LETTER

Cannibalism can drive the evolution of behavioural phase polyphenism in locusts

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Abstract

During outbreaks, locust swarms can contain millions of insects travelling thousands of kilometers while devastating vegetation and crops. Such large-scale spatial organization is preceded locally by a dramatic density-dependent phenotypic transition in multiple traits. Behaviourally, low-density 'solitarious' individuals avoid contact with one another; above a critical local density, they undergo a rapid behavioural transition to the 'gregarious phase' whereby they exhibit mutual attraction. Although proximate causes of this phase polyphenism have been widely studied, the ultimate driving factors remain unclear. Using an individual-based evolutionary model, we reveal that cannibalism, a striking feature of locust ecology, could lead to the evolution of density-dependent behavioural phase-change in juvenile locusts. We show that this behavioural strategy minimizes risk associated with cannibalistic interactions and may account for the empirically observed persistence of locust groups during outbreaks. Our results provide a parsimonious explanation for the evolution of behavioural plasticity in locusts.

Keywords

adaptation, behavioural plasticity, collective migration, collective animal behaviour, locust plagues, phase-change, spatial evolutionary ecology, self-organization.

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INTRODUCTION

Mass migration of insects such as locusts and Mormon crickets are spectacular examples of collective animal movement. During outbreaks, locust swarms can contain millions of individuals, extend up to several kilometers and may travel over continental scales (Farrow 1990; Lovejoy *et al.* 2006). To meet their nutrient requirements, these insects primarily feed on plants, but may also consume animal matter and often cannibalize each other (Simpson *et al.* 2006; Bazazi *et al.* 2008). The insects themselves also serve as a mobile prey resource for their predators. Therefore, insect mass migrations can influence the ecology of a number of plant and animal species spread over large spatial scales. By virtue of their negative agricultural impacts, locust plagues are estimated to influence the livelihood of one in ten people in the world (Simpson & Sword 2008). As such, an understanding of proximate and ultimate factors that drive their mass migrations can not only reveal general principles of collective motion and the ecology of migration, but also potentially contribute to designing preventive pest-management strategies (Sword *et al.* 2010).

A key step preceding formation of marching migratory bands of juvenile locusts is the expression of a dramatic form of phenotypic plasticity mediated by local conspecific density. The two phenotypic phases, solitarious and gregarious, exhibited by locusts can be distinct in many traits, such as colouration, neurophysiology or behaviour (Uvarov 1921; Roffey & Popov 1968; Collett *et al.* 1998; Simpson *et al.* 1999; Anstey *et al.* 2009; Simpson & Sword 2009;

Pener & Simpson 2009; Ayali and Yerushalmi 2010; Ma *et al.* 2011; Guo *et al.* 2011). The differences can be so dramatic that in one species, *Locusta migratoria*, individuals in different phases were previously considered to belong to separate species (Uvarov 1921). However, it is the behavioural transition that responds most rapidly, within a few hours, to changes in local population density (Anstey *et al.* 2009; Pener & Simpson 2009). In the Desert locust, *Schistocerca gregaria*, local density of conspecifics is assessed by tactile and/or visual and olfactory stimuli (Simpson *et al.* 1999; Simpson *et al.* 2001; Pener & Simpson 2009). At low population densities, locusts are solitary individuals where they avoid contact with one another. As the local density increases beyond a critical value, behavioural repulsion among insects declines, and subsequently they begin to be attracted towards others. Full gregarious behavioural characteristics including increased activity levels and mutual attraction are acquired within 2–4 h of forced crowding.

As gregarious-phase insects are attracted to others crowding them, they provide a positive feedback that can result in the maintenance and spread of the gregarized state, leading to the formation of mass-moving-migratory bands of juveniles and flying swarms of adults (Buhl *et al.* 2006; Simpson & Sword 2009). Thus, density-dependent gregarisation is a crucial process preceding, and potentially providing an early indicator of devastating locust outbreaks (Sword *et al.* 2010). The expression of density-dependent phase polyphenism in locusts has independently evolved several times in multiple lineages on different continents (Pener & Simpson 2009), thus raising an important

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question: What are the key evolutionary forces that have repeatedly shaped this form of extreme phenotypic plasticity?

Previous studies have proposed that selection from interspecifc interactions, namely predation, has been important in the evolution of density-dependent polyphenism. Under such scenarios, the benefits accrued through active aggregation as local population densities increase can include evading, swamping and/or signalling toxicity to predators through their colouration (Sword 1999; Sword *et al.* 2005; Simpson & Sword 2009) and/or disrupting the connectivity of predators' food-patches, thereby reducing risks of predation (Reynolds *et al.* 2009). However, recent experiments have revealed that individual desert locusts (*Schistocerca gregaria*) and Australian plague locusts (*Chortoicetes terminifera*) may both benefit from, and pay a significant cost of group membership due to, cannibalism (Bazazi *et al.* 2008; Hansen *et al.* 2011). Therefore, the role of inter-vs. intra-specific processes and how trade-offs in the costs and benefits of gregarisation have influenced the evolution of the density-dependent behavioural phase-change remains unclear.

In this article, we use an individual-based and spatially explicit evolutionary model, implemented on massively parallel graphics processing units (GPUs) (Guttal & Couzin 2010, 2011), to investigate the influence of risks of cannibalism on the evolution of behavioural strategies in locusts. This is based on empirically motivated models (Romanczuk *et al.* 2009; Bazazi *et al.* 2011) which have been successful in explaining a range of experimental data on the formation and dynamics of coherent bands (Buhl *et al.* 2006; Buhl *et al.* 2011; Bazazi *et al.* 2011). A key (and differentiating) aspect of our model is that we consider a framework in which behavioural interactions and plasticity are not pre determined, but rather they evolve. This allows us

to explore the selection pressures, and evolutionary stable strategies/states, of individual movement and local interactions relevant to migratory band formation and spatial movement. We test generality of our results to various modifications of the model and discuss its implications to our understanding of proximate and ultimate factors underlying locust ecology.

MATERIALS AND METHODS

Evolutionary model for local interactions and movement

We introduce a modelling framework for the collective dynamics of locusts, consisting of an individual-based model for the motion and interaction of individual insects in two spatial dimensions (Box 1), coupled to an evolutionary algorithm (Box 2) for the social response of individuals.

The ability of locusts to modify their direction of motion in response to the relative motion of nearby individuals (Bazazi *et al.* 2008; Romanczuk *et al.* 2009; Buhl *et al.* 2011), defined as those within a sensory radius of l_s, is taken into account via two continuous evolvable social traits. The first trait, denoted by ω_{ai}, determines how an individual i moves in response to a perceived approach by others, i.e., when the relative velocity between them is negative. A negative value of ω_{ai} will result in a focal individual moving away from approaching locusts. In the following we will refer to this response as an 'escape' behaviour, in analogy to the neurophysiologically characterized response to looming visual stimuli in locusts (Rind *et al.* 2008; Rogers *et al.* 2010). A positive value of ω_{ai} will have the opposite effect, i.e., movement towards insects that approach.

Box 1 Individual-based model of locust movement and local interactions

We consider self-propelled motion of individuals with a constant speed s_0 in two spatial dimensions. The equations of motion for the position vector $\mathbf{r}_i(t)$ of the focal individual i and its instantaneous direction of motion, given by the unit vector $\hat{\mathbf{v}}_i = \left(\cos\theta_i(t), \sin\theta_i(t)\right)^T$ read

$$\frac{d}{dt}\mathbf{r}_i = \mathbf{v}_i = s_0\hat{\mathbf{v}}_i, \qquad \frac{d}{dt}\theta_i = \frac{1}{s_0}\left(f_{Si,\theta} + \sigma_\theta\xi_{i,\theta}(t)\right), \tag{1}$$

where, $f_{Si,\theta} = \mathbf{f}_{Si,\theta} \cdot \hat{\mathbf{v}}_{i,\theta}$, with $\hat{\mathbf{v}}_{i,\theta} = \left(-\sin\theta_i(t), \cos\theta_i(t)\right)^T$, is the component of the total 'social force' $\mathbf{f}_{Si}$ perpendicular to the direction of motion, which induces turning of the individual due to interactions with others. The last term accounts for the randomness in the motion of individuals with $\sigma_\theta\xi_{i,\theta}(t)$ being an uncorrelated Gaussian random number with mean zero and variance σ_θ^2 determining the strength of angular fluctuations.

The total social force consists of three terms: $\mathbf{f}_{Si} = \mathbf{f}_{ai} + \mathbf{f}_{mi} + \mathbf{f}_{ri}$. The first two terms model the response to approaching ($\mathbf{f}_{ai}$) and moving-away individuals ($\mathbf{f}_{mi}$) within a finite sensory range l_s. The focal individual i distinguishes approach from moving away of individual j via the sign of the relative velocity $v_{ji} = \left(\mathbf{v}_j - \mathbf{v}_i\right) \cdot \hat{\mathbf{r}}_{ji}$. The first two response terms read

$$\mathbf{f}_{ai} = \frac{\omega_{ai}}{n_{ai}}\sum_{j \neq i}|v_{ji}|\hat{\mathbf{r}}_{ji} \quad \text{if} \quad v_{ji} < 0 \quad \text{and} \quad r_{ji} < l_s, \tag{2}$$

$$\mathbf{f}_{mi} = \frac{\omega_{mi}}{n_{mi}}\sum_{j \neq i}|v_{ji}|\hat{\mathbf{r}}_{ji} \quad \text{if} \quad v_{ji} > 0 \quad \text{and} \quad r_{ji} < l_s, \tag{3}$$

where ω_{ai}, ω_{mi} are evolvable response strengths which might be positive or negative, corresponding to attraction or repulsion. Both forces act along the unit vector $\hat{\mathbf{r}}_{ji} = \left(\mathbf{r}_j - \mathbf{r}_i\right)/|\mathbf{r}_j - \mathbf{r}_i|$ pointing from individual i towards individual j and are normalized by the corresponding number of interacting partners n_{ai}, n_{mi}. Furthermore, the response is assumed proportional to $|v_{ji}|$, leading to stronger response to faster approaching or moving-away individuals.

The third force term ($\mathbf{f}_{ri}$) is a short-range repulsion, modelling the tendency of individuals to maintain a minimum distance $l_b < l_s$ to others, independent of their relative velocities (see Appendix S1 for further model details, and Appendix S3 for discussion of a variable speed model).

Box 2 Evolutionary algorithm

The behavioural strategy given by the response strengths may evolve freely within a rectangular two-dimensional phenotype space $-\Omega \leq \omega_{ai}, \omega_{ri} \leq \Omega$ with $\Omega > 0$.

During the numerical integration of the individual-based model, the fitness $\mathcal{F}_i$ of individual i corresponding to phenotype $(\omega_{ai}, \omega_{mi})$ changes due to encounters with other individuals. It evolves according to

$$\frac{d}{dt}\mathcal{F}_i = \mathcal{G}_i(t) = \sum_{j \neq i} \begin{cases} (1 - \omega_b)C - \omega_b B & \text{if } r_{ji} < l_b \\ 0 & \text{else} \end{cases} \tag{4}$$

where $\mathcal{C}$ and $\mathcal{B}$ are cost and benefit functions which in general depend on the positions and velocities of the encountering individuals $\mathcal{C} = \mathcal{C}(\mathbf{r}_i, \mathbf{r}_j, \mathbf{v}_i, \mathbf{v}_j)$, $\mathcal{B} = \mathcal{B}(\mathbf{r}_i, \mathbf{r}_j, \mathbf{v}_i, \mathbf{v}_j)$ (see Appendix S1, S3, S6, S7 and S8 for different forms of cost-benefit functions). The term w_b is a measure of relative importance of benefits of nutrients obtained through cannibalizing others to the costs of being cannibalized by others. In general, this implies asymmetric pay-offs to interacting individuals. Please note that, according to Eq. 4, encounters between more than two individuals may take place at a given point in time.

The fitness $\mathcal{F}_i$ is reset to 0 after a finite transient time τ_{tr} to exclude influence of initial conditions and then integrated over a finite time

$$\tau_{\text{fit}} : \mathcal{F}_i = \int_{\tau_{tr}}^{\tau_{tr} + \tau_{\text{fit}}} dt' \mathcal{G}_i(t').$$

Finally, the fitness for each individual (phenotype) is averaged over different realizations of the system.

To determine the next generation, a bout of selection according to the individual fitness is performed, where individuals (phenotypes) with higher relative fitness have a higher probability to be selected. The phenotypes of offspring undergo a mutation, which is modelled by an additive Gaussian noise with zero mean and a small variance (σ_μ^2).

After a sufficient number of generations (typically 100–1000) the evolved traits approach a stationary distribution. For unimodal trait distributions, we define the ESS as the average phenotype $(\bar{\omega}_{ai}, \bar{\omega}_{mi})$. Stationary trait distributions with multiple peaks can be interpreted as a coexistence of different strategies (mixed strategies; Maynard–Smith 1984), corresponding to the different maxima of the evolved distribution. In the cases studied here only unimodal stationary phenotype distributions were obtained.

Due to the possible extremely high fitness costs of aggression (e.g. injury, death), a special emphasis is put on costs-dominated pay-off functions, whereby different types of pay-off functions have been studied. Our analysis shows that the general results on the ESS are insensitive to the detailed dependence of the pay-offs (in particular costs) on the encounter geometry. Furthermore, we have performed additional simulations with heterogeneous but non-inheritable pay-offs (different costs/benefits for different individuals), accounting for individual variations in tendency to cannibalise, or to be cannibalised by, others. The corresponding results confirm our general findings for constant pay-offs, even for large pay-off variations (see Appendix S1, S3, S6, S7 and S8 for details).

The second evolvable trait captures individuals' response to those moving away, denoted by ω_{mi}. Here, a positive value of ω_{mi} will make them move towards those moving away. Again, relating this social behaviour to the visual loom response, we will refer to the selective attraction to moving-away individuals ($\omega_{mi} > 0$) as 'pursuit' behaviour. This is further supported by the structural similarity of the simulated collective dynamics of identical individuals with $\omega_{mi} > 0$ to the corresponding social response in a model of collective motion introduced by Romanczuk *et al.* 2009. In this previous model, where individuals can have variable speeds, it has been shown that pursuit behaviour will lead to reduced distance between individuals. A negative value of this trait (ω_{mi}) will lead individuals to turn away from those moving away resulting in increased distance between individuals and is therefore equivalent to a repulsive behaviour. Our simulations show that these features continue to hold even when speeds of both individuals are equal and constant. Therefore, we employ a simpler constant speed version of the model which allows us to perform a more comprehensive analysis of evolutionary dynamics. We have verified that a more complex variable-speed model does not affect the qualitative nature of the key results of our article (Appendix S3 and S4).

For both ω_{ai} and ω_{mi}, the larger the magnitude of the trait, the faster is the rate at which individuals turn, and thus move toward

their desired direction (see Box 1, and Appendix S1, for details of the model implementation).

These local interaction rules capture a deliberately wide range of both individual and group behaviours, including a solitary correlated random walk (when $\omega_{ai} \approx 0$ and $\omega_{mi} \approx 0$), avoidance behaviour (ω_{ai} and ω_{mi}), polarized swarms (ω_{ai} and $\omega_{mi} \geq 0$), head-to-head attraction ($\omega_{ai} > 0$ and ω_{mi}) and the formation of unpolarized aggregations ($\omega_{ai} > 0$ and $\omega_{mi} > 0$; see Appendix S2 for representative spatial patterns).

Locusts that do not detect and/or respond to the approach of others, in particular to approach from behind, are vulnerable to cannibalism (Bazazi *et al.* 2008; Hansen *et al.* 2011). We incorporated this empirical observation by assigning costs to individuals that are approached by others within a small radius l_b (with l_b), comparable to their body size. Individuals who cannibalize others may also be able to compensate for nutritional deficiencies in a resource-limited environment (Hansen *et al.* 2011). This is incorporated by allowing individuals to accumulate benefits when they are within a small distance l_b of others' abdomens i.e., able to feed upon others' rear ends (see Appendix S3 and S7 for alternative implementations of costs and benefits). It is the behaviour of individuals, in the context of the strategies employed by others in the population, which results in the relative fitness of their

strategy (based on the balance of costs and benefits accrued by them, and by others). Individuals reproduce with a probability that is proportional to their relative fitness and pass on their social traits (ω_{ai} and ω_{mi}) to offspring with a small rate of mutation.

We evolve populations in this way until an evolutionary stable distribution of these behavioural traits is reached (see Box 2 and Appendix S1; also see Maynard-Smith 1982; Guttal & Couzin 2010). We note that our focus is not the evolution of cannibalism, which is widespread in a diverse range of taxa from protozoa to mammals (Elgar & Crespi 1982; Polis & Holt 1992), but to examine how the threat of cannibalism that already exist in insects can influence evolutionary stable strategy (ESS) of local interactions. Having obtained such ESS at a range of fixed population densities, we then determine whether behavioural plasticity (polyphenism) can evolve when individuals are exposed to fluctuating population densities. We also investigate extensions of the model, such as inclusion of variable speed, modification of local interactions and how cannibalistic costs and benefits are accrued, individual variations in costs and benefits of cannibalism, and find that these do not affect the qualitative nature of our results (see Appendix S3, S4, S5 and S8).

RESULTS

Risk of cannibalism can select for density-dependent behavioural strategies

We begin by exploring how (any) costs of cannibalism affect the evolution of individual behaviours as a function of insect density. For a wide range of cost functions, and their parameter values, we find that evolved interaction strategies exhibit a sharp non-linear transition as a function of conspecific density (Fig. 1a; Appendix S3). At low population densities, individuals evolve 'avoidance behaviour' (ω_{ai}, ω_{mi}; both large in magnitude) whereby they avoid all neighbours, regardless of whether they are approaching or moving away. Above a critical density, denoted by ρ_c, individuals evolve an 'escape-pursuit behaviour' (ω_{ai}, $\omega_{mi} > 0$; both large in magnitude), which involves selective repulsion and attraction with other individuals. Specifically, they move away from those moving towards them (escape) and are attracted towards those moving away from them (pursuit).

In the low-density avoidance behaviour, individuals typically spread out in space and do not exhibit coordinated motion (1c–d). Beyond ρ_c, however, the evolved escape-pursuit behaviours result in individuals aligning locally their direction of motion, resulting in the
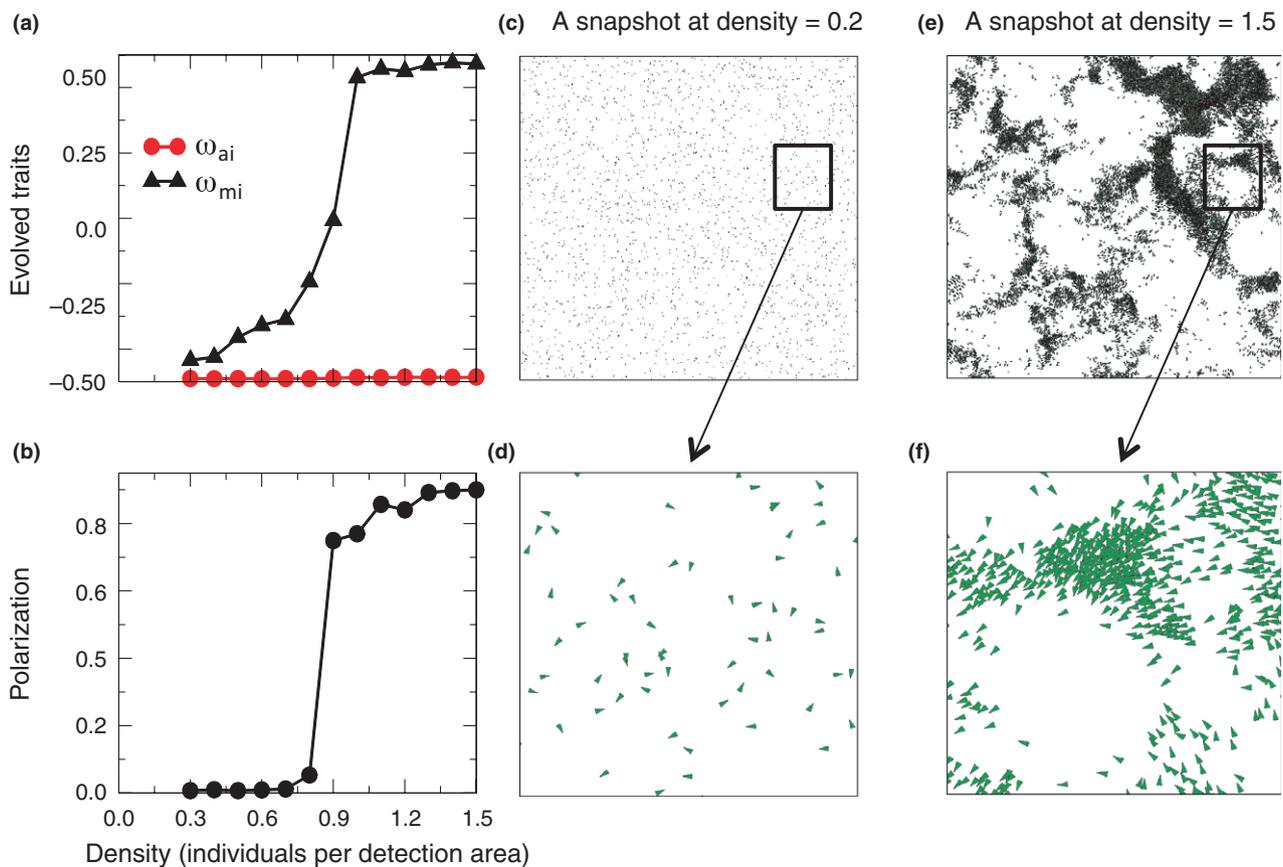
Figure 1 The evolution of behavioural polyphenism and swarm formation (a) The evolutionary stable strategy (ESS) in 'response to those approaching' (ω_{ai}), and 'response to those moving away' (ω_{mi}), as a function of density (ρ). (b) Polarisation, a measure of coherence in motion of the evolved population, as a function of density. (c and e) Spatial patterns of solitarious ($\rho = 0.2$) and gregarious ($\rho = 1.5$) behaviours, respectively. (d and f) Close up views of boxed regions from (c) and (e). Parameters: size of population $N = 16384$, degree of nutritional benefits $w_b = 0$. For other parameter values, details of methods and generality, see Appendix S1–S3.
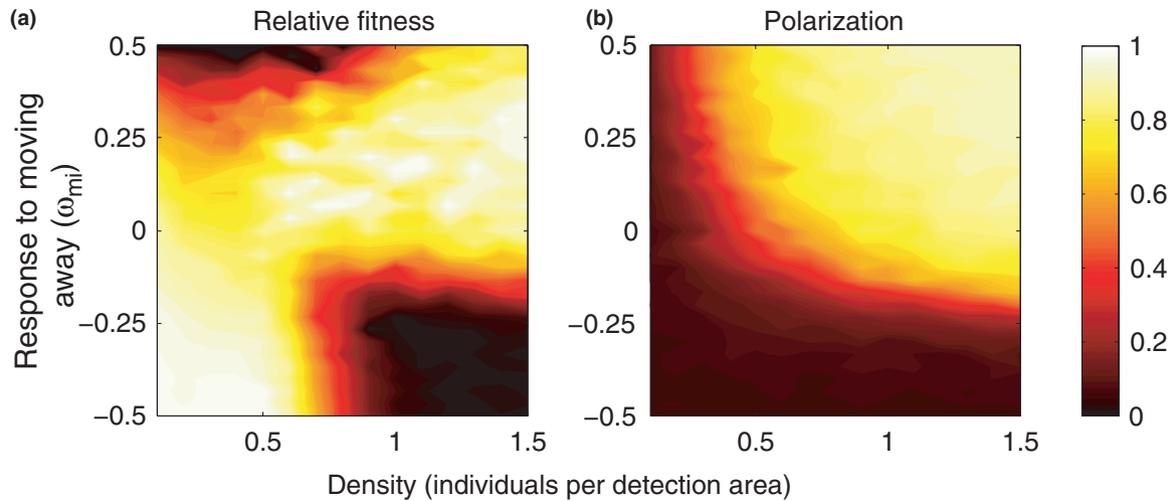
Figure 2 Density-dependent polyphenism as an adaptive strategy to reduce costs of cannibalism. (a) Relative fitness, and (b) Polarisation, of unimodal phenotypic populations given by a narrow Gaussian distribution around mean behavioural traits as a function of density (ρ) and mean response to moving away ($\omega_{mi}s$). Here, we set $\omega_{ai} = -0.5$. $N = 256$ and the width of the Gaussian phenotype distribution $\sigma_\omega^2 = 0.02$. See Appendix S4 for details of computing relative fitness landscapes.

formation of large mobile bands (Fig. 1e–f), as exhibited by real locusts (Buhl *et al.* 2006; Buhl *et al.* 2011). Consequently, polarisation, a measure of coordination in movement of individuals within and across groups (Vicsek *et al.* 1995; Couzin *et al.* 2002), of the evolved populations display an abrupt density-dependent transition resembling the sudden onset of locust swarms in the real world (Simpson & Sword 2008).

To determine the adaptive significance of a density-dependent shift in behavioural strategy, we compute the risks of cannibalism as a function of density and the two social traits, ω_{ai} and ω_{mi} (see Appendix S4 for related methods). We find that, at low densities, the evolved avoidance behaviour (ω_{ai} and ω_{mi}; i.e., the tendency to turn away from any nearby individual) reduces the number of encounters, and thus the risk of cannibalism (Fig. 2a). Therefore, an invasion by an escape-pursuit strategy (ω_{ai} and $\omega_{mi} > 0$) is not evolutionarily stable. However, encounters become unavoidable beyond a critical density (ρ_c). At such densities, avoidance-behaviour individuals continue to move away from all nearby individuals. However, an individual with an escape-pursuit strategy in a population of avoidance-phase individuals moves in the direction of those moving away. This kind of movement strategy exploits the areas left vacant by other individuals, thus reducing its own frequency of contacts with others and thereby the risks of cannibalism. As a result the escape-pursuit strategy is selected for and eventually it dominates the population (Fig. 2a). It is this evolved behaviour that results in the formation of mobile and coherent groups (Fig. 2b).

In summary, the low-density evolved strategy is to avoid all nearby individuals. At high densities, the evolved escape-pursuit behaviour, corresponding to selective repulsion and attraction, mediates large-scale coordinated movement (Bazazi *et al.* 2008). This density-dependent strategy reduces collisions, and thus minimizes the costs of cannibalism. These evolved individual behaviours closely resemble the behaviour of real locusts; the avoidance behaviour is analogous to the solitarious phase whereas the escape-pursuit strategy relates to the gregarious phase. Put simply, our model suggests that both the solitarious and gregarious phase behaviours expressed by locusts can be an outcome of selection on the insects to reduce costs of cannibalism by minimising the frequency of contact with each other.

The evolution of density-dependent behavioural polyphenism

Thus far, we have obtained the ESS in local interactions among locusts for fixed global population densities; consequently, we assumed individuals use the same strategy at all times within a generation. In reality, however, the size of insect populations can be highly dynamic, and the locusts themselves express behavioural plasticity mediated by local population density (Simpson & Sword 2009). We, therefore, also investigate whether cannibalism can select for density-dependent behavioural polyphenism (or plasticity) when faced with density-fluctuating environments within the lifetime of individuals. We do so by devising a version of the above model that allows individuals to sense and respond to local population density. Here, individuals may adopt behaviourally fixed strategies, such as being solitarious or gregarious throughout their lifetime, or behaviourally plastic strategies such as density-dependent transition from solitarious to gregarious, or gregarious to solitarious phases. We incorporate variable environments by assuming that individuals spend a fraction, denoted by f_l, of their lifetime in relatively low global population densities with the rest being in relatively high densities (see Appendix S5 for details of model implementation).

For a wide range of values of f_l, and choices of low and high densities, we find that individuals evolve a behaviourally plastic strategy, i.e., when at a local density below a threshold value, and thus encountering relatively few individuals, they adopt avoidance behaviour. If individuals experience higher local densities, however, they switch to a gregarious strategy whereby they are attracted to those moving away, thereby forming groups and mobile bands. Thus, we demonstrate that selection to reduce the risk of cannibalism can also account for the evolution of density-dependent behavioural polyphenism (or plasticity) that corresponds to locusts' behavioural phase-change in response to changing local densities.

Memory effects in gregarisation

Experimental studies of *Schistocerca gregaria* demonstrate that behavioural gregarisation within an individual's lifetime occurs more rapidly,
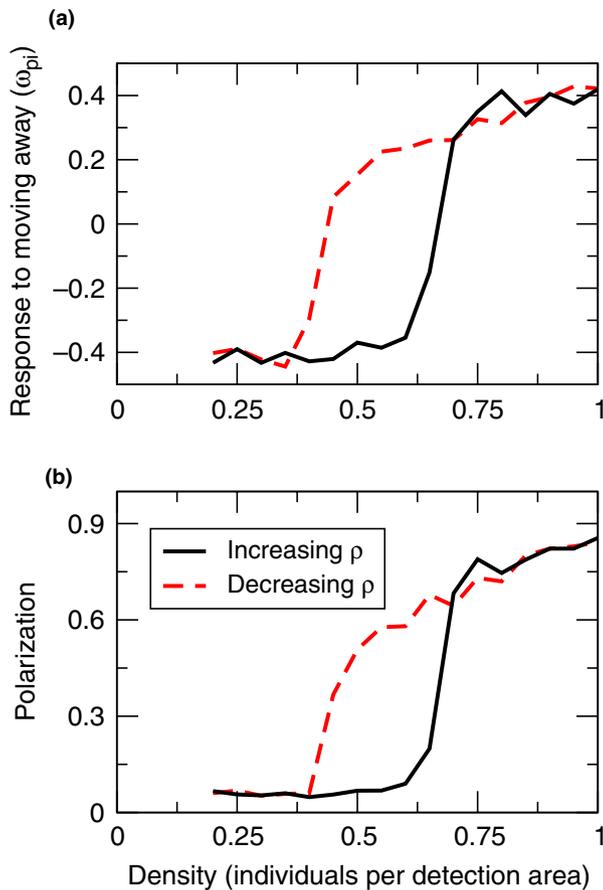
Figure 3 Memory effects in gregarisation. (a) Evolved ω_{mi} as a function of density. The solid black line represents response to increasing ρ, whereas broken red line is the response to declining ρ. The evolved ω_{ai}, as in Fig 1a, is independent of density and does not show hysteresis. (b) Polarisation of the evolved population. Here, $N = 256$ and $w_b = 0$.

e.g., within 2 h (Anstey *et al.* 2009; Pener & Simpson 2009), in comparison to the reverse process of behavioural solitarisation, which may take several developmental stages or even generations (via a parentally mediated epigenetic mechanism) to complete (Ellis 1963a, , b; Miller *et al.* 2008; Tanaka & Maeno 2010).

Motivated by these observations, we investigate memory effects in the evolved behavioural strategies. To do so, we revert to the original model (see Materials and Methods, and Appendix S1, for details) and determine an evolutionary stable state for a given population. We then make small changes to the values for insect density (either increasing, or decreasing), and employ the evolved state from the previous values of density as the input for further adaptation of traits (ω_{ai} and ω_{mi}); this mimics the empirical observation that the phase state of a parent can be transferred to an offspring. Note that this method determines a locally stable ESS, which is in contrast to our results shown in Fig. 1 where we focused on obtaining a robust ESS among many possible evolved states (see Appendix S1 for details; also see Ellis 1963b).

As before, we find a non-linear transition from solitarious to gregarious behaviour as a function of increasing population density (3a, b). However, when we restore the population density to lower values, gregarisation does not decline at the same value at which it first appeared. It continues to persist until lower densities, i.e., it exhibits
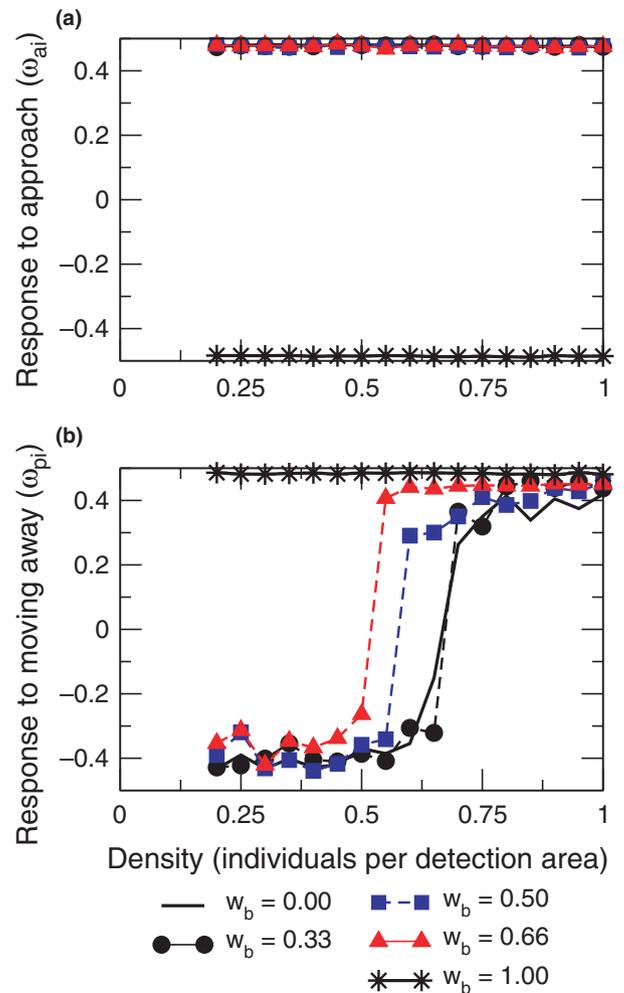
Figure 4 Role of nutritional benefits of cannibalism. Evolved strategies (a) ω_{ai}, and (b) ω_{mi} as a function of density for different degrees of nutritional benefits w_b. See Appendix S6–S8 for generality and relative fitness landscapes.

memory, or hysteresis (Fig. 3a). As a consequence, once a band of locusts are on the march, it may require a much greater reduction in population density to return insects to the solitarious state (Fig. 3b).

Limited resources and nutritional benefits of cannibalism

So far we have shown that the costs of cannibalism alone can drive the evolution of phase-change behaviour. We note that cannibalism is a common response to nutritional deficiency in animals, especially when environments are limited in resources (Elgar & Crespi 1982; Richardson *et al.* 2010) and it may lead to either nutritional imbalance or benefits. For example, when insects that are carbohydrate deficient consume protein-rich conspecifics, they will be even more nutritionally imbalanced resulting in potential fitness costs (Simpson *et al.* 2004). This is equivalent to increasing the cost of cannibalism, and thus the density-dependent gregarisation remains the ESS. On the other hand, cannibalism can provide critical nutritional benefits when insects are locally deprived of protein and salt, as in Mormon crickets and desert locusts (Simpson *et al.* 2006; Bazazi *et al.* 2008; Bazazi *et al.* 2011). Therefore, we consider the role of nutritional

benefits that cannibalism may provide. Our simulations show that even if the costs of cannibalism are relatively small, but outweigh the nutritional benefits, the density-dependent phase-change strategy continues to be evolutionarily stable (Fig. 4a,b; also see Appendix S6 and S7). When the benefits of nutrition exceed the costs of cannibalism, however, the evolved behaviour for all densities is that of 'pure attraction' ($\omega_{ai} > 0$ and $\omega_{mi} > 0$; i.e., individuals move towards those who approach, or move away from, the focal individual). This results in formation of aggregates which typically remain unpolarised and are not mobile.

DISCUSSION

We propose, and provide evidence for, the hypothesis that cannibalism could have been a key factor in the evolution of behavioural phase polyphenism in locusts. We demonstrate that at low insect densities, the evolutionarily stable strategy is to avoid all nearby individuals leading to spatial spread across the landscape. As local density increases above a critical value (ρ_c), however, the favoured strategy is for individuals to move away from those who approach while being attracted to those moving away. This results in the formation of dense mobile aggregates. Counter-intuitively, our results suggest that a low-density avoidance behaviour followed by a transition to a gregarious behaviour beyond the critical density are both adaptations to reduce risks of cannibalism. This is favored as a plastic strategy across a wide range of fluctuating density regimes.

Results of our model are broadly consistent with the behaviour of locusts at the level of both individuals and collectives. That solitarious locusts avoid each other, and that gregarious locusts are attracted towards other individuals has been known for a long time (Ellis 1963a; Roessingh & Simpson 1994). Recent experiments provide evidence that gregarious individuals tend to move away from those who approach them to avoid risks of cannibalism, resulting in formation of migratory bands of locusts (Bazazi *et al.* 2008). Our cannibalism hypothesis is also shown to account for the observed hysteresis, or memory, effect evident in individual desert locust phase-change behaviour (Ellis 1963a, , b; Miller *et al.* 2008; Tanaka & Maeno 2010).

We test the robustness of our results by considering other realistic biological scenarios, such as role of nutritional benefits of cannibalism, more complex cost–benefit structures, and the movement of individuals at variable speeds. These modifications did not affect the qualitative nature of our results as long as the benefits of cannibalism are less than the costs. When benefits did exceed costs, however, we do not find conditions that favour the evolution of density-dependent behavioural polyphenism. Instead, for all densities, we find a 'pathological' strategy of moving towards those who are approaching, as well as those running away, resulting in repeated head-to-head interactions and grouping unlike that seen in nature. Thus, our work provides evidence that the cost of cannibalism may be a significant ecological factor influencing the evolution of behavioural phase-change.

Our model predicts that behaviour of locusts will change from gregarious to solitarious at much lower densities compared to that at which the solitarious individuals become gregarious. At a qualitative level, this is consistent with the empirical observation that memory effects exist in the transition between the two phases (Ellis 1963a; Pener & Simpson 2009). This suggests that to control locust outbreaks by reducing the number of mass-migrating gregarious-phase individuals, insect population densities must be reduced to substantially lower levels than those at which gregarisation occurs. This further emphasizes the need for preventive measures that take into account the fact that gregarisation may occur in local populations well before widespread outbreaks and swarm formation (Sword *et al.* 2010).

Although individuals in our model interact locally, for tractability purposes we did not include other realistic features such as roles of individual nutritional state (e.g., that protein-deprived individuals are more likely to cannibalize) and heterogeneity within populations and in the habitat structure (e.g., arising from patchiness in vegetation). An explicit incorporation of these features is unlikely to alter the qualitative nature of our results. As an example, we considered the role of individual variations in locusts' ability to cannibalise and/or be cannibalised by others. Such variability may arise due to inherent differences among individuals, differences in their nutritional states and/or differences in environmental conditions experienced by them. We found that such variations do not affect the qualitative nature of our results (Appendix S8). With regards to spatial heterogeneity, it has been shown both empirically and computationally that even in sparsely spread populations, locally high concentrations of resource patches can promote crowding of locusts, thus creating conditions favorable for gregarisation (Roffey & Popov 1968; Collett *et al.* 1998; Simpson & Sword 2009). Furthermore, protein-deprived insects are likely to be attracted towards both other individuals and to patchy resources, which further facilitates crowding. Within our model framework, these can be thought of as effectively increasing the mean population density. Therefore, incorporating landscape features will alter the critical mean population density ρ_c at which gregarisation evolves (but does not affect the principles elucidated). More specifically, we predict that the higher the clumpiness of resource distribution, the smaller will be the critical global population density ρ_c at which behavioural phase-change occurs.

Several other factors influence costs and benefits accrued by insects when they are swarming. For example, locusts and other insects are likely to be most vulnerable to cannibalism after moulting (Pener & Simpson 2009); therefore, swarming can exacerbate the risk of cannibalism in moulting individuals. It has been recorded during an earlier field study of our group (Simpson *et al.* 2006) that insects enter a period of quiescence prior to moulting that functions to separate individuals from the band. However, studies have shown evidence for synchronization in moulting, mediated through a combination of pheromones that act as developmental accelerators and retarders (Hassanali *et al.* 2005; Pener & Simpson 2009), which may further reduce risks of cannibalism. In addition, swarming may provide both increased opportunities and competition for mating. Although we do not consider these features explicitly in our model, our approach of considering costs of cannibalism and benefits of nutrition as a function of contacts among individuals could allow us to include payoffs of other biological features by modifying to the cost–benefit parameter values.

Prior considerations of the evolution of locust behavioural-phase polyphenism have relied heavily on predation as the principal selective factor (Sword 1999; Sword *et al.* 2000; Sword *et al.* 2005; Reynolds *et al.* 2009). In contrast, we have shown that the expression of behavioural phase-change mediated by changes in local population density can evolve exclusively due to intraspecific interactions. We employed a spatially explicit computational framework where behaviours can undergo evolutionary change and provide evidence for a

new hypothesis that the threat of cannibalism, i.e., conspecific predation, may account for the evolution of density-dependent behavioural polyphenism. We do not argue that cannibalism and predation are mutually exclusive, but rather that cannibalism provides a generally applicable, intrinsic, and parsimonious mechanism that should similarly favor the evolution of behavioural polyphenism across species. The additional anti-predator benefits of aggregation at high density undoubtedly occur (Sword *et al.* 2000; Sword *et al.* 2005), but such benefits are contingent upon a host of other ecological factors that are likely to be both temporally and spatially variable including the presence or absence of predators and specific host plants, predator movement patterns and abundance, and the availability of alternative prey items to name just a few.

Our study assumed nutrient-deficient conditions where the risks as well as benefits of cannibalism contribute significantly to an individual's fitness. When alternative resources are available to supplement individual's nutrient deficiencies, locusts may remain herbivores and thus not indulge in cannibalism. It is also worth noting that heterogeneous environmental conditions are often considered to play an important role in the evolution of phenotypic plasticity in various organisms (West-Eberhard 2003). It would be interesting to extend our computational model to investigate relative roles of cannibalism with other such plausible ecological factors, as mentioned above, in shaping the behavioural polyphenism in locusts. Furthermore, it would be interesting to explore the role of various ecological factors, including that of cannibalism, in the evolution of proximate mechanisms such as mechanosensory receptors, and phase-specific genes that induce phase-change in locusts (Anstey *et al.* 2009; Miller *et al.* 2008; Tanaka & Maeno 2010; Guo *et al.* 2011).

In summary, we provide evidence that the risk of cannibalism could have been a key ecological factor underlying the evolution of density-dependent polyphenism in locusts. We demonstrate that phase-change behaviours minimize the costs of cannibalism. In conjunction with recent empirical works demonstrating the role of cannibalism and nutrition in the march of locust migratory bands (Sword *et al.* 2005; Bazazi *et al.* 2008; Romanczuk *et al.* 2009; Simpson & Sword 2009; Bazazi *et al.* 2011; Hansen *et al.* 2011), this work provides insights into both proximate and ultimate factors that shape individual locust behaviour, local interactions between insects and how these local behaviours scale to landscape-level dynamics of locust migratory bands.

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