

Predator Percolation, Insect Outbreaks, and Phase Polyphenism

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Summary

Apart from being notorious outbreak pests, locusts are of interest because of their expression of density-dependent “phase polyphenism.” In this remarkable form of phenotypic plasticity, changes in local population density generate distinct solitary and gregarious phases that differ in behavior, physiology, and appearance [1, 2]. A hallmark of phase polyphenism in outbreak species is the transition from solitary living to group formation and subsequent mass movement in migratory bands or swarms, yet there has been no convincing general explanation for the evolution of these density-dependent switches in spatial distribution. Using a model from “percolation theory” [3], we show that it would be highly detrimental for locust individuals to continue indefinitely in a dispersed spatial distribution as their population densities increase. Switching to an extremely clumped distribution is advantageous because it disrupts the connectivity of predators’ food-patch networks. Thus, selection pressure from predators has probably been an important factor underlying the initial evolution of conditional switches between “dispersed” and strongly aggregative behavior, which will also affect outbreak dynamics. Although group formation is the best alternative for high-density populations, it brings its own set of severe problems, resulting in secondary selection for many of the traits seen in gregarious-phase individuals [4–6].

Results

“Percolation” Model Development

Foraging theory predicts that mobile predators [7] will sacrifice feeding effort within a food patch (e.g., a clump of desert plants harboring locusts) if the reward/risk ratio falls below

a certain level. For lizards, small mammals, and some invertebrate predators, a patch may represent a single clump of plants, whereas to a highly mobile predator such as a bird, a patch can comprise several neighboring clumps. In either case, a predator can be expected to cease foraging and abandon a clump once the density of locusts falls below the “giving-up density” [8]. If a single locust is a worthwhile food item for a predator, and if locusts are relatively obvious to the predator, then all of the locusts might be caught, and in this case the giving-up density would be zero. More generally, however, some locusts are likely to remain within the patch, either because they have remained undetected by the predator or because the predator has become satiated. Locust numbers within that clump may eventually recover, but until that time, the clump is effectively depleted. The predator may then explore several neighboring food patches and subsequently commence foraging within one of these if it is found to contain locusts in sufficiently high abundance—otherwise, it will cease foraging in that locality, perhaps flying to a new location within the landscape to begin foraging there. From the perspective of predators, the landscape can therefore be regarded as a random network of food patches. A food patch is connected with probability p to nearest neighbors if it contains locusts in sufficiently high numbers to sustain foraging in that locality; otherwise, it is disconnected (Figure 1). A predator can move directly to neighboring patches if they are within visual range; otherwise, they can be located with an area-restricted search.

A predator can forage indefinitely only if it happens to find itself on a connected pathway of food patches that spans the landscape. The probability of the predator being on such an indefinitely long path is equal to the probability of not being on a finitely long path:

$$P_{\infty}(p) = 1 - P_{\text{finite}}(p). \quad (1)$$

The probability P_{finite} can be calculated as follows. For the patch currently containing the predator to belong to a finite pathway, it must either contain locusts in low abundance (i.e., be disconnected from neighboring patches) with probability $1 - p$, or it must contain locusts in high abundance with probability p and then be connected to a finitely long pathway by one of the n neighboring patches. Mathematically, this can be expressed as

$$P_{\text{finite}}(p) = (1 - p) + pQ^n, \quad (2)$$

where Q is the probability that a neighboring patch belongs to a finite pathway. One of these n neighboring patches is itself connected to $n - 1$ neighbors, and so

$$Q(p) = (1 - p) + pQ^{n-1} \quad (3)$$

(see Figure 1). Underlying this is the assumption that the predator does not loop back to previously visited patches. This is reasonable given that predators are not expected to return to previously visited depleted patches but instead tend to move unidirectionally across a landscape (Figure 1). Even if a predator, having given up on local area-restricted foraging,

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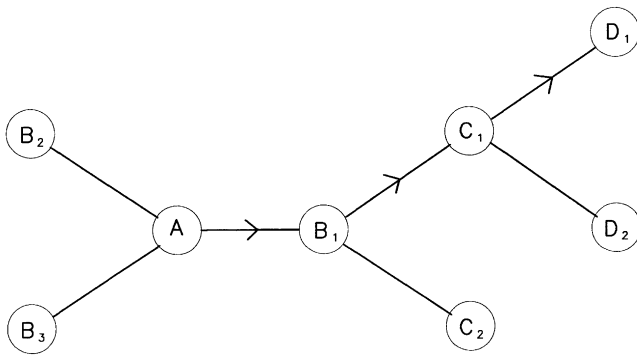


Figure 1. An Example of the Movement Pattern of a Predator through a Landscape Containing Randomly Distributed Food Patches

In this case, the food patches are clumps of desert vegetation that may contain one or many locusts. A predator that first began to forage in patch A will cease foraging in that patch when the locust density falls below the giving-up density. The predator will then forage in one (say B₁) of the three neighboring patches (B₁, B₂, and B₃), assuming that patch contains locusts in sufficiently high abundance; otherwise, the foraging activity ends. After leaving B₁, the predator will not return to patch A because it is known to be depleted, but the predator instead will forage in one of the two neighboring patches (C₁ or C₂), assuming one of those patches (say C₁) contains locusts in high abundance; otherwise, the foraging activity ends. The cycle repeats indefinitely if the predator is located on a connected pathway of high-yielding food patches that spans the landscape.

chooses a random angle for ranging, the chances are low that it will return to an earlier patch. The presence of loops complicates the calculation considerably, but it does not change key predictions.

For the simplest food-patch network, a linear chain corresponding to $n=2$, Equation 3 has the solution $Q=1$ when $p \neq 1$. Substitution of this solution, $Q=1$, into Equation 2 gives $P_{\text{finite}}(p)=1$, and as a consequence, there is no possibility of the predator foraging indefinitely. Only when locusts are in

high abundance in every patch can predation be sustained indefinitely. This is not true of more complex food-patch networks. Consider, for example, the $n=3$ hexagonal or honeycomb network shown in Figure 1. In this case, Equation 3 has two roots: $Q=1$ valid for $p < 1/2$ and $Q=(1-p)/p$ valid for $p > 1/2$. The latter solution, together with Equations 1 and 2, reveals that an indefinitely long pathway of connected food patches exists and that the probability of a food patch being on this pathway is $P_{\infty} = p + (1-p)^3/p^2$. The probability $p=1/2$ is said to be the “threshold of percolation.” Below the percolation threshold, the landscape is composed solely of isolated clusters of connected food patches. Above the threshold, the probability of a predator being on the landscape-spanning cluster of patches grows very quickly as the density of locusts increases (see Figure 2 and Figure 3, which show the relationships between population density, cluster size, and per capita mortality rate). These properties of networks above and below the threshold of percolation are not specific to the hexagonal network of patches but are, in fact, applicable to almost any network, including networks in which there is spatial correlation in the density of patches [3, 9]. However, in most cases the percolation threshold can only be found numerically.

As a consequence, a ground-foraging predator can only move continually across a landscape, consuming locusts as it goes, if locusts occur at sufficiently high density and once the predator is on the landscape-spanning pathway of connected food patches. If the predator is not initially on this pathway, then it will, on average, find itself on the pathway after encountering $1/P_{\infty}$ dead ends and subsequently relocating (and perhaps in the case of the bird predator, flying some distance) so as to explore a new part of the landscape. Below the critical density, however, there is a sufficient probability that the predator will locate too few locusts to sustain itself even after making several flights. In this picture, predation “flips” rather than changes gradually with increasing locust density from being unsustainable to being sustainable. The situation does not

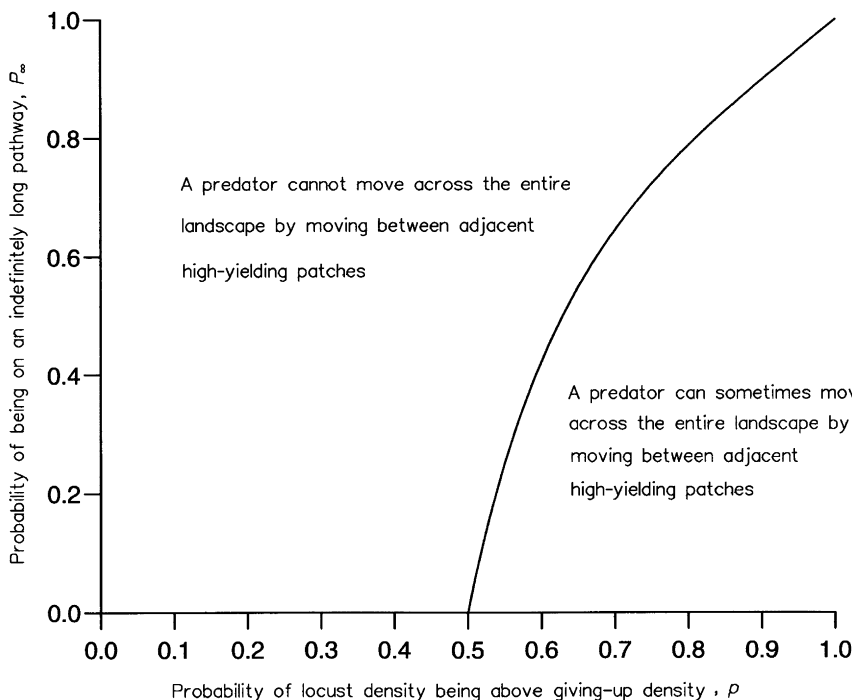


Figure 2. The Likelihood of Sustained Predation
The probability, P_{∞} , that a predator arriving at random within a landscape finds itself on an indefinitely long pathway formed from adjacent high-yielding patches, each with densities of locusts above the giving-up density. A predator can only move across the entire landscape when the probability, p , that the density of locusts within any given patch is above the giving-up density exceeds the threshold of percolation ($p=0.5$). Therefore, the per capita survival of locusts can be enhanced by those individuals that switch to aggregative behavior and thereby reduce p to a value below the threshold for percolation.

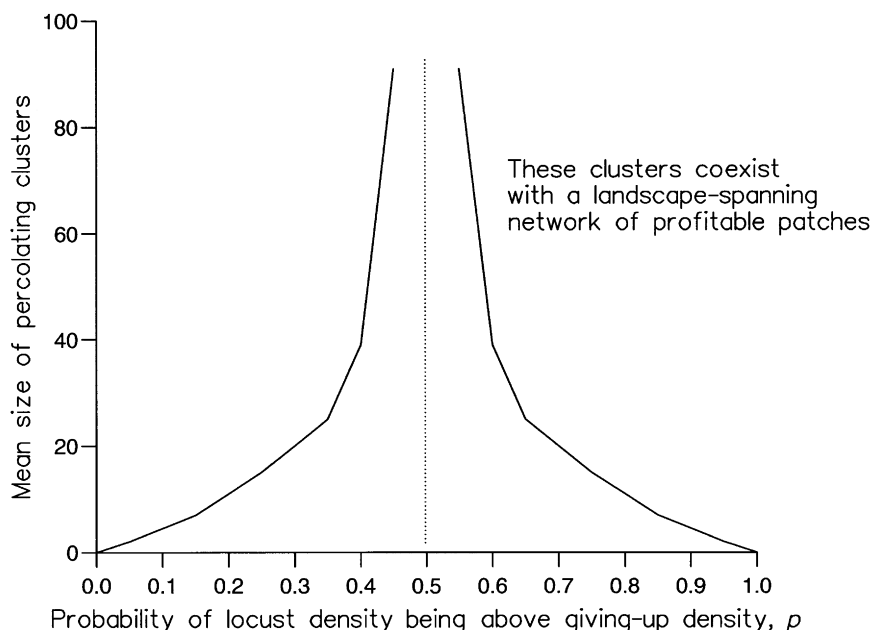


Figure 3. Predicted Mean Size of Percolating Clusters of Prey in the Absence of Aggregation as Total Prey Population Size Increases

Predators can move across these percolating clusters, which consist of networks of adjacent “profitable” high-yielding patches. The predicted mean size of the clusters approaches, but is strictly less than, the landscape size as p approaches the percolation threshold ($p = 0.5$) because of the emergence of interconnected network patches that span the landscape. As p increases above the percolation threshold, the mean percolating cluster size necessarily decreases because the clusters coexist with the increasingly large network of patches that span the entire landscape. Prey aggregation into discrete patches as population density increases keeps p below the percolation threshold and thus prevents predators from foraging indefinitely on a landscape-spanning network of profitable prey patches.

change if there are multiple predators that can be attracted to a food patch by the sight of their conspecifics (or another predator species) actively feeding. After exploiting the patch, a group of predators will either soon find themselves on a landscape-spanning pathway of connected food patches, or they never will.

From the perspective of the locusts, it is therefore advantageous when under pressure of predation to flip over from a cryptic and dispersed solitary state to tight cohesive groups when numbers become sufficiently high, for instance, after (weather-driven) explosive growth in the local locust population. This is because group formation can reduce the number of connections between patches to a value below the threshold allowing for continual predation (in the language of percolation theory, the locusts act collectively to keep the connectivity of the food patches, p , below the threshold of percolation, P_c). This response, coupled with the mobility of locusts, would lead to the merging of groups and the formation of large bands or swarms. The intermediate state (i.e., high densities of dispersed solitaires) would be highly disadvantageous because small groups will be more apparent to predators and within the satiation threshold. This condition, in general, is not observed. Aggregation is neither observed nor expected when locusts are in low density because locusts can then distribute themselves evenly, such that all plant patches have a prey density below the predator’s giving-up threshold. The locusts are then “unprofitable” for the predator to harvest.

The derivation presented here is a classic example of “percolation on a Bethe network” [3], recast in the language of predation. Importantly, key predictions do not depend sensitively on the details of the underlying model of predation.

Discussion

Percolation theory provides a novel and general approach to the antipredator benefits of gregariousness, an approach that, as far as we know, has not been considered in reviews of group living [e.g., 10–12]. It illustrates the conditions

favoring the evolution of gregariousness at a very early stage, perhaps similar to that seen in grasshoppers that show some density-related tendency to aggregate, and occasionally form small marching bands of nymphs and loose swarmlets of adults, but do not express the extreme phase transformation seen in locusts [13]. Having transitioned from solitary living to grouping behavior, the gregarious individual will then have some additional advantages, such as selfish concealment in the group [14, 15]. However, as the level of gregariousness escalates, which is often the case in outbreaking species, individuals in huge, highly visible and “apparent” bands or swarms would then be subject to a whole set of new selection pressures, e.g., having to deal with those predators that happen to be in the vicinity of, and able to attack, the band or swarm. Characteristic gregarious-phase features, such as aposematic coloring in the desert locust, *Schistocerca gregaria* [4, 5], the flurry of movements that lead to predator deterrence or confusion [16], and speeded-up development of the gregarious phase [17], can thus be viewed as a consequence of group formation, rather than the reason the gregariousness evolved in first place. This may also apply to changes in the selection of toxic food plants and acquisition of enhanced immune responses [18–20]. The former, in which protection from predators is mediated by toxic gut contents [5], is important when bridging the gap between populations of highly dispersed cryptic individuals and the formation of conspicuous aggregations. There is increasing evidence that living in large bands imposes considerable costs, but it nonetheless represents the best of a bad situation. The case of the Mormon cricket (*Anabrus simplex*) is instructive—isolated individuals suffered high levels of predation [6], so the crickets were better off living in the large migratory bands despite the real drawbacks of increased intraspecific competition for food and increased risk of cannibalism [21].

The probability of reaching high local density and thus becoming gregarious is itself a function of habitat patchiness in locusts [22–26], as well as other organisms [11]. Thus, the initial congregation that precedes the switch to active aggregation and other phase changes in locusts is driven by the

underlying patchy distribution of resources, such as basking, roosting, or oviposition sites, type of host plant, and even nutritional variation among plants. Other mechanisms at different scales can also cause initial congregation; for example, weather systems can concentrate flying locusts [27]. However caused, this initial patchiness together with the potential for explosive population growth are crucial ingredients in our model. With respect to the explosive population outbreaks exemplified by locusts, percolation effects are predicted to further contribute to the process. Under conditions favorable for population growth, the lower per capita mortality rate experienced by the gregarious phase at high densities (Figure 3) will result in a greater intrinsic rate of population increase, thereby contributing to the ongoing outbreak.

Hence, the conditions that might serve to break down connectivity for predators are the same as those that initially encourage local prey congregation. One problem for the locusts in being crowded in restricted habitat patches is that they will locally deplete food resources. But, by virtue of their individual-based interactions, including cannibalism [28, 29], they commence marching en masse in random directions—effectively making them harder for predators to track. Thus, aggregated locusts become patchy both in space and time. Although static, our model remains applicable in this situation provided that the predators are faster than their prey because from the perspective of the predators, their prey are quasi-stationary.

A key requirement for the percolation model is that prey demonstrate active aggregation at high densities, rather than not responding to others or else being repelled. In other words, passive congregation within a patchy environment is not sufficient; there needs to be active aggregation if prey are to form extremely clumped distributions and disrupt predator foraging within habitats where resources are less extremely clumped. Locusts demonstrate density-dependent (i.e., facultative) mutual attraction. At low densities, they actively avoid one another, but individuals that experience crowding switch and actively orient toward other locusts. In contrast, migratory-band-forming Mormon crickets do not show this phenotypic switch [30], but rather seem to be constitutively attracted by others and aggregate when environmental conditions provide high local population densities.

There are clear parallels between predator-percolation theory and aspects of existing models of grouping behavior. Notably, the “attack abatement” model of Turner and Pitcher [31] considers the combined effects of detection and attack risk on the evolution of prey gregariousness. Because it is based on individual prey, it is inherently intuitive to see from Turner and Pitcher’s model [31] how selection would favor the fixation of alleles for gregariousness within a prey population. The percolation and attack-abatement models share having dispersing and aggregating forms of prey. Similarly, the combined effects of key terms in the attack-abatement model (predator satiation, as well as detectability as a function of prey density) are operationally interchangeable with the giving-up density as used in the percolation model. Percolation theory, however, exposes a previously unconsidered and equally general advantage of aggregation that is not dealt with in existing models and that only becomes apparent when the spatial consequences of prey aggregation on predator foraging success are considered, namely the existence of a percolating threshold. Turner and Pitcher’s model predicts that prey-abundance thresholds for sustained predation arise when isolated individual prey coexist as a single aggregation.

Percolation thresholds are distinctly different, spatially explicit values that indicate long-range connectivity across a landscape and do not coincide with the prey-abundance thresholds in Turner and Pitcher’s model. Importantly, recognition of the percolation threshold provides a theoretical basis for attempts to predict insect outbreaks from assessments of vegetation or prey abundance across the landscape. Indeed, the predicted percolation-threshold effect on prey population dynamics strongly augments models and data showing how locust population size interacts with local resource abundance and distribution patterns to determine the likelihood of gregarization and subsequent swarm formation [22–26].

There are also parallels between percolation theory and the hypothesis that aggregation behaviors may have evolved in insects as an antiparasite defense mechanism because, by aggregating in groups, there is a greater probability that a parasite or pathogen will fail to breach the gap between infectious hosts [32–34]. We note that percolation theory has recently been applied in the context of disease epidemiology [35]. Thus, for any natural enemy that exploits patches of hosts, percolation theory warrants consideration as a generally applicable model underlying the ecology and evolution of aggregative behavior.

In summary, we postulate that selection pressure from predators has been an important factor in the evolution and ecology of gregarious behavior in prey species subject to high population densities and great fluctuations in abundance. Our model from percolation theory shows that it would be highly disadvantageous for prey to continue indefinitely in a dispersed spatial distribution of small local clumps in the face of greatly increasing population densities. Switching to an extremely clumped distribution (with most of the population in a few highly cohesive bands or swarms) was shown to confer a benefit to prey because it disrupts the connectivity of the predators’ food-patch network. A whole suite of density-dependent traits (behavior, color, et cetera) may then be favored in the prey population, leading eventually to the extreme manifestations of phase polyphenism seen in locusts.

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References

1. Simpson, S.J., and Sword, G.A. (2008). Locusts. *Curr. Biol.* 18, R364–R366.
2. Pener, M.P., and Simpson, S.J. (2009). Locust phase polyphenism: An update. *Advances in Insect Physiology*, in press.
3. Gouyet, J.-F. (1996). *Physics and Fractal Structures* (Paris: Masson).
4. Sword, G.A. (1999). Density-dependent warning coloration. *Nature* 397, 217.
5. Sword, G.A., Simpson, S.J., El Hadi, O.T., and Wilps, H. (2000). Density-dependent aposematism in the desert locust. *Proc. Biol. Sci.* 267, 63–68.
6. Sword, G.A., Lorch, P.D., and Gwynne, D.T. (2005). Migratory bands give crickets protection. *Nature* 433, 703.
7. Greathead, D.J. (1966). A brief survey of the effects of biotic factors on populations of the desert locust. *J. Appl. Ecol.* 3, 239–250.

8. Brown, J.S. (1988). Patch use as an indicator of habitat preference, predation risk, and competition. *Behav. Ecol. Sociobiol.* 22, 37–47.
9. Falconer, K. (2003). *Fractal Geometry: Mathematical Foundations and Applications*, Second Edition (Chichester, UK: John Wiley & Sons).
10. Prokopy, R.J., and Roitberg, B.D. (2001). Joining and avoidance behavior in non-social insects. *Annu. Rev. Entomol.* 46, 631–665.
11. Krause, J., and Ruxton, G.D. (2002). *Living in Groups* (Oxford: Oxford University Press).
12. Sword, G.A. (2008). Gregarious behaviour in insects. In *Encyclopedia of Entomology*, Second Edition, J.L. Capinera, ed. (Dordrecht, Netherlands: Springer), pp. 1733–1740.
13. Uvarov, B.P. (1966). *Grasshoppers and Locusts, Volume 1* (Cambridge, UK: Cambridge University Press).
14. Hamilton, W.D. (1971). Geometry for the selfish herd. *J. Theor. Biol.* 31, 295–311.
15. Viscido, S.V., Miller, M., and Wetthey, D.S. (2002). The dilemma of the selfish herd: The search for a realistic movement rule. *J. Theor. Biol.* 217, 183–194.
16. Gillett, S.D., and Gonta, E. (1978). Locusts as prey: Factors affecting their vulnerability to predation. *Anim. Behav.* 26, 282–289.
17. Cheke, R.A. (1978). Theoretical rates of increase of gregarious and solitary populations of the desert locust. *Oecologia* 35, 161–171.
18. Despland, E., and Simpson, S.J. (2005). Surviving the change to warning colouration: Density-dependent polyphenism suggests a route for the evolution of aposematism. *Chemoecology* 15, 69–75.
19. Despland, E., and Simpson, S.J. (2005). Food choices for solitary and gregarious locusts reflect cryptic and aposematic antipredator strategies. *Anim. Behav.* 69, 471–479.
20. Wilson, K., Thomas, M.B., Blanford, S., Doggett, M., Simpson, S.J., and Moore, S.L. (2002). Coping with crowds: Density-dependent disease resistance in desert locusts. *Proc. Natl. Acad. Sci. USA* 99, 5471–5475.
21. Simpson, S.J., Sword, G.A., Lorch, P.D., and Couzin, I.D. (2006). Cannibal crickets on a forced march for protein and salt. *Proc. Natl. Acad. Sci. USA* 103, 4152–4156.
22. Collett, M., Despland, E., Simpson, S.J., and Krakauer, D.C. (1998). Spatial scales of desert locust gregarization. *Proc. Natl. Acad. Sci. USA* 95, 13052–13055.
23. Despland, E., and Simpson, S.J. (2000). Small-scale vegetation patterns in the parental environment influence the phase state of hatchlings of the desert locust. *Physiol. Entomol.* 25, 74–81.
24. Despland, E., Collett, M., and Simpson, S.J. (2000). Small-scale processes in desert swarm formation: How vegetation patterns influence gregarization. *Oikos* 88, 652–662.
25. Despland, E., Rosenberg, J., and Simpson, S.J. (2004). Landscape structure and locust swarming: A satellite's eye view. *Ecography* 27, 381–391.
26. Babah, M.A.O., and Sword, G.A. (2004). Linking locust gregarization to resource distribution patterns across a large spatial scale. *Environ. Entomol.* 33, 1577–1583.
27. Farrow, R.A. (1990). Flight and migration in acridoids. In *The Biology of Grasshoppers*, R.F. Chapman and A. Joern, eds. (New York: John Wiley & Sons), pp. 227–314.
28. Buhl, J., Sumpter, D.J.T., Couzin, I.D., Hale, J.J., Despland, E., Miller, E.R., and Simpson, S.J. (2006). From disorder to order in marching locusts. *Science* 312, 1402–1406.
29. Bazazi, S., Buhl, J., Hale, J.J., Anstey, M.L., Sword, G.A., Simpson, S.J., and Couzin, I.D. (2008). Collective motion and cannibalism in locust migratory bands. *Curr. Biol.* 18, 735–739.
30. Sword, G.A. (2005). Local population density and the activation of movement in migratory band-forming Mormon crickets. *Anim. Behav.* 69, 437–444.
31. Turner, G.F., and Pitcher, T.J. (1986). Attack abatement: A model for group protection by combined avoidance and dilution. *Am. Nat.* 128, 228–240.
32. Watve, M.G., and Jog, M.M. (1997). Epidemic diseases and host clustering: An optimal cluster size ensures maximum survival. *J. Theor. Biol.* 184, 165–169.
33. Wilson, K., Knell, R., Boots, M., and Koch-Osborne, J. (2003). Group living and investment in immune defence: An interspecific analysis. *J. Anim. Ecol.* 72, 133–143.
34. Wilson, K. (2005). Evolutionary ecology of insect host-parasite interactions: An ecological immunology perspective. In *Insect Evolutionary Ecology*, M.D.E. Fellowes, G.J. Holloway, and J. Rolff, eds. (Wallingford, UK: CABI Publishing), pp. 289–341.
35. Davis, S., Trapman, P., Leirs, H., Begon, M., and Heesterbeek, J.A.P. (2008). The abundance threshold for plague as a critical percolation phenomenon. *Nature* 454, 634–637.