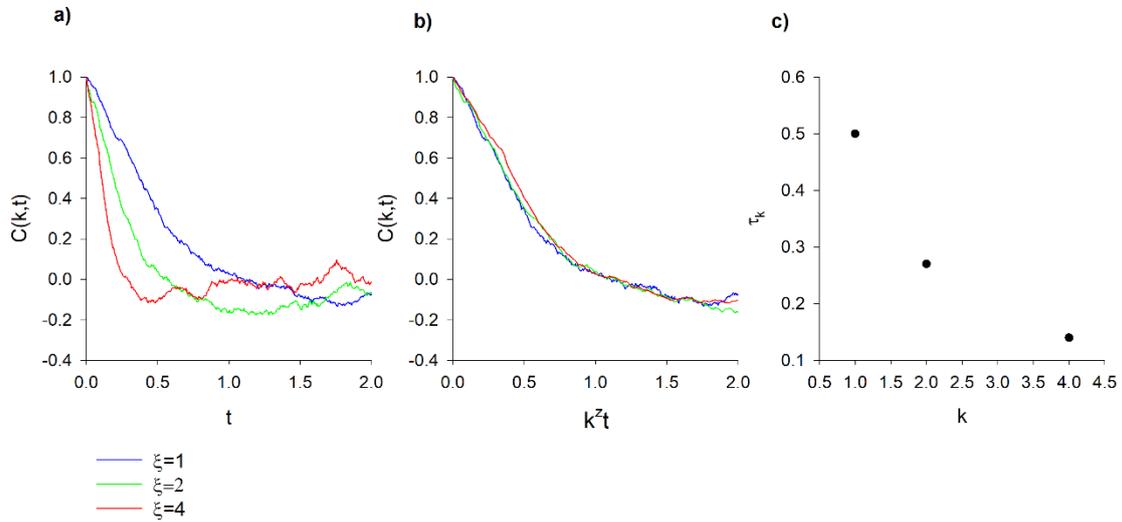


Figure 3. Spaces within simulated laboratory swarms of non-interacting individuals move like insects in natural swarms. **a)** Normalized time correlation functions, $C(k,t)$, were
 325 evaluated at $k = 1/\xi$ where $\xi = \sigma_r$ is the root mean square size of the swarm. **b)** $C(k,t)$ as a
 function of the scaling variable $k^z t$ for the same cases as shown in panel a). **c)** Characteristic
 timescales, τ_k , computed at $k = 1/\xi$ as a function of k . Predictions are shown for the model
 of Reynolds et al. [2017] for swarms containing 100 non-interacting individuals with root-mean
 square velocity and velocity autocorrelation timescale $\sigma_u = 1$ and $T = 1$. Root mean square
 330 swarm sizes σ_r range between 1 and 1/4.

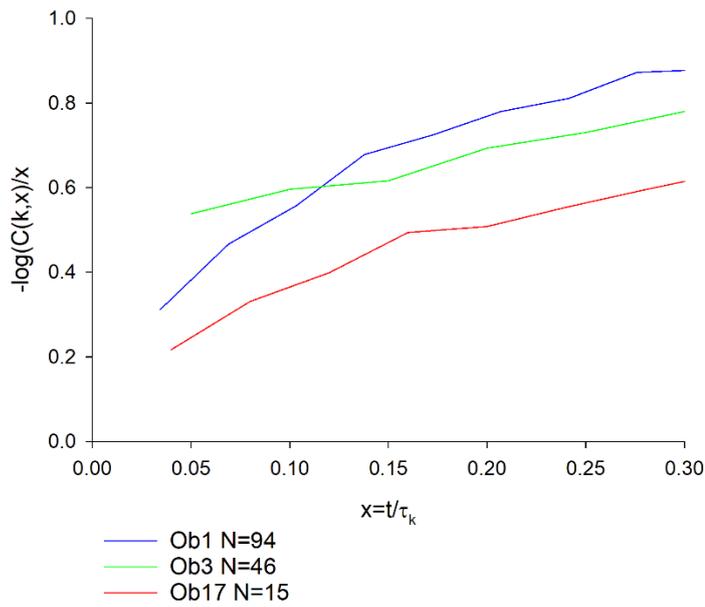


Figure 4. Non-exponential relaxation of spaces within laboratory swarms. Spatio-temporal correlation functions characterizing the spaces within laboratory swarms are non-exponential for times $t < \tau_k$. Purely exponential relaxation is characterized by $-\log(C(k,x))/x \rightarrow 1$ for $x \rightarrow 0$. The concave shapes seen here mirror that obtained by Cavagna et al. [2015] for insects in natural swarms. Normalized time correlation functions, $C(k,t)$, were evaluated at $k = 1/\xi$ where $\xi = \sigma_r$ is the root mean square size of the swarm. Data are taken from Sinhuber et al. [2019]. Ob1 is the latest swarm in the dataset. root-mean-square size 230 mm. Ob17 is the smallest dusk time swarm with root-mean-square size 188 mm.

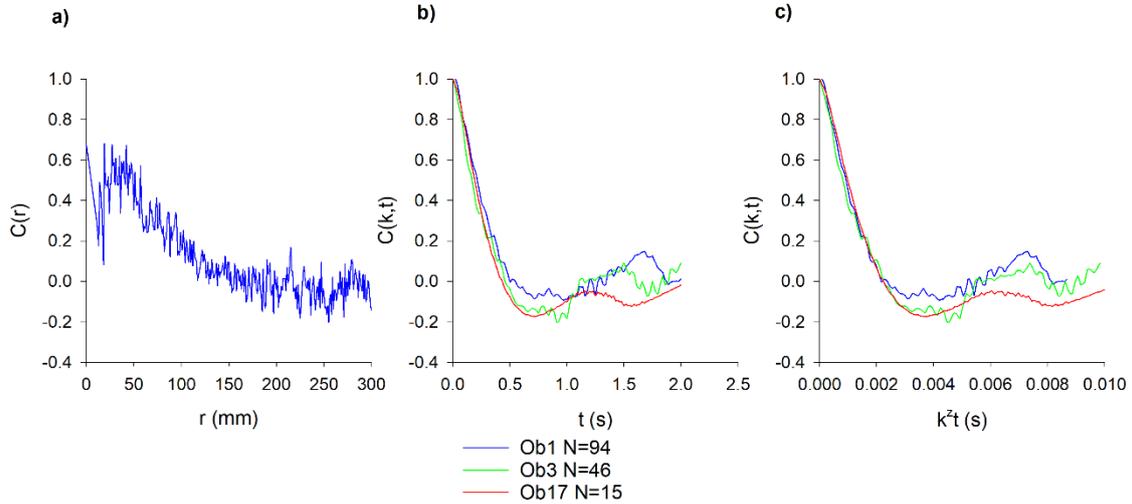
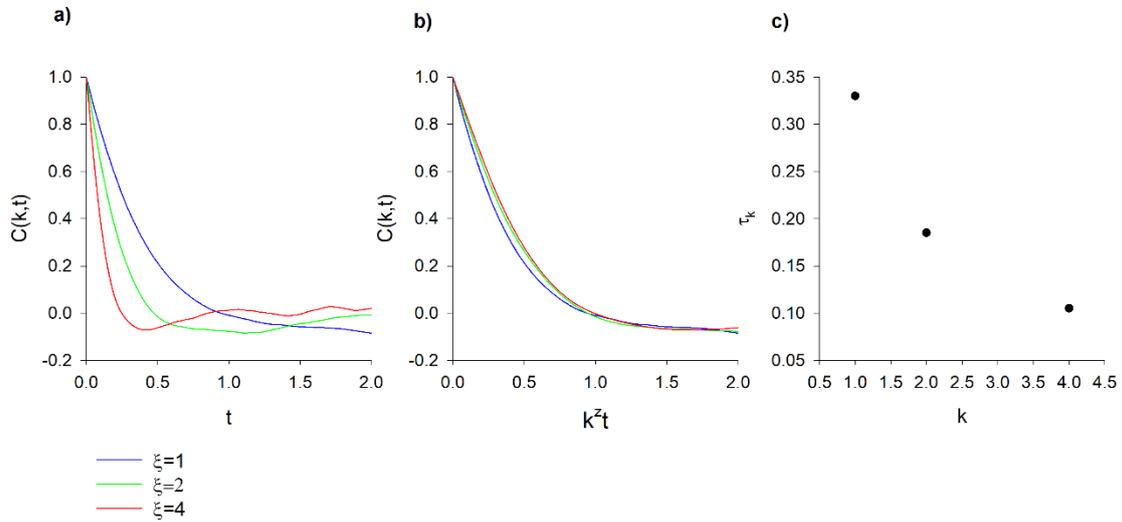


Figure 5. Spaces that are not tied to individuals within laboratory swarms move like insects in wild swarms. a) The connected correlation function, $C(r)$ and the cumulative correlation for insects and spaces within a laboratory swarm Ob1 containing on average 94 individuals and with root-mean-square size 230 mm. **b)** Normalized time correlation functions, $C(k, t)$, were evaluated at $k = 1/\xi$ where $\xi = \sigma_r$ is the root mean square size of the swarm. **c)** $C(k, t)$ as a function of the scaling variable $k^z t$ for the same cases as shown in panel b). Data are taken from Sinhuber et al. [2019]. Ob1 is the latest swarm in the dataset. Ob17 is the smallest dusk time swarm with root-mean-square size 188 mm. The partial collapse of the

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data under the rescaling is here quantified with $\Delta = \frac{1}{N} \sum_{t, i \neq j} (C(k, t)_i - C(k, t)_j)^2 = 0.026$ and $\hat{\Delta} = \frac{1}{N} \sum_{k^z t, i \neq j} (C(k, k^z t)_i - C(k, k^z t)_j)^2 = 0.003$ where i and j refer to the swarms Ob1, Ob3 and Ob17 and where N is the number of positional fixes.



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Figure 6. Spaces that are not tied to individuals within simulated laboratory swarms move like insects in natural swarms. **a)** Normalized time correlation functions, $C(k,t)$, were evaluated at $k = 1/\xi$ where $\xi = \sigma_r$ is the root mean square size of the swarm. **b)** $C(k,t)$ as a function of the scaling variable $k^\xi t$ for the same cases as shown in panel a). **c)** Characteristic timescales, τ_k , computed at $k = 1/\xi$ as a function of k . Predictions are shown for the model of Reynolds et al. [2017] for swarms containing 100 non-interacting individuals with root-mean square velocity and velocity autocorrelation timescale $\sigma_u = 1$ and $T = 1$. Root mean square swarm sizes σ_r range between 1 and 1/4.