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Social Learning: Parents May Not Always Know Best

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ABSTRACT

The efficiency with which animals learn new skills depends on their ability to choose good tutors. A new study shows that early-life stress causes young zebra finches to switch tutor preference from parents to unrelated adults.

For over half a century, we have been fascinated by the way in which animal populations acquire novel behavioural skills that spread from individual to individual. The copying of behaviour, and the regional differences that often develop, can shine a light on the evolution of human culture [1]. One of the earliest examples of the spread of innovative behaviour in animals was made by Fisher and Hinde [2], who described the diffusion of the stealing of cream from foil-capped milk bottles by various British tit species—a behaviour that spread across the country from the 1920s to 1940s. While this original study was observational, and could potentially have been caused by individual learning, a recent experimental study [3] revisited this classic example and demonstrated that blue tits (*Cyanistes caeruleus*) can efficiently acquire the necessary skills to exploit this very unnatural — but rich — resource by observing others.

‘Social learning’ refers to individuals acquiring important life skills by watching their peers. This important route to new skills is found widely across the animal kingdom, and has been particularly well studied in primates, rodents, birds and fishes [4]. Social learning has been observed in many different contexts — from finding and processing food, to avoiding predators and choosing mates [5–7]. An intriguing new study by Farine et al. [8] published in a recent issue of *Current Biology* now shows that the social learning strategy of an individual is dependent on experience early in life. The implications of this study are important, because such condition-dependent social learning strategies may be able to alter diffusion patterns of behaviour through a population. The study also suggests that there may be a critical period early in life that sets an individual’s cognitive developmental trajectory.

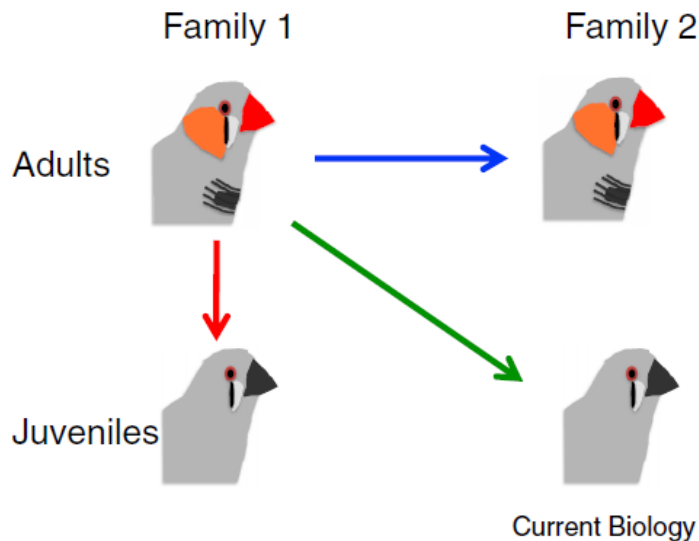
Social learning is widespread in the animal kingdom. This is because much behaviour is openly apparent to most members of a population, if they pay attention to this ‘social’ or ‘public’ information. For example, hatchery-reared salmonids rapidly learn to eat live prey items when partnered with a tutor because the behaviour of the tutor is highly salient [9]. Alternatively, it may pay for one individual to pass on a particular behaviour to another, perhaps because of close kinship. In birds and mammals, where there is often prolonged and extensive parental care, individuals acquire much information from their parents, during ‘horizontal social learning’. However, other adults in the population can also be valuable tutors to young (‘oblique social learning’; Figure 1) and their accessibility will depend upon the social structure of the wider population.

Our ability to identify the pathway by which information flows through natural populations has improved through sophisticated analytical methods that consider the social networks in which animals live. For example, a recent study used a network-based approach to demonstrate how a novel hunting method (tail slapping combined with a bubble net), may have spread from a single individual through a population of humpback whales over a period of 27 years [10]. A similar diffusion of novel skills through a social network has also been recently demonstrated in monkeys and birds [5,11].

Social learning increases the speed with which a population can adapt to new situations — rats are particularly good at learning socially about opportunities and risks in the human world [4]. However, evolution acts at the individual level, and social learning can be viewed as a form of ‘information parasitism’ [12]. Social learners can prosper by ‘scrounging’ new behavioural solutions at the expense of ‘producers’ that are likely to bear some cost for their own propensity to explore and innovate. However, the benefits of social learning are frequency dependent: if too few individuals are actively sampling the environment, then socially learned information may be out of date. Individuals often actively weigh the relative costs and benefits of social and asocial learning, which can be context specific and vary between individuals [13].

Figure 1. Three different pathways of social learning in a population.

Vertical transmission where information is transmitted from parents to their offspring (red). Horizontal transmission where information is transmitted within a generation (blue). Oblique transmission where information passes between generations but to unrelated individuals (green). In the study by Farine et al. [8] juveniles that were stressed at an early stage of development switched from the red to the green pathway illustrated to acquire foraging skills.



In highly gregarious species, an inquisitive tutee has a whole network of adults from which it can potentially learn. However, for every winning strategy, there will be lots of alternatives that are off-target with respect to their effect on individual evolutionary fitness. In animals, as in human culture, there will be good role models as well as bad ones. Two recent studies have found evidence that in some situations the best solution to this challenge is to conform to a social norm, even though it might not provide the best solution [5,14]. In these ground-breaking studies (in a species of bird and monkey, respectively), wild animals were taught foraging skills that were

locally common and readily transmitted socially to newcomers that adopted them even when they ran counter to the benefit of their own experience. These studies provided compelling evidence of the potency of social learning and its ability to establish local cultures and fashions.

In highly social species a major challenge has been to understand how individuals judiciously choose the best tutors [15]. Who is best to copy and learn from? Often the best tutors will be highly placed in the social hierarchy or may be particularly good at a certain task. For example, guppies prefer tutors that are familiar and of large size [16].

Figure 2. The social network.

Wild zebra finches are gregarious and move around together in small social groups. Inexperienced individuals have lots of potential tutors, but which one to follow?



In the new study, Farine et al. [8] studied the development of foraging skills in a captive population of zebra finches (*Taeniopygia guttata*; Figure 2). These birds live in the Australian arid zone, a challenging landscape, where the unpredictability of rainfall can result in long periods of 'boom and bust'. Wild zebra finches breed in loose colonies and routinely move around in small groups to forage [17]. In their experiment, half of the chicks in each of the experimental nests were exposed to elevated levels of the stress hormone corticosterone for about two weeks early in their development. Their siblings (in the same nest), were given a control treatment at the same time. When the youngsters were old enough to leave their parents, whole families were moved into experimental aviaries that contained multiple families for twenty days, thus providing opportunity for the youngsters to interact with adults other than their parents and other peers of the same age. The temporal associations between individuals when visiting feeding stations were used to delineate a social network.

After this period, in which the baseline social network between individuals was established, a novel foraging task was introduced into the aviaries—the zebra finch equivalent of the blue tit 'milk bottle challenge'. Spinach was provided in small wells covered with cardboard lids that had

to be removed by foraging birds. Spinach is a treat for these birds that normally survive on a diet of dry seed. Despite only being given a relatively brief period to acquire this novel skill, individuals were motivated to learn and overall 62% of the juveniles and 42% of the adults learned how to get the food reward.

A comparison of the best models to fit the social networks with the time taken by individuals to learn the skill indicated that individuals learned from adults rather than juveniles. This is consistent with findings in a number of other species. The important breakthrough was that the control group offspring typically learned from their parents, while the offspring exposed to higher levels of stress hormone during development learned faster, and learned almost entirely from other adults, even though they still associated with their parents to about the same degree as their siblings [8].

The mechanism underlying this switch from a vertical to an oblique pattern of social learning is not clear from the current study. A previous study of the same species found that exposure to stress hormones early in life increased an individual's learning ability in isolation through trial-and-error learning [18]. Exposure to stress hormones during the same period or early life has also been shown to change the rate of development, with manipulated individuals smaller and in poorer condition at that stage, but managing to catch up later in their development to full adult size [19]. In the new study [8], corticosterone-treated juveniles spent marginally more time with unrelated adults which provided further opportunity for social transmission of foraging behaviour.

An intriguing possibility suggested by the authors, and worthy of further attention, is that it may be adaptive for an individual to switch social learning strategies when they have suffered a poor start to life. In animals that have extensive parental care, such as many mammals, birds and fish, a stressful start to life may be indicative of parents that are struggling to cope with conditions. It might make sense under those circumstances to switch one's learning attention to other adults whom may be doing better. It's news that will bring joy to many teenagers: maybe parents don't always know best after all?

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