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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Animal cultures

Kevin N. Laland

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.

Perhaps the most obvious of these is that culture is a source of adaptive behavior; individuals can efficiently acquire solutions to problems such as 'what to eat?' and 'with whom to mate?' simply by copying others.

The fascination of culture, however, also relates to its ability to propagate behavior in a manner that is to some degree independent of the ecological environment. For instance, it is a fundamental assumption of evolutionary biology that natural selection will shape organisms to reflect environmental conditions. However, culture can violate this premise; it can cause the characteristics of organisms to become partially disconnected from their environments. This is most obvious in humans where studies of different societies have found that most human behavioral and social traits correlate with cultural history — were handed down as traditions — rather than with a society's ecology. The same applies to at least some animals. Bluehead wrasse mating sites, for instance, cannot be predicted from knowledge of environmental resource distributions. Rather, removal and replacement experiments demonstrate that mating sites are maintained as 'traditions', for multiple generations, with young fish and newcomers adopting the mating sites of residents.

Culture can also generate patterns of phenotypic variation in space. Evolutionary biologists and ecologists set out to understand the processes underlying geographical variation in gene frequencies and phenotypic characters. However, cultural processes, like gene-frequency clines, can generate geographical patterns in behavioral phenotypes. Clines in behavioral characteristics attributed to culture have been reported for primate behavior, birdsong, whale vocalizations and human language.

A third challenging feature of cultural transmission is that, under restricted circumstances, arbitrary and even maladaptive information can spread. Once again, this is well documented in humans, where fitness-reducing habits, such as smoking or contraceptive use, can become fashionable. However, there are instances where arbitrary and maladaptive traits appear to spread among animals too. An example

is *informational cascades*, where individuals base behavioral decisions on prior decisions of others. If animals think that a particular behaviour must be good because others are doing it, then all kinds of arbitrary traditions can result. A study of lekking sage grouse found that the decisions of females using social information to decide with whom to mate were less closely correlated with male traits indicating quality than were the decisions of females making their own judgments about males. This copying of mate choices obscures the relationship between male quality and mating success, resulting in unpredictable 'fads' in the characters that females find attractive and a lower intensity of sexual selection. This is not to say that the capability for social learning is a maladaptive trait, but rather that the occasional transmission and acquisition of maladaptive information is an unavoidable byproduct of a largely adaptive knowledge-gaining system.

Moreover, cultural traditions often impact on the environment to modify the selection acting on the population, an instance of *niche construction*. This is most obvious in humans and a great deal of mathematical theory by evolutionary biologists and anthropologists has investigated gene–culture co-evolution, whereby human cultural traits modify the selective environment. A good example is the cultural practice of dairy farming, which spread prior to the allele for lactose absorption, creating the environmental context in which this gene was favoured in some pastoralist societies. Similar interactions occur in other animals: theoretical models of mate-choice copying have revealed that learned preferences could plausibly co-evolve with gene-based traits, models of birdsong suggest that song learning affects the selection of alleles influencing song acquisition and preference, and other models have found that animal social learning could lead to the evolution of brood parasitism, affect levels of genetic diversity, and facilitate speciation.

Such gene–culture co-evolution is suggested by the observation that the frequency of social learning usage co-varies with brain size in non-human primates. It would seem that big-brained primates copy each other more than do small-brained

primates; they also invent more novel behaviour. This has led to the suggestion that the ability to learn from others, and to devise novel solutions to challenging problems, may have given individual primates a selective advantage in the struggle for existence. Since these abilities are no doubt underpinned by neural substrate, it is conceivable that the capabilities for social learning and innovation could have driven brain evolution in primates, culminating in *Homo sapiens*, the most innovative and most culturally dependent primate with the largest brain.

In short, cultural processes in a broad range of animal species exhibit a number of properties that change the evolutionary dynamic, including detaching the behaviour of animals from their ecological environments, generating geographical patterns in phenotypic characters, allowing arbitrary and even maladaptive characters to spread, influencing evolutionary rates and trajectories, and modifying selection to precipitate and direct evolutionary events. This different way of adapting and evolving is not unique to humans but shared with many other species capable of social learning, including species only distantly related to ourselves. Animal culture is much more than a window onto humanity: it is an evolutionary player.

The animal cultures debate
Groups of white-faced capuchin monkeys in Costa Rica exhibit extraordinary and bizarre social conventions, sniffing each other's hands and placing fingers in each other's mouths, behaviors not seen in other capuchin populations. Some orangutans in Borneo make leaf-bundle 'dolls', others use tools as sexual stimulants, and still other orangutans blow raspberries at bedtime. Humpback whales from different regions sing different songs, as do white crowned sparrows and a host of other bird species.

At first sight, such reports of behavioral differences among species members living in different locations are evocative of human cultural variation. Just as people from different regions of the world eat different foods, have varying customs and speak different languages, some animals also appear to have local traditions. Much circumstantial

Box 1.

Social learning processes: definitions and examples.

Social learning: any process through which one individual ('the demonstrator') influences the behaviour of another individual ('the observer') in a manner that increases the probability that the observer learns.

Various social learning processes have been proposed, including:

Local enhancement: a demonstrator inadvertently attracts an observer to a specific location, leading to the observer learning.
Example. Naïve guppies follow informed individuals to food.

Stimulus enhancement: a demonstrator inadvertently exposes an observer to a particular stimulus, leading to the observer learning.
Example. Blue tits learn to open milk-bottle tops faster after being exposed to bottles opened by other birds.

Observational conditioning: a demonstrator's behaviour inadvertently exposes an observer to a relationship between stimuli, allowing the observer to form an association between them.
Example. Blackbirds learn to recognise predators through observing birds mobbing unfamiliar objects.

Response facilitation: the presence of a demonstrator performing an act increases the probability of an animal that sees it doing the same, leading to the observer learning.
Example. The rate at which chickens initiate bouts of preening is strongly related to the number of birds already preening in the same locality.

Contextual imitation: through observing a demonstrator perform an action in a specific context, an observer becomes more likely to perform that action in the same context.
Example. Pigeons that watch demonstrators step or peck on a treadle for a food reward are more likely to solve the task using the method they had seen.

Production imitation: after observing a demonstrator perform a novel action, sequence or combination of actions, an observer becomes more likely to perform that same action or sequence of actions.
Example. Humans learn tennis strokes and improve golf swings through observing sports coaches.

Emulation: after observing a demonstrator interacting with objects in its environment, an observer becomes more likely to act to bring about a similar effect on those objects.
Example. Chimpanzees learn to gain out-of-reach food with a tool through observing a demonstrator, but do not reproduce its motor pattern.

and some experimental evidence suggests that these traditions are learned from others, and handed down across generations. But are the similarities between animal 'cultures' and those of humans meaningful or superficial?

Part of the disagreement over animal culture is definitional, reflecting diverse perspectives across academic disciplines: here biologists tend to employ less exacting definitions than do anthropologists. However, the controversy is more over the evidence necessary to establish that within-species behavioural variation results from social learning rather than from genetic differences or the way diverse ecologies shape behavioral development. Researchers vary in the degree to which they are willing to

rely on circumstantial evidence and plausibility arguments, with laboratory experimentalists and field researchers often taking different sides. Common chimpanzees, for instance, are very good at social learning; experimental demonstrations in captivity clearly show that they are capable of transmitting learned foraging skills through populations, while in the field behavioural repertoires vary between populations, with youngsters spending long hours close to competent adults foraging, before adopting the local variants. In other words, the circumstantial support for chimpanzee culture is strong. However, for no single natural chimpanzee behaviour, including termite fishing and nut cracking, is there conclusive evidence that it is socially learned.

This issue is likely to be resolved within the next decade, as new mathematical and experimental methods are developed for identifying social learning in animal populations. Many such tools, which include an array of statistical methods, are currently in development, and offer great promise for the future. Countless species, from oystercatchers to orangutans, exhibit inter-population variation in their behavioural repertoires, and in all probability the next decade will confirm that a sizeable proportion of this variation is cultural.

Mechanisms of culture
Behavioural traditions are not restricted to clever or large-brained animals: laboratory and field studies imply that a capacity for social learning is taxonomically widespread among animals, including invertebrates. There are now, quite literally, many hundreds of reports of novel behaviour patterns increasing in frequency over time, too rapidly to be plausibly interpreted as manifestations of selection, migration or demographics. It would seem such animals must be learning their new behaviour, and to all appearances they seem to be learning from each other. Combined with the aforementioned inter-populational variation in behaviour, the data from the field imply that social learning is pervasive.

We can also be fairly certain that animal social learning is multi-faceted in its underlying mechanisms. Laboratory studies, largely carried out by experimental psychologists, reveal a multitude of means by which one animal can learn from another. The question of whether animals learn by imitating others has attracted an especially high level of interest, since imitation is often assumed to rely on complex cognitive processes — such as an ability to understand what the other is doing, or to adopt another's perspective, or even conscious awareness — assumptions that remain highly contentious. Nonetheless, reasonably compelling evidence for imitation has been provided for a variety of species of birds, primates and cetaceans.

Much effort has gone into defining alternative social learning processes that might superficially resemble imitation, and that must be ruled out if researchers are to isolate cases
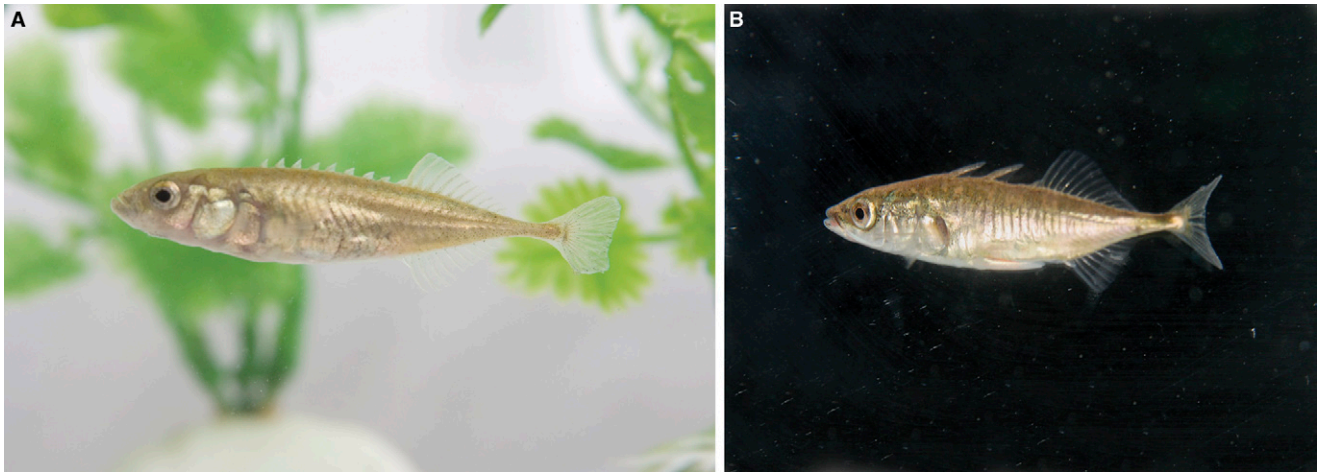
Figure 1. Social learning in sticklebacks.
(A) Nine-spined stickleback and (B) three-spined stickleback. Experimental studies reveal that nine-spined but not three-spined sticklebacks are capable of learning the richness of a food patch by observing other fish, a form of social learning known as 'public-information use'. This difference, in two closely related species with very similar lifestyles, is thought to be an adaptive specialization in social learning. The weaker morphological defenses of the nine-spines leaves them more vulnerable to predation than the more robust three-spines, leading them to spend more time hiding in refuge, from where selection has seemingly fashioned their ability to monitor the success of others at food patches.

of 'true' imitative learning. As a result, there are a plethora of terms used to describe different social learning phenomena, including *local enhancement, stimulus enhancement, contagion, emulation, observational conditioning,* and *social facilitation* (see Box 1). These, and other, terms have been organized into a number of classification schemes, but there is little consensus in the field over terminology or underlying mechanism: indeed considerable confusion and major differences of opinion remain. For instance, 'imitation' is frequently described as complex, and 'local enhancement' as simple, because, intuitively, reproducing a motor pattern through observation appears more challenging than having one's attention directed to a location. However, there is currently little neuro-scientific basis to social learning research, and the processes described in classifications are not tied to neural mechanisms. In the absence of a strong biological understanding, such use of terms like 'simple' and 'complex' could be profoundly misleading. It is, for instance, plausible that a large proportion of social learning phenomena can be understood as the result of a single psychological mechanism, priming (in which experience has at least a temporary effect on the relative probabilities of evoking stored mental representations).

Also up for grabs is the relative frequency of alternative social learning processes in the natural world. For instance, it is widely thought that the processes of local and stimulus enhancement are common and imitation is rare in nature (see Box 1 for definitions). However, a recent review found just a handful of cases that could unambiguously be designated in the former categories, while the apparent rarity of imitation may merely reflect the stance, widely adopted within the field, that imitation can only be claimed when alternative processes have been ruled out. Ironically, *response facilitation*, a process that relatively few social learning researchers even recognize, is arguably the process that commands the most empirical support. Even the assumption that one or other of these processes will explain most natural cases of animal social learning is contestable: in any given instance, multiple processes may be operating, while there can be little confidence that current classification schemes are non-overlapping or complete. Once again, however, there are grounds for confidence that these uncertainties will be eroded in the near future, since experimental studies that disassociate alternative social learning processes increasingly appear.

Evolution of culture
The extent to which the learning abilities of animals are shaped by natural selection in response to species-specific ecological challenges or general processes that vary little across taxa has long been a matter of contention. This issue lay at the centre of the debate between ethologists and comparative psychologists from the 1940s to 1960s, and has resurfaced in recent discussions of evolutionary psychology and cognitive ecology. However, some consensus is beginning to appear. While many learning mechanisms are extremely general, there is limited evidence for psychological mechanisms that guide and direct learning and associated perceptual processes in response to specific ecological problems. For example, scatter-hoarding birds like the marsh tit can store and retrieve many hundreds of food items, while non-storing members of the same genus do not seem to possess this spatial memory capacity. Similar adaptive specializations in social learning exist. When exposed to songs of multiple species, juveniles of a number of bird species preferentially learn conspecific song, while several monkeys appear predisposed by past natural selection to acquire a fear of snakes (as opposed to other objects) on seeing other monkeys behave fearfully in the presence of a snake.

A particularly instructive example is an experimental study of public-information use (the ability to assess the quality of a resource on the basis of the success of other individuals) in two closely related species of sticklebacks (Figure 1). Isabelle Coolen and colleagues recently found that nine-spined sticklebacks, after watching conspecific or heterospecific 'demonstrator' fish feeding at two patches, when tested alone, tend to approach the former location of the richer patch. As their observational experience was restricted to the relative success of their demonstrators, and potential alternative explanations could be ruled out, they surmised that nine-spined sticklebacks were capable of public-information use. However, three-spined sticklebacks, when subject to the same test, swam with equal frequency to the former locations of rich and poor patches. These species were collected from the same streams, frequently shoal together, and feed on similar foods. Why should one species and not the other exhibit this specific form of social learning?

The answer to this conundrum comes from a surprising source: mathematical analyses of the adaptive advantages of human culture. Californian anthropologists Rob Boyd and Peter Richerson postulated a *costly information hypothesis*, which proposes an evolutionary trade-off between reliable but costly self-acquired information and potentially less reliable but cheap socially transmitted information. Here, the relative cost of acquiring personal information varies between the two stickleback species, which determines the value of public information. Three-spines have large spines and armoured body plates, robust structural defenses that allow them to sample alternative food patches directly, in relative safety. Such sampling by nine-spines, which have weaker physical defenses, would leave them vulnerable to predation, and hence in fitness terms would be extremely costly. Consequently, nine-spines spend much of their time in refuge, from where selection seemingly has favoured the ability to monitor the foraging success of others. Further

research confirms that this species difference is robust.

In fact, considerable evidence is accumulating among fish, birds and mammals that animals will ignore social information under specific and predictable circumstances. For instance, nine-spine sticklebacks will ignore public information if they have reliable, up-to-date personal information, yet switch to exploiting public information if their personal information is unreliable or outdated. Social and personal information are not weighted equally, and animals will toggle between the two in a conditional manner, according to their respective reliability and cost. Evolved rules, labelled *social learning strategies*, dictate the circumstances under which individuals copy others, and when they rely on personal experience. One such rule — copy when asocial learning is costly — has already been described for sticklebacks, but there are likely to be many social learning strategies in nature (conform, copy the most successful individual, copy anyone doing better than you, and so on) and researchers are only now just beginning to investigate them.

The study of animal culture is unmasking a fascinating and rich interplay between two inheritance systems — genes and culture — in which each has, to some extent, been shaped by the other.

Further reading
Boyd, R., and Richerson, P.J. (1985). Culture and the Evolutionary Process (Chicago: Chicago University Press).
Byrne, R.W., Barnard, P.J., Davidson, I., Janik, V.M., McGrew, W.C., Miklósi, A., and Wiessner, P. (2004). Understanding culture across species. Trends Cogn. Sci. *8*, 341–346.
Coolen, I., Day, R.L., and Laland, K.N. (2003). Species difference in adaptive use of public information in sticklebacks. Proc. Roy. Soc. Lond. B *270*, 2413–2419.
Heyes, C.M., and Galef, B.G. Jr. (1996). Social Learning in Animals: The Roots of Culture. (San Diego: Academic Press).
Hoppitt, W., and Laland, K.N. (2008). Social processes influencing learning in animals: a review of the evidence. Adv. Stud. Behav., in press.
Laland, K.N. (2004). Social learning strategies. In Special edition on Studies of Social Learning and Imitation, B.G. Galef Jr. and C.M. Heyes., eds. Learn. Behav. *32*, 4–14.
Laland, K.N., and Janik, V. (2006). The animal cultures debate. Trends Ecol. Evol. *21*, 542–547.

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Chimpanzees infer the location of a reward on the basis of the effect of its weight

Daniel Hanus and Josep Call

The extent to which animals in general, and non-human primates in particular, understand physical causality is currently unclear [1,2]. One way to assess an animal's causal understanding is to test its ability to analyze a causal chain backwards — to infer cause from an effect [3]. In the study reported here, chimpanzees saw a given outcome (effect) of an action and had to infer the preceding event (cause) in order to solve the problem. More specifically, subjects saw a banana being hidden inside one of two opaque cups mounted on opposite sides of a balanced beam, but they were kept ignorant about the banana's exact location. Subsequently, the subjects witnessed the balance beam tilting to one side after the experimenter released it from its equilibrium position (the Balance condition). The chimpanzees preferentially (and from trial one) selected the lower, compared to the upper, cup. Two control conditions demonstrated that the chimpanzee subjects lacked an intrinsic preference for the lower cup when there was no movement involved (the Wedge condition) or when the balance beam was tilted by the experimenter's action (the Non-causal balance condition). We conclude that the chimpanzee subjects of our experiments demonstrated evidence of causal inference based on an object's weight.

In our experiments, the chimpanzee subjects selected the baited cup significantly above chance in the Balance condition (see the Supplemental data available on-line for details). We compared the Balance condition to two control conditions. In the Wedge condition, the cups were mounted