Current Biology
Dispatches

Animal Behaviour: Conformity and the Beginnings of Culture in an Insect

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https://doi.org/10.1016/j.cub.2019.01.023

Culture in animals is defined as socially learnt, group-specific behaviour, and has been found in many species. The discovery of social learning and cultural conformity in mate choice in *Drosophila* might allow for the investigation of the mechanistic underpinnings of gene–culture co-evolution.

Culture is a second form of inheritance that is based on behavioural traditions maintained within a population and transmitted to naïve individuals via social learning [1]. Cultural evolution may interact with genetic inheritance and evolution [2]; for example, humans' cognitive architecture may have evolved to facilitate the storage and transmission of culturally acquired knowledge. Indeed, our ability to capitalise upon information gained from innovators of many generations has led to the cumulative cultural processes that make our species uniquely successful. Perhaps for this reason, culture was historically thought to be an exclusively human trait, and the question of whether animals have culture was a matter of intense debate. A wealth of evidence now supports the existence of culture in great apes: foraging techniques and tool use are socially transmitted and maintained as traditions by chimpanzees, gorillas and orangutans, and the specific techniques vary among wild populations [1]. But it might be misguided to suspect that the learning mechanisms that support culture are inherently complex or difficult to evolve, or that these might exist only in our closest relatives. For example, in the 1980s, Martin Lindauer first explored culture-like phenomena in insects by investigating behavioural traditions of early and late-rising honeybees [3]. More recently, it was discovered that in bumblebees object manipulation skills can spread from single skilled demonstrators to sequential generations of observers [4,5]. In a new study, Etienne Danchin and colleagues [6] discovered that in *Drosophila melanogaster* mating preferences can be transmitted through social learning and may be maintained within populations for many generations.

Danchin's group coloured males either green or pink, and first confirmed that mate preference is socially transmitted in fruit flies. Virgin females that watched a pink or green male mount another female through a glass screen preferentially chose a mate of the same colour once they were allowed to choose a partner themselves. If they were given multiple opportunities to watch such pairings, they even exhibited the same preference when the daintily-coloured suitors were presented 24 hours later. These results are far from trivial, as they suggest that the observing female identifies what she sees on the other side of the glass as a mating couple of her own species (not, for example, a predator eating a fly, or a strange 12-legged arthropod). On some level, she also appears to comprehend that the successful individual is a male whose features are worth memorising — even though the colourful individual looks different from any naturally occurring fruit fly.

To explore whether these preferences were the result of a form of imprinting, where the females simply memorised the traits of the first male seen copulating, or whether more extensive sampling took place, observer females were placed in the central chamber of a hexagonal set-up. Here, they could watch six demonstrator females mate with pink or green males, each pair accompanied by a lone male of the other colour who had been rejected by the female (Figure 1A). This set-up allowed the experimenters to manipulate the ratio of green and pink mating males that was presented to the observers. Observers were subsequently permitted to make their own choice between the two types of coloured males.

In the control condition, where three green and three pink males could be seen copulating, observer females had no preference when they were allowed to make their own choice. Remarkably, whenever successful males of one colour or another were in the majority, no matter how slight, observers displayed a strong 'conformist bias' — a significant preference for males of the majority colour. There was also no difference in the strength of preference between a majority of 60% and one of 100%. Female flies, like many adolescent humans, seem to acquire their partner preferences from the majority choices that can be observed around them. This suggests that fruit flies engage in substantial sampling before forming their own mate preference — conformity can only emerge when individuals have sampled a substantial fraction of the preferences expressed by others around them.

Such a conformist bias in learning has previously been found in great tits [7], swamp sparrows [8] and chimpanzees [9]. Conversely, in the most elaborate example of collective decision making in the animal kingdom, the honeybee swarm, no individual appears to assess the choices of the majority. In this process, scouts from the swarm examine the suitability of multiple potential nesting locations, and indicate these different locations using the 'dance language' [10]. In the end, a complete consensus must be (and is) reached, as individuals cannot survive on their own and must agree on a common choice. However, no single bee counts the votes for one or another option as flies appear to do in their mate choice. The study of Danchin and colleagues [6] shows that insects, like some vertebrates, can sample social information more

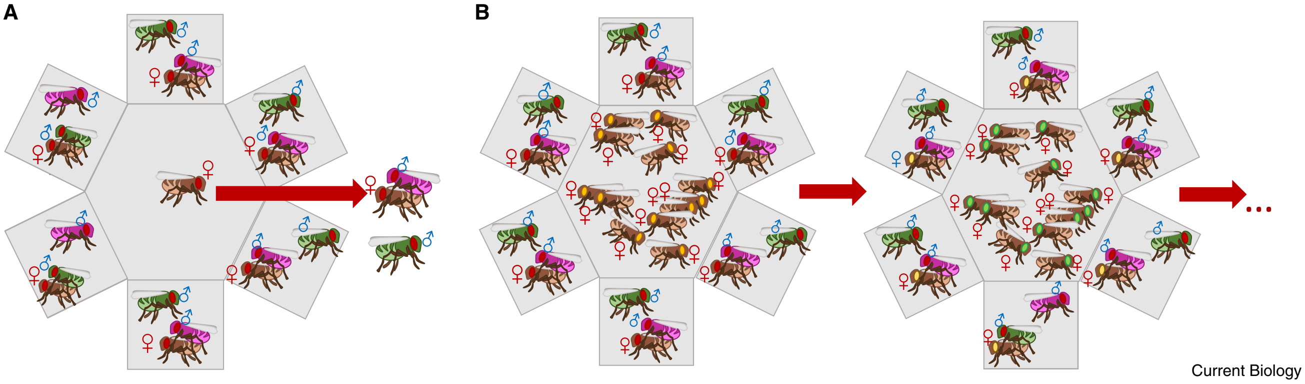

Figure 1. Sexual conformity and transmission chain experiments in fruit flies.
(A) To test conformist bias, a single virgin female is placed in the central observation chamber. In the peripheral compartments, females mate with pink or green males (rejected male also in view). In this example, the majority of matings are with pink males. When the observer female subsequently chooses between pink and green males, she is more likely to choose the majority colour (here pink). (B) In transmission chain experiments, different 'generations' of virgin females are symbolised by different eye colours. Twelve females (yellow eyes, left) are placed in the central observation chamber; in the peripheral compartments all females mate with pink males (rejected green males also visible). Right panel: observer females then choose between pink and green males, and the first six to choose become demonstrators for the next generation of 12 virgin females (green eyes). The majority of observers here copy the majority colour (pink). Such transmission chains can be continued for multiple sequential 'generations'.

extensively before making their own choices. It is obvious why the exploration of conformist biases is of relevance for studies of culture: such biases mean that, even in the absence of any adaptive advantage of a learnt, group-specific behavioural pattern, variation between cultures can be sustained over extended periods if individuals tend to copy the behaviour of the majority in their vicinity [11,12]. Here, conformity can act as a 'repair mechanism' of sorts, by correcting deviations from the group norm that could lead to dissolution of the tradition.

However, while conformist social learning is conducive to maintaining culture, it is useful to demonstrate empirically that preferences persist in a population across time and generations. To this end, Danchin and colleagues [6] performed a transmission-chain experiment (Figure 1B). Each chain began with all of the six demonstrators choosing males of the same colour and ended when the majority was lost. Twelve observers were present in the central chamber to watch these choices and were then permitted to choose between males themselves in isolation. The first six to begin copulation with a male were placed in the peripheral compartments of the set-up and used as demonstrators for a new set of twelve observers. Mate choice 'traditions' were upheld in these experimental populations for an average of eight 'generations' before the majority was lost and the transmission chains ended. Over a quarter of all chains collapsed after the very first step.

This result appears slightly unexpected in light of the apparently strong conformist bias shown by females in the single-step experiments. According to those results, fruit flies should copy even a small majority with the same vigour as they would a large majority, so one or two observers picking the minority male colour should have little effect on the propensity of future observers to copy the majority. The authors suggest that this effect may have occurred due to copying errors having a greater impact on small populations. It is also possible that there was an effect of the different numbers of females in the observation chamber: in the single-step experiments that suggested conformist bias, a single observer female was placed in the central chamber of the hexagon. Here, in close proximity to all six demonstrations, she had little else to do other than observe. In the transmission-chain experiments, twelve females were present in this chamber. Could interactions with other present females, and the ensuing distraction, have led to the eventual collapse of the transmission chains? This is of relevance for the question of whether cultural traditions are likely to persist under natural conditions, where environments are more cluttered than they might be in the laboratory. If, however, the question is whether insects have the cognitive capacities that form the necessary ingredients of between-group cultural variation, the answer is a clear yes.

Why, then, are animal cultures not more common in the wild, especially the cumulative variety seen in humans, where new innovations build on previous ones? Why don't flies build vehicles to travel over land, why do bees not construct walls around their territory to keep competitors away from their flower patches? The conventional way of answering such questions is that they do not have the required brain power. Behavioural experimental studies on multiple invertebrates, however, indicate that the basic problem-solving skills required, and the capacity to learn from observation, are present in a number of invertebrates [13]. Many seemingly advanced cognitive capacities have recently been shown to be computationally trivial, and the required neural circuits could certainly be implemented in some of the smallest brains [14,15]. So, the reason why culture, or cumulative culture, is so rarely seen in nature, might simply be that the conditions that favour its emergence are quite rare. It is easy to see how an animal might benefit, for example to cope with rapid man-made global change, if it were given the benefit of a fully-fledged cumulative culture tomorrow. But one would have to develop a scenario by which the first tiny steps in the direction of such a culture would already be beneficial and maintained in a population — and in such a manner that such variation could not be more beneficially just cemented into genes. A laboratory setting under which culture emerges in a free-flowing experiment (i.e. without significant experimenter intervention) is actually quite hard to conceive for any animal. Even if you gave insects all the tools and parts to build a bicycle, there would be little incentive for them to begin building anything in the right direction. Another potential answer to this question may lie with conformity itself. Conformist biases are a useful way to maintain traditions. However, if these biases are so strong that they result in discrimination against new phenotypes, whether brought about by mutation or individual innovation, such novelty may be discriminated against even if it could be of adaptive benefit. This would prevent the accumulation of improvements characteristic of cumulative culture.

Nonetheless, fruit flies are an interesting choice of model for cultural processes due to the feasibility of selection experiments in relatively short time spans, and thus the potential of exploring interactions between cultural and genetic evolution. In addition, the expansive molecular-genetic toolkit that is available in *Drosophila* should make it possible to explore the neural mechanisms underpinning social learning, as well as the processes mediating evolutionary change under conditions in which certain forms of social learning and culture are selectively advantageous.

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Systematics: The Cohesive Nature of Bacterial Species Taxa

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https://doi.org/10.1016/j.cub.2019.01.033

A survey of bacterial genomes suggests that the diversity within recognized species is constrained by a force of cohesion. However, recognized bacterial species do not adhere to another species-like property—that of being the newest lineages that can coexist indefinitely.

Are bacterial species real? Species, and indeed taxa at all levels, are real in that they represent clusters of similar organisms that are separated by gaps. That is to say, the gaps between taxa represent intermediate organisms that we can imagine but don't actually exist. This cluster-and-gap pattern emerges inevitably from the genealogical continuity of all organisms, in which some lineages have succeeded to the present whereas others have gone extinct, yielding gaps in