cells. Regardless, increasing evidence supports the idea that invadopodia are the subcellular structures required for ECM remodeling activity. Molecules such as the transmembrane metalloproteinase MT1-MMP are essential for invadopodia activity *in vitro* and have been shown by Steve Weiss' laboratory and others to be important for tumor growth and invasion *in vivo*, suggesting that invadopodia are likely to enhance tumor growth at secondary sites through removal of space constraints.

Why do cells need invadopodia? why can't they just secrete proteinases at large to degrade ECM? At this point it is not fully clear why ECM degradation appears to take place only at invadopodia. This might represent a regulatory point of control, such that efficient ECM degradation only occurs where many signals and processes converge. One possibility is that proteinase activation and/or delivery occurs 'on-site' at invadopodia. The invadopodia metalloproteinase MT1-MMP is an activator of other invadopodia proteinases and could function as a critical upstream catalyst of proteinase activity for focal ECM degradation. Why Src kinase signaling and branched actin assembly are required in this process, however, is an open question.

Any outstanding controversies? Many of the points raised above. Open questions include: what are the differences between podosomes and invadopodia? Do invadopodia exist *in vivo* (and if so what they would look like)? What are the stages in invadopodia formation and function? And are invadopodia as structures truly required for ECM degradation?

Where can I find out more?

Ayala, I., Baldassarre, M., Caldieri, G., and Buccione, R. (2006). Invadopodia: a guided tour. Eur. J. Cell Biol. *85*, 159–164.

Buccione, R., Orth, J.D., and McNiven, M.A. (2004). Foot and mouth: podosomes, invadopodia and circular dorsal ruffles. Nat. Rev. Mol. Cell Biol. *5*, 647–657.

Linder, S. (2007). The matrix corroded: podosomes and invadopodia in extracellular matrix degradation. Trends Cell Biol. *17*, 107–117.

Weaver, A.M. (2006). Invadopodia: specialized cell structures for cancer invasion. Clin. Exp. Metastasis *23*, 97–105.

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Locusts

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What is a locust? A special type of grasshopper (Orthoptera: Acrididae) distinguished by expression of a remarkable and potentially devastating form of phenotypic plasticity, known as density-dependent phase polyphenism. Changes in local population density cause the development of strikingly different phenotypic forms, or 'phases' (Figure 1). Low population densities produce the shy, well-camouflaged 'solitarious' phase, whereas crowded conditions produce the aggregating, migratory 'gregarious' phase. Solitarious phase locusts avoid one another, but gregarious locusts can form huge groups and embark on spectacular mass migrations, travelling as marching bands of flightless juveniles and vast flying swarms of winged adults.

Of the more than 12,000 described grasshopper species, fewer than 20 are considered locusts. Swarming locusts have evolved independently a number of times in a variety of different grasshopper lineages throughout the world. It seems as though a combination of ecological factors has repeatedly favoured the evolution of locusts from their more grasshopper-like ancestors. The relationship between locusts and their environment and how this interaction leads to swarm formation is an active area of research.

What is phase polyphenism? Although phenotypic changes in colouration as seen in Figure 1 may often be the most conspicuous feature, solitarious and gregarious phase locusts differ in a variety of other traits, including morphology, food selection and nutritional physiology, reproductive physiology, metabolism, neurophysiology, endocrinology, molecular biology, immune responses, longevity and pheromone production. In the Migratory locust of Africa, Asia and Australia (*Locusta migratoria*), the phenotypic differences are so extreme that the two phases were originally classified by Linnaeus as separate species, a mistake that was not appreciated until 1921 when Russian biologist Boris Uvarov proved that the two phases are not even different genotypes. The genetic instructions for producing the two phases are packaged within a single genome, with expression of one or other suite of genes depending on cues associated with crowding. Different locust species vary in the number of phase traits that they express. The Australian Plague locust (*Chortoicetes terminifera*), for example, shows extreme density-dependent behavioural changes, but appears to lack the colour and shape changes seen so prominently in *L. migratoria* and the Desert locust, *Schistocerca gregaria*.

Why are locusts of interest? Locusts have been feared agricultural pests since the dawn of civilisation with plagues documented in ancient texts including the Qur'an, Bible and Torah. Locust outbreaks can occur on all of the continents with the exception of Antarctica and have the potential to affect the livelihoods of one in ten people on the planet. A single locust

Figure 1. The two extreme phases of juvenile Migratory locusts, *Locusta migratoria*.
The solitarious phase insect on the left was reared alone, whereas the gregarious phase insect was reared in a crowd. (Image courtesy of Gabriel Miller.)

swarm can contain billions of insects and travel hundreds of kilometres each day. On occasion they can even cross oceans, as happened most recently in 1988 when Desert locust swarms from West Africa flew across the Atlantic Ocean and reached the New World. For these reasons alone, locust biology has long been the object of intense scientific study, to try to find ways to control them.

From a purely scientific perspective, locusts are of considerable interest as a model for studying phenotypic plasticity. Thanks to recent behavioural, ecological, neurophysiological and mathematical modelling experiments, locust phase change has emerged as one of the best understood examples of a complex plastic phenotype. A major gap in the otherwise well-rounded understanding of locust phase change is its underlying genetic basis. The recent development of genomics resources offers researchers new opportunities to elucidate the genetic mechanisms underlying phase change. These new approaches combined with the well-developed understanding of locust behaviour and ecology make locusts uniquely suited for integrating basic genetic, physiological and behavioural mechanisms with higher order ecological and evolutionary processes. In locusts we now have the potential to understand how fundamental processes such as gene transcription, translation, and their regulation scale up to behavioural and ecological interactions involved in outbreaks, collective movement and mass migration, and even continental patterns of biogeography.

Why is behavioural phase change so important? Behaviour is the first phase trait to change in response to crowding and lies at the heart of swarm formation and migration. A solitarious locust will switch from avoiding other locusts to exhibiting gregarious behaviour after only a few hours of crowding. Once locusts become attracted rather than repelled by others, a positive feedback loop is established that can drive an initially solitarious population to the gregariousness phase. Because behavioural change occurs before changes in other traits appear, its autocatalytic effect serves to couple a diverse suite of continuous plastic traits into a coordinated threshold trait, both at the individual and population levels.

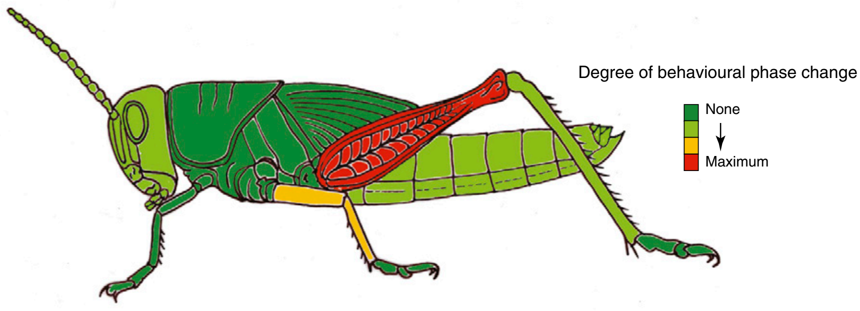

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Figure 2. Stroking the hind legs, but no other body region, with a paintbrush causes a solitarious phase locust to change phase and start behaving gregariously. (Reproduced with permission from Simpson *et al*., 2001.)

What physiological mechanisms are involved? The ability to quantify behavioural phase and follow its time course in behavioural assays has facilitated ongoing investigations into the stimuli, neurophysiological and ecological mechanisms involved in locust phase change, particularly in *S. gregaria* which has been most intensively studied to date. The sight and smell of other locusts together trigger behavioural phase change, but direct contact with other locusts is the most powerful gregarising stimulus. The critical site of mechanical stimulation during contact has even been localised to a region of touch-sensitive receptors on the jumping hind legs (Figure 2).

Different stimuli and mechanisms are involved in producing changes in other phase characters. In nymphs of *S. gregaria*, the smell of other locusts is sufficient to induce the characteristic black patterning of gregarious phase juvenile locusts, but it does not elicit yellowing of the background colour, which requires direct contact with conspecifics, presumably indicating the action of a contact chemical cue. The production of black patterning in juveniles is controlled by the neuropeptide $[\text{His}^7]$-corazonin, which also changes body shape towards the gregarious phase, but has no effect on behavioural phase state. Much attention has been paid to the possible roles of hormones, such as ecdysteroids and juvenile hormone, but it is clear that these are not primary controlling agents of phase change.

Phase characteristics, including behaviour, not only change within the life of an individual, they also accumulate epigenetically across generations. Solitarious *S. gregaria* females can produce hatchlings that are behaviourally gregarious to an extent that reflects when the mother was last crowded. If the mother is crowded for the first time ever while laying her eggs, she will produce offspring that behave gregariously upon hatching. In contrast, if a gregarious phase female is alone when laying her eggs, she will produce hatchlings that tend to express solitarious phase behaviours. This maternal effect is mediated by a chemical that the mother adds to the egg foam that surrounds her eggs in the soil. In effect, female locusts use their own experience of being crowded to predict the population density that their young will experience, and predispose them to behave appropriately.

An exciting new frontier in locust research lies ahead. The advent of genomics and proteomics approaches has the potential to reveal the molecular genetic and epigenetic mechanisms underlying locust phase change. An expressed sequence tag (EST) library recently developed for the Migratory locust, *L. migratoria*, found over 12,000 unigenes of which 532 were differentially expressed between the solitarious and gregarious phases. A majority of these genes had no identifiable homologues among other insects' genomes. Comparative genomics and RNA interference (RNAi) gene-silencing studies are underway to attempt to characterise the phenotypic effects of these phase change genes and elucidate the regulatory networks involved.

How and why do swarms form?

Weather plays a critical role in locust population growth and swarm formation, because it promotes growth of host plants and provides soil moisture for egg development. Individual-based computer simulations, laboratory and field experiments have shown that the fine-scale spatial distribution and quality of resources in the habitat can either promote or deter contact among individuals, and hence influence the probability of locusts entering the gregarious phase. Clumping of food plants or areas of favourable microclimate encourages solitarious locusts to come into contact and gregarise, despite their initial tendency to be repelled by one another. In contrast, more dispersed resources allow solitarious locusts to avoid one another and inhibit gregarisation.

The expression of phase polyphenism itself may enhance local population growth and promote further gregarisation by altering local ecological interactions. Juvenile *S. gregaria* in pre-outbreak populations feed on a variety of plants that contain secondary compounds toxic to vertebrates, and they become even more willing to do so as they become gregarious. When this happens, their conspicuous gregarious phase colour patterns serve as a warning colouration to vertebrate predators, signalling that the locusts are toxic prey by virtue of feeding on noxious plants. Gregarious *S. gregaria* are also more resistant to pathogen infection than solitarious individuals, another adaptation to life in a crowd that will reduce mortality and contribute to local population growth.

Why do locusts mass migrate?

Locust swarms often fly with prevailing winds that take them to regions where air masses may collide, produce rainfall, and potentially generate suitable habitat. Until recently, the mechanisms and adaptive significance of migratory band movements over smaller scales on the ground was largely unknown. In part because of the comparative studies involving the migratory band-forming Mormon cricket (*Anabrus simplex*), the past few years have seen the rapid development of a unifying framework that explains both how and why such mass movements occur. It has been shown that bands form as an anti-predator strategy in which individuals are much less likely to be killed by predators than insects that are on their own. Despite this benefit, band members suffer from increased intraspecific competition for nutritional resources as well as an increased risk of cannibalism by other hungry band members. These costs, in turn, are precisely the factors that drive the subsequent mass movement of individuals in migratory bands. Migratory bands are a “forced march” driven by cannibalism, in which individuals must keep moving both to find new resources and avoid being attacked by cannibalistic conspecifics approaching from behind.

Because swarms are composed of many interacting individuals, locusts are powerful model organisms for studies of collective movement. The group-level movement patterns of migratory bands and flying swarms are similar to those observed in many other animals, suggesting that general mechanisms underlie collective movement across taxa. In fact, the laws generating collective movement in animals may be so general that they can be modelled as interacting particles. Self-propelled particle models developed for statistical physicists have recently been used to explain transition from wandering individuals to cohesive marching locust bands at high population density.

Where can I find out more?

Buhl, J., Sumpter, D.J.T., Couzin, I.C., Hale, J., Despland, E., Miller, E., and Simpson, S.J. (2006). From disorder to order in marching locusts. Science *312*, 1402–1406.
Kang, L., Chen, X.Y., Zhou, Y., Liu, B.W., Zheng, W., Li, R.Q., Wang, J., and Yu, J. (2004). The analysis of large-scale gene expression correlated to the phase changes of the migratory locust. Proc. Natl. Acad. Sci. USA *101*, 17611–17615.
Simpson, S.J., Despland, E., Haegele, B.F., and Dodgson, T. (2001). Gregarious behaviour in desert locusts is evoked by touching their back legs. Proc. Natl. Acad. Sci. USA *98*, 3895–3897.
Simpson, S.J., and Sword, G.A. (2007). Phase polyphenism in locusts: mechanisms, population consequences, adaptive significance and evolution. In Phenotypic Plasticity of Insects: Mechanisms and Consequences, D. Whitman and T.N. Ananthakrishnan, eds. (Plymouth: Science Publishers Inc), pp. 93–135.
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.
Sword, G.A., Simpson, S.J., El Hadi, O.T.M., and Wilps, H. (2000) Density-dependent aposematism in the desert locust. Proc. R. Soc. Lond. B *267*, 63–68.

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Primer

Animal cultures

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For most biologists, ‘culture’ is either some agar-bound growth in a Petri dish or the nebulous domain of fashion, art and theatre that lies at the edge of scientific understanding. For an increasing number of animal behaviourists, however, ‘culture’ has a quite different meaning: the learning and social transmission of knowledge and skills among animals. The best-known examples include the opening of milk bottles to drink cream by European birds, the washing of food by Japanese macaques, and the habit, of some East African chimpanzees, of fishing for termites with stalks. Animals as diverse as ants, sticklebacks and killer whales are now known to pick up foraging skills, dietary preferences, mating preferences and predator evasion tactics, and to learn calls, songs, and migratory routes, by observing more experienced others. But the claim that humans are not the only species immersed in a cultural realm is shrouded in controversy.

Why study animal culture?

Why is culture of interest? Many people who study animal cultures, particularly primatologists, do so because they believe their research will shed light on the evolution of human cognition. Animal social learning, it is argued, lies at the roots of human culture. If we can get to grips with termite fishing in chimpanzees or macaque food washing, they surmise, we can gain insights into homologous processes that led to the emergence of ‘full-blown’ culture in humans, the conditions that favored the cognitive underpinnings of our own cultural capability, or the evolutionary trajectory of our cultural ancestors.

Whatever the merits of that argument, from the evolutionary biologist’s perspective, animal culture is inherently interesting. That is, there are broader issues that validate investigating animal cultural processes over and above the light such study sheds on our own species.