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Nutritional state and collective motion: from individuals to mass migration

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In order to move effectively in unpredictable or heterogeneous environments animals must make appropriate decisions in response to internal and external cues. Identifying the link between these components remains a challenge for movement ecology and is important in understanding the mechanisms driving both individual and collective motion. One accessible way of examining how internal state influences an individual's motion is to consider the nutritional state of an animal. Our experimental results reveal that nutritional state exerts a relatively minor influence on the motion of isolated individuals, but large group-level differences emerge from diet affecting inter-individual interactions. This supports the idea that mass movement in locusts may be driven by cannibalism. To estimate how these findings are likely to impact collective migration of locust hopper bands, we create an experimentally parametrized model of locust interactions and motion. Our model supports our hypothesis that nutrient-dependent social interactions can lead to the collective motion seen in our experiments and predicts a transition in the mean speed and the degree of coordination of bands with increasing insect density. Furthermore, increasing the interaction strength (representing greater protein deprivation) dramatically reduces the critical density at which this transition occurs, demonstrating that individuals' nutritional state could have a major impact on large-scale migration.

Keywords: mass migration; desert locust; swarming; nutrition; animal movement

1. INTRODUCTION

The phenomenon of collective behaviour in nature, such as the formation of coordinated swarms of insects, schooling fish or flocks of birds, has fascinated scientists from a wide range of disciplines [1–4]. Understanding the way in which such patterns emerge from interactions between individuals remains a challenging and important problem. It is central not only to our knowledge of animal groups but also in understanding the functioning of tissues where individual cells behave collectively, as in the case of tumours [5] and in sensory system processes, where information is gathered and processed into behavioural responses through the collective action of neurons [6,7]. Common principles, such as positive feedback or threshold responses, are shared by coordinated swarms and sensory system processes [8,9]. Furthermore, understanding the governing factors and resulting consequences of mass animal movements is useful for the control of pest species, such as locusts, and is an important component of many other ecological and evolutionary processes (for example, the spread of diseases [10]).

One of the most striking examples of collective movement is exhibited by locusts. Swarms of the desert locust *Schistocerca gregaria* can devour large areas of vegetation and have a large social and economic impact on humans [11]. Marching bands of juvenile locusts form as a result of individuals interacting with one another [2,4,12–15]. Once the density of locusts in the group increases beyond a critical threshold, there is rapid transition from disordered movement to highly aligned collective motion [12]. This is analogous to phase transitions in statistical physics [16,17], which show a rapid shift from one state to another: for example, a liquid can suddenly change to a solid state or a gas as a result of a very small change in temperature. The existence of such transitions has a fundamental implication for the understanding of collective motion in general as it is likely to be prevalent in collective animal behaviour, particularly in response to the changing density of organisms [4,12,14].

An individual's movement is influenced by several basic components: internal state, motion and navigation capacity, and external factors [18]. Individual internal state can include states of hunger, thirst or fear, but these are difficult to assess as they are often hidden or only inferable [19]. In addition, the interactive effect of internal state and external factors, such as the presence of other individuals or of environmental cues, on animal movement has largely been unexplored [18].

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One accessible way of examining how internal state influences an individual's motion is to consider the nutritional state of an animal. Nutritional state, notably protein and carbohydrate status, plays an important role in individual locust behaviour (for example, in their foraging patterns [20]) and has been suggested to affect mass migration in the Mormon cricket, *Anabrus simplex* [21]. The state of protein deprivation in particular affects the probability of individual crickets moving and cannibalizing, with salt deprivation also having an effect on cannibalism [21].

Cannibalism has also been shown to play an important role in the onset and maintenance of collective motion in locusts [22]. Individuals move in order to reduce their own risk of being cannibalized and in doing so are likely to contact conspecifics, leading to an auto-catalytic process where cannibalism drives the marching behaviour [22]. Romanczuk *et al.* [15] developed a model of swarming to demonstrate that such interactions can account for the long-range order (alignment) of individuals within a group. In this model, individuals have varying velocities and show increased movement away when approached from behind (or 'escape behaviour') and attraction to those ahead (or 'pursuit behaviour'), and hence coordinated group motion does not necessarily rely on explicit alignment among near neighbours.

Here we take an integrated experimental and theoretical approach in order to investigate how the internal state of animals and social interactions lead to collective motion. We carry out an experimental investigation to explore how the internal state—in particular the nutritional state—of an individual locust affects its motion. We then consider the interactive effects of internal state and external factors, namely social cues from conspecifics, on individual motion. Under highly controlled laboratory conditions, we provide locusts with one of three artificial diets for 48 h: a high-protein, low-carbohydrate diet; a balanced diet with equal parts of protein and carbohydrate; and a low-protein, high-carbohydrate diet. We then examine the movement of individuals in an experimental arena when alone (in 'single locust experiments') or with other individuals (in 'group experiments').

Animal movement is often not a continuous state of motion but instead consists of punctuations in locomotion with random fluctuations of movement variables, such as displacements, reorientations and pausing bouts [23,24]. The role of stochasticity in animal movements has only recently been considered to have an adaptive role, particularly in animal foraging strategies [23,25,26]. We use the probabilistic nature of movement to both gain insight into our experimental data and to develop a model of individual and collective motion using an individual-based approach, parametrized by our single locust experimental results (for details see §5). We incorporate the intermittent ('stop and go') nature of animal movement, and selective attraction and repulsion interactions between individuals, to reflect various social interaction strengths that we suggest may result from different nutritional states based on our experimental results. Such social interactions lead to collective motion and, using our model, we reveal how changes in the strength of these interactions are likely to change the critical point at which collective migration occurs. These findings demonstrate how individual internal state can have a major impact on large-scale collective motion.

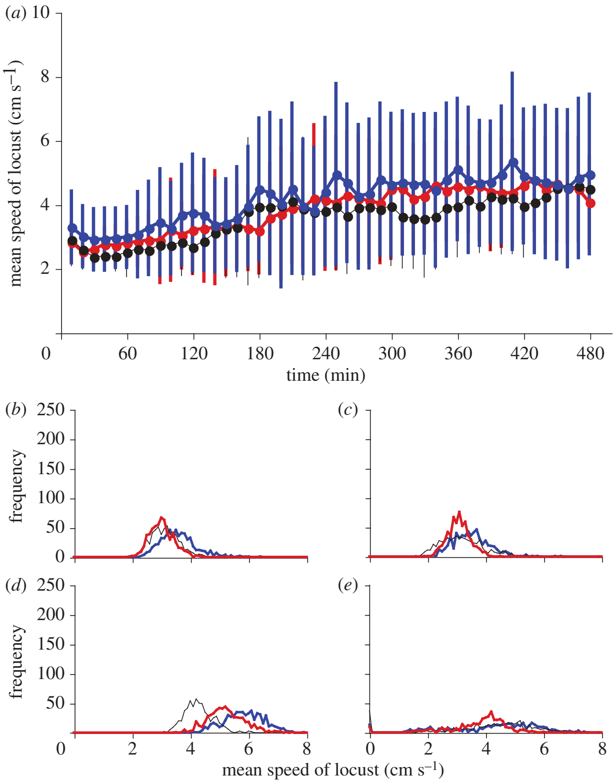

Figure 1. The mean speed of a locust when alone. (*a*) The time series showing the mean speed (cm s^{-1}) of a locust when alone in the arena for each of the diet treatments: high protein (red), balanced (black) and low protein (blue). Thirty experimental trials were carried out for each treatment. Error bars show ± one s.d. (*b–e*) The frequency distributions for the mean speed (cm s^{-1}) of a locust fed on each diet calculated over different two-minute time-windows during the experiment: (*b*) 8–10 min, (*c*) 58–60 min, (*d*) 238–240 min and (*e*) 478–480 min, illustrating how the speeds of individuals fed on different diets change over time.

2. EXPERIMENTAL RESULTS

(a) *The role of diet on locust motion when alone*

To examine the motion of locusts, we consider the mean speed of moving locusts and the proportion of time spent moving by individuals (where moving is defined as a speed greater than 1.5 cm s^{-1} [12,22]). There is no significant effect of diet on the mean speed of an individual in single locust experiments (figure 1; linear mixed-effects model (LME): $F_{2,87} = 1.013$, $p = 0.3674$). Diet also shows no significant influence on the proportion of time spent moving by an individual (electronic supplementary material, figure S1*a*; LME: $F_{2,87} = 0.641$, $p = 0.5293$).

As the experiment progresses, the mean speed of a locust increases (figure 1*a*) and no difference between different diets is observed (figure 1*b–e*). While time does not have a significant effect on the mean speed of an individual within a 2 h time scale, either at the beginning or end of the experiment (figure 1; LME: $F_{1,909} = 0.492$, $p = 0.483$), nor the proportion of time spent moving by an individual (electronic supplementary material, figure S1*a*; LME: $F_{1,987} = 0.027$, $p = 0.869$), it does have a significant effect on the mean speed and the proportion of time spent moving over a larger time scale, when comparing the first and last 2 h of the

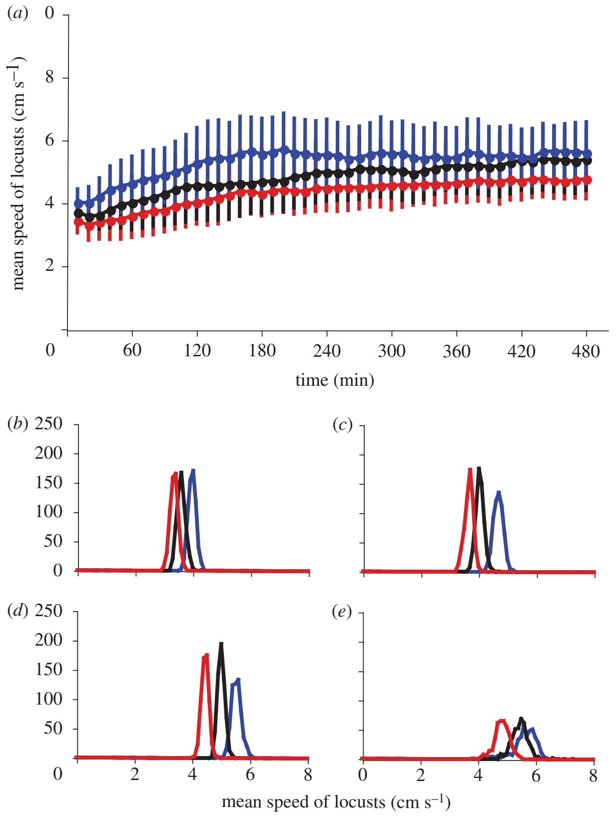

Figure 2. The mean speed of a locust when in a group. (*a*) The time series showing the mean speed (cm s^{-1}) of a locust when in a group of individuals fed on different diet treatments: high protein (red), balanced (black) and low protein (blue). Thirty experimental trials were carried out for each treatment. Error bars show ± one s.d. (*b–e*) The frequency distributions for the mean speed (cm s^{-1}) of a locust in a group fed on different diets calculated over two-minute time-windows at different points during the experiment: (*b*) 8–10 min, (*c*) 58–60 min, (*d*) 238–240 min and (*e*) 478–480 min, illustrating how the speeds of individuals fed on different diets change over time.

experiment (figure 1; LME: $F_{1,909} = 438.827$, $p < 0.0001$ and the electronic supplementary material, figure S1*a*; LME: $F_{1,987} = 379.30$, $p < 0.0001$, respectively).

(b) *The role of diet on locust motion when in groups*

When in groups, individuals fed on a low-protein diet move approximately 40 per cent faster than those on a high-protein diet (figure 2). A balanced diet shows speed levels intermediate to low- and high-protein diets. The effect of diet on the mean speed of individuals and the proportion of moving locusts when in groups is different between the first and last 2 h of the experiment (figure 2; LME: $F_{1,\,985} = 5.802$, $p < 0.005$ and the electronic supplementary material, figure S1*b*; LME: $F_{1,985} = 22.449$, $p < 0.0001$, respectively). Furthermore, when we examine single locust and group experiments together, the effect of diet on the mean speed of individuals is dependent on whether the locust is alone or in a group (electronic supplementary material, figure S2; LME: $F_{2,174} = 3.663$, $p = 0.0276$).

Similarly time shows a significant effect on the mean speed of individuals and the proportion of moving locusts within groups within a 2 h time period. This changes between the first and last 2 h of the experiment, resulting in a significant interactive relationship (figure 2; LME: $F_{1,985} = 54.782$, $p < 0.0001$ and the electronic supplementary material, figure S1*b*; LME: $F_{1,985} = 30.158$, $p < 0.0001$, respectively). At the end of the experiment, the mean proportion of moving locusts for all diets reaches an asymptote at values between 0.5 and 0.7 (electronic supplementary material, figure S1*b*).

3. MODEL

(a) *Model description*

In order to explore the influence of nutritional state on the onset of large-scale migration in locust swarms, we extend Romanczuk *et al.*'s [15] model of collective motion, where individuals have selective repulsion and attraction interactions from escape and pursuit behaviour, respectively. This was an abstract model of swarming and thus unsuitable for direct comparison with our data, lacking key features such as biologically derived motion characteristics.

Here, we present a model motivated by our experimental results in order to help explain and make predictions about the real system. We employ a generic stochastic model that incorporates the intermittent movement dynamics observed in locust behaviour (see electronic supplementary material, figure S3*a*) by considering individuals to be in one of two kinematic states: a moving state and a non-moving state, with stochastic transitions between them (see §5 for details). Individuals in the moving state move actively with speed v and orientation φ, which both fluctuate owing to social interactions or noise (representing such intrinsic stochasticity as is inherent in sensory and locomotory circuits, as well as that resulting from environmental factors).

Furthermore, in our model, individuals have varying diet-dependent social interaction strengths (movement towards, or away from, other individuals). Locusts themselves are a source of protein to other locusts [22] and thus protein-deprived individuals are predicted to show a greater interaction strength (increased escape or pursuit behaviour) than are protein-replete insects.

We have previously shown that the contact and/or sight of others' approach from behind strongly influences a locust's propensity to move [22]. Therefore in our model, we consider an escape-dominated social response to other individuals within a finite sensory range. Note that a single parameter (the interaction strength, χ) controls how individual insects change their speed and direction of motion in response to their neighbours. Low χ values, which correspond to a weak impact of social interactions on individual movement dynamics, are associated with low protein deprivation, whereas large χ values, leading to a strong and fast response to other individuals, are identified with large protein deprivation. The parameters of the model, excluding the interaction strength χ, were chosen according to the single locust experimental results (see §5 for details).

(b) *Comparison with experimental data and estimation of the interaction strength* (χ)

As described above, different nutritional conditions have a minor influence on individual speed dynamics in the absence of social interactions. We test the hypothesis

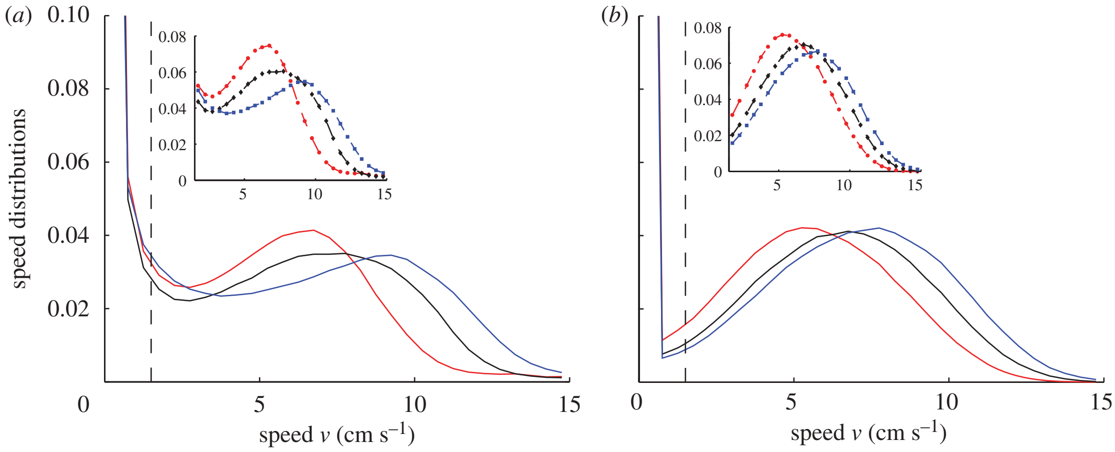

Figure 3. (*a*) Probability speed distributions of individuals for different diets (red: high protein; black: balanced; blue: low protein) obtained from experiments for $t > 300$ min and (*b*) from simulations for different response strengths (red: $\chi_{\mathrm{high}} = 4.0$; black: $\chi_{\mathrm{balanced}} = 8.0$; blue: $\chi_{\mathrm{low}} = 12.0$). The probability speed distribution is the frequency of the different speeds (histogram) normalized by the total number of speed measurements. The dashed line represents $\nu = 1.5\ \mathrm{cm\ s^{-1}}$. The insets show the corresponding probability speed distributions of only moving individuals (which we define as $\nu > 1.5\ \mathrm{cm\ s^{-1}}$).

that the relatively major increase in the speed of individuals in the group experiments for different nutritional conditions (figure 2) originates from diet-dependent social interaction strengths.

First we obtained the mean speed $\langle \nu \rangle_g$ of moving individuals (those with speeds greater than $1.5\ \mathrm{cm\ s^{-1}}$) from our group experiments for different diets (figure 3*a*):

$$\langle\langle \nu \rangle\rangle_{g(\mathrm{high})} = 5.98\ \mathrm{cm\ s^{-1}}, \quad \langle\langle \nu \rangle\rangle_{g(\mathrm{balanced})} = 6.74\ \mathrm{cm\ s^{-1}}, \quad \langle\langle \nu \rangle\rangle_{g(\mathrm{low})} = 7.28\ \mathrm{cm\ s^{-1}}.$$

Here $\langle\langle\ \rangle\rangle$ denotes the average for all individuals and for all times in the experiment (temporal average).

We then performed simulations for different values of the interaction strength, χ (for visualizations of the model see electronic supplementary material). All model calculations were performed with constant interaction strengths (representing the constant nutritional conditions found in our experimental treatments); thus, the interaction strength does not change in each model run. The mean speeds of individuals from simulations increase with increasing interaction strength χ (figure 3*b*). To estimate interaction strengths that correspond to the different diets, we select the values of χ that yield individual mean speeds in agreement with the experimental results, up to a relative error of 1 per cent ($|\langle \nu \rangle_{\mathrm{exp}} - \langle \nu \rangle_{\mathrm{sim}}| / \langle \nu \rangle_{\mathrm{exp}} < 0.01$). For the simulation parameters used (see §5) these interaction strengths are: $\chi_{\mathrm{high}} = 4$, $\chi_{\mathrm{balanced}} = 8$, $\chi_{\mathrm{low}} = 12$.

A comparison of the probability speed distributions from experiments and simulations shows the same qualitative shape with a large peak at $\nu = 0$ and a second maximum at $\nu = 5{-}10\ \mathrm{cm\ s^{-1}}$ (figure 3). Furthermore an increase in the interaction strength χ leads to a shift of the second maxima, also observed in experiments with increasing protein deprivation (figure 3*a*). The quantitative differences between the simulation and experimental distributions, in particular the different peak heights of the maximum, are due to the deviations at small speeds ($\nu = 0.5{-}2\ \mathrm{cm\ s^{-1}}$). The discontinuous shape of the distributions obtained from simulations originates from the discrete formulation of the model, whereas the smoothness of the experimental curves can be due to errors (from noisy position recordings) in measuring the speed of individuals.

(c) *Estimating the impact of diet on collective migration*

If our estimates of the social interaction strength χ are indeed associated with the respective diets, it is possible to use the model to estimate the impact of the different diets on the onset of collective migration by varying the density for the corresponding interaction strengths. The density was varied for different interaction strengths by keeping the number of particles constant ($N = 576$) and changing the size of the simulation domain L.

The onset of collective motion was measured using the global migration speed U and the corresponding order parameter Φ, where $\Phi = 0$ represents fully disordered motion and $\Phi = 1$ represents perfect alignment (collective motion):

$$\langle U \rangle = \left\langle \frac{1}{N} \left| \sum_{i=1}^{N} \vec{\nu}_i \right| \right\rangle \tag{3.1}$$

and

$$\langle \Phi \rangle = \left\langle \frac{\left| \sum_{i=1}^{N} \vec{\nu}_i \right|}{\sum_{i=1}^{N} |\vec{\nu}_i|} \right\rangle. \tag{3.2}$$

Here $\langle\ \rangle$ represents an average over 10 independent simulations each running for 2000 s after the system reached a stationary state.

The simulations suggest that the mean speed (figure 4*a*) and order parameter (figure 4*b*) as a function of density are strongly dependent on the interaction strength. An increase in density results in an increase in both the mean speed and order parameter for all interaction strengths. We define the critical density ρ_c for the onset of collective motion where the order parameter passes the value 0.5. For the parameter set used, the critical

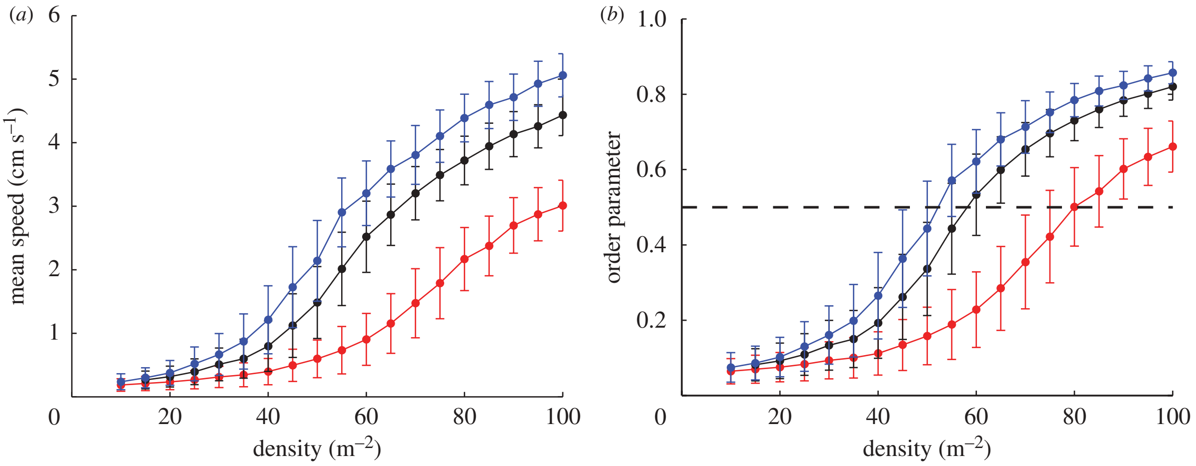

Figure 4. Simulation results for different densities. The (*a*) global migration speed and (*b*) order parameter as a function of density for individuals with different response strengths (red: $\chi_{\text{high}} = 4.0$; black: $\chi_{\text{balanced}} = 8.0$; blue: $\chi_{\text{low}} = 12.0$). Error bars show ± one s.d. The dashed line in (*b*) represents the threshold of the order parameter $\Phi = 0.5$, which we define as the critical density. Each point was calculated as an average over time series from 10 independent simulations. The time series of each run was recorded for time interval $\Delta t = 2000$ after the system reached a stationary state (numerical time step $dt = 0.006$).

density decreases with increasing interaction strength, from $\rho_c \approx 80\ \text{m}^{-2}$ for $\chi_{\text{high}} = 4$, to $\rho_c \approx 58\ \text{m}^{-2}$ for $\chi_{\text{balanced}} = 8$, and finally $\rho_c \approx 52\ \text{m}^{-2}$ for $\chi_{\text{low}} = 12$. Therefore, stronger escape and pursuit behaviour lead to mass migration occurring at a much lower density (figure 4). The qualitative result of the differences in critical densities for different χ, in particular the large shift of the critical density for high-protein diet, also holds for different parameter sets, but the quantitative results may shift.

4. DISCUSSION

We examined the role of individual locusts' nutritional (internal) state on motion in the presence and absence of social interactions (external factor). We could detect no statistical effect of diet on the movement patterns of individual locusts when alone in our assay system. It has been reported previously that individual locusts fed a nutritionally balanced diet rest longer between meals than those fed either an equally protein- or carbohydrate-biased diet [27,28]. Hence, if any effect were to be predicted on locomotion of individuals in our assay, it would be that locusts fed a balanced diet would have lower speeds and spend less time moving than those fed imbalanced diets. Such a tendency is indeed apparent in the data in figure 1 and the electronic supplementary material, figure S1, but is too weak to be a significant effect.

In contrast to isolated locusts, individuals fed on a low-protein diet moved approximately 40 per cent faster than individuals fed on a high-protein diet when in groups (figure 2). The mean proportion of moving individuals was also significantly greater for the low-protein diet groups. This difference is particularly evident within the first 2 h of experiments (electronic supplementary material, figure S1*b*), when the influence of diet treatment would be expected to be most pronounced and before general effects of food deprivation swamped nutrient-specific effects of the pre-treatment [20]. Locust groups fed on a balanced diet initially showed speeds similar to those fed on a high-protein diet, but as the experiment progressed their mean speed increased and became similar to groups of individuals fed on a low-protein diet (figure 2*b*–*e*), presumably as all individuals became generally nutrient-deprived over time [20].

Our results indicate that the nutritional manipulations used in our study had a relatively limited influence on individuals' internal programme of movement, but strongly affected their response to environmental stimuli—in this case, cannibalistic interactions. Consequently, nutritional state can have a major impact on the dynamics of group movement, and the effect of nutritional state at the group level differs from the effects on the behaviour of isolated individuals. To test the prediction that this difference emerges from the way in which nutritional state alters the nature of social interactions between locusts, we created a stochastic model of individuals with intermittent movement and selective attraction and repulsion interactions. The simulation results support our prediction and show a similar shift in the maximum of the probability speed distribution of the moving individuals as observed in our experiments (figure 3). Our model results also show a transition in the mean speed and order parameter with increasing density (figure 4), a feature often observed in animal groups [12,29–31]. The model also suggests that increasing the interaction strength between individuals significantly decreases the critical density at which this transition occurs (from high to low protein). A higher interaction strength corresponds to higher levels of escape behaviour when individuals are approached from behind and higher levels of pursuit behaviour of those ahead, and simulates an increase in protein deprivation of the internal nutritional state of the individuals.

When locusts are in a group, internal nutritional conditions affect social interactions since other locusts provide a source of high-protein food. Locusts are known to possess highly effective mechanisms to regulate the intake of protein and carbohydrate [20]. Our empirical results show that groups of individuals fed on a high-protein diet moved and had mean speeds similar to if they were alone, unlike low-protein-fed individuals (electronic supplementary material, figure S2), suggesting that lack of protein has a greater effect on group motion. Those fed on low-protein diets need to restore their nutritional balance and obtain more protein [20]. When within groups, an abundant source of protein is other locusts, and interactions with other locusts provide opportunities for cannibalism [22]. In naturally occurring marching bands, cannibalism may not only provide locusts with additional protein, but may activate others to march and increase the degree of collective motion in the population, thereby driving the band to cover substantially greater distances than individual insects [21,22], thus effectively searching larger areas for new sources of food required by individuals within the group. This further supports the contention that reducing protein state results in stronger social interactions, and thus higher levels of collective motion. Additionally, travelling with conspecifics as a potential food source may enable locusts in bands to persist longer while traversing unfavourable parts of a patchy nutritional environment.

The results of this study help improve our understanding of animal movement, increasing our knowledge of some of the factors (internal and external) that influence an individual's movement and their interactive effects on animal motion. Not only is this information important in our understanding of collective motion in animals, particularly in pest species, but it may also be useful in predicting when and where collective animal migrations, which can have a significant impact on the environment, are likely to occur.

5. MATERIAL AND METHODS

(a) *Experiments*

Healthy, intact freshly moulted gregarious desert locusts (*S. gregaria*) in the 5th (final nymphal) instar, reared under conditions described in [32], were placed in groups of 20 individuals in plastic cages (30 × 20 × 10 cm) with a mesh roof containing sawdust, an expanded aluminium perch and a water supply. Locusts were fed one of three dry, granular synthetic diets: low-protein, balanced (equal proportions of carbohydrate and protein) and high-protein (for details of diet composition see the electronic supplementary material) ad libitum for 48 h. Marching and feeding behaviour are low and irregular 24 h post moult [33], but by 48 h locusts have high and uniform marching, and maintain a high food intake.

After 48 h, either individual locusts in 'single locust experiments' or a group of 15 insects in 'group experiments' (above the threshold density for coordinated marching in the arena [12,33]) were placed in a ring-shaped experimental arena (80 cm diameter, walls 52.5 cm high and a central dome 17.5 cm diameter), as described in [12,22]. The motion of the locusts in the arena was then filmed for 8 h using a digital video camera (Canon XM2). Thirty trials were carried out for each treatment for group and single locust experiments (a total of 180 trials).

Automated digital tracking software [12,22], which captured images at a rate of five times per second, was used to analyse the video footage and thereby determine any differences in the behavioural parameters for each treatment. Information regarding the position, speed and direction of all the individuals in the marching band was obtained.

(b) *Statistics*

The time series of the mean speed of an individual, the proportion of time spent moving by an individual when alone and the proportion of moving individuals within a group were analysed using a LME. Since we are dealing with time series analysis there is temporal autocorrelation, thus two data points collected in quick succession are more similar than ones that are far apart in time. To reduce the effects of temporal autocorrelation, the data were averaged into 20 min intervals. Only the first and last 2 h were included in the model (to examine the short-term time effect within 2 h and the long-term time effect between the beginning and the end of the experiment). Thus, our LMEs included the following response variables: diet, time and session (first or last 2 h of the experiment), treating experimental trial as a random factor. All proportion data (p) were transformed using arcsin $\sqrt{p}$ transformation [34]. The data were checked for normality and homogeneity of variance, and non-normally distributed data were transformed using an inverse transformation (mean speed in single locust experiments). Statistical analysis was carried out in R v. 2.8.0.

(c) *Model implementation*

In order to model the experimental results, we introduce a simplified individual-based description of the locust dynamics in two spatial dimensions. Each individual is considered as a particle, which can move actively and interact with neighbours within a sensory range l_s (set to $l_s = 14$ cm according to [12]). The response of an individual i to other individuals is described by an effective social force $\vec{F}_i^s$, which is the sum of three different components: escape behaviour, where individuals move away when they are approached from behind; pursuit behaviour, where an individual moves towards another individual moving forwards in front of it; and a repulsion component, which ensures individuals maintain a preferred minimal distance from neighbours (the details of the social force calculations can be found in the electronic supplementary material). The escape and pursuit interactions are similar to those described in [15] and only take place if individuals have a distance greater than the repulsion range, but still within the sensory range. There are no escape and pursuit interactions with stationary individuals. Here, we set the repulsion range to 4 cm (typical locust's size). Thus, at small distances (less than the repulsion range) repulsion dominates the individual dynamics and individuals increase their distance away from close neighbours irrespective of the escape/pursuit interaction scheme.

In our simulations, we consider escape-dominated social responses [22], with a constant ratio $\chi_e/\chi_p = 5$. This gives us a single parameter determining the strength of the social interaction $\chi = \chi_e$, which we assume is correlated with the nutritional state.

Based on the experimental observations of intermittent movement (electronic supplementary material, figure S3), we consider each individual to be in one of two kinematic states: moving or non-moving. In the moving state, an individual moves actively with a preferred (mean) speed and orientation, which may fluctuate owing to social interactions or noise (for details of speed and orientation fluctuation calculations see the electronic supplementary material). In the non-moving state, individuals are at rest (speed equals zero) and keep their orientation from their last position in the moving state.

The change of the kinematic state of a solitary individual, owing to various internal and external factors, is described as stochastic processes with the transition rates r_{nm} and r_{mn} (probabilities of transition per unit time). In general, for an individual within a group, both transition rates depend on its social interactions within its sensory range. In our experiments, the proportion of moving individuals shows a weak dependence on the diet and at the end of experiments (after 300 min) approaches an asymptotic value of 0.5–0.7, independent of the diet (electronic supplementary material, figure S1*b*). Furthermore previous experiments show no significant dependence of the proportion of moving individuals on the density [12]. Thus for simplicity we set both rates as constant: $r_{mn} = 0.025$ and $r_{nm} = 0.040$, which yields a proportion of moving individuals in the simulations that is comparable to the experiments. In order to confirm that this simplification does not have a major impact on the model predictions for the onset of collective motion, we tested two additional extensions of the model with transition rates (between the moving and non-moving states) dependent on the strength of the social force acting on an individual or on the nutritional state (see electronic supplementary material, materials and methods and figures S4 and S5). All tested variants yield similar qualitative and quantitative predictions on the onset of collective motion. Simulations of the model with transition rates dependent on the social force show a strong effect of density of individuals on the proportion of moving individuals in groups, which contrasts with previous experimental results in this species [12]. The model with transition rates dependent on nutritional state shows diet differences in the proportion of time spent moving in single individual simulations, which was not observed in our experimental results (electronic supplementary material, figure S1). We therefore select the simplest model with constant transition rates in our study.

For a solitary individual, the new direction of motion after a transition from the non-moving to moving state is chosen randomly, whereas for a socially interacting individual it is chosen to be the direction of the total social force acting on the individual at the time of the transition. The initial speed after a transition is set to the preferred speed.

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