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Animal Behavior: Social Learning by a Whisker

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Banded mongoose pups learn foraging preferences from unrelated group members rather than their parents, suggesting that cultural transmission maintains behavioral diversity in groups.

> "Learning would be exceedingly laborious, not to mention hazardous, if people had to rely solely on the effects of their own actions to inform them what to do".
>
> Bandura and Walters (1977) [1]

Few things are more important than learning what is safe and nutritious to eat — after all, eat the wrong thing and you may die. For many mammals, all of which are born relatively altricial and in need of early care, offspring usually learn from their mothers what to eat. Dietary preferences can be transmitted through mother's milk in rats and humans, suggesting that early food preferences are formed from physiological transmission of foraging knowledge [2,3]. However, dietary preferences can also be learned later in life by copying others. Black rat pups, for instance, learn from an adult demonstrator how to acquire food by stripping pine cones [4]. Rat pups also learn which foods are safe to eat by choosing sites where they see adults feeding [5]. This non-genetic phenomenon, called 'cultural transmission', allows learned information to be transmitted across generations and has been demonstrated in apes, dolphins and birds [6–8]. Yet, to convincingly identify learning, and specifically whom animals learn from, it is essential to isolate vertical learning from parents, and horizontal or oblique learning from other group members. One way to understand the relative importance of maternal influence and environmental experiences is to switch animals at birth — for instance when birds' eggs are cross-fostered by moving them between nests [9] or between species [10]. If an individual exhibits a trait from their parents and not their foster, then the trait can be assumed to be largely genetic or parental in origin, while if they show a trait from their foster and not their parents, the trait can be assumed to be largely environmental in origin. Cross-fostering is even possible with marsupials, where joeys have been moved between pouches [11] but is more technically challenging for placental mammals in the wild where many young are born in burrows. In this issue of *Current Biology*, Catherine Sheppard, Harry Marshall, Mike Cant and colleagues capitalize on a unique mammalian rearing system of the banded mongoose, which naturally mimics cross-fostering, to convincingly show that the foraging preferences of pups are shaped not by their mothers' preferences but by exposure to specific non-relatives [12].

Banded mongooses live in groups of approximately 20 adults plus offspring. They are plural breeding cooperative breeders, meaning that many females breed at once and all members of the group contribute to rearing the young.

Mike Cant and his colleagues have been studying the social dynamics of a Ugandan population of banded mongooses for over two decades [13]. When mongoose pups emerge from their natal burrows (about a month after birth), they form a foraging relationship with one or more unrelated adults (Figure 1). Pups follow these animals closely and eat what they eat. These 'escorts' spend their days with pups until they are nutritionally independent, at about three months of age. This makes the mongoose system unique in that after weaning, pups are not reared by their mother, but by unrelated helpers.

Prior work by this group showed that pups learn from escorts to obtain food from puzzle boxes [14]. To further investigate whether pups learn about food from their escorts, Sheppard, Marshall and colleagues [12] capitalized on a nifty trick. As you are what you eat, stable isotopes of carbon and nitrogen from different consumed plants and animals are assimilated into body tissues and can be measured through their unique isotopic signatures. Thus, the researchers collected 4–5 whiskers from each mongoose and asked whether the carbon and nitrogen isotopic signature in pups resembled those of their escorts or their parents. As whiskers are fully replaced after about 6 months, they expected that younger mongooses would show isotopic signatures similar to their mothers due to maternal provisioning, while isotopic signatures of older mongooses would reflect diet preferences learned from escorts.

Younger pups did indeed show similar isotopic signatures to their mothers [12], while the isotopic signature of older pups more closely resembled that of their escort(s) than that of a randomly selected animal and these similarities persisted into adulthood. From this, Sheppard, Marshall and colleagues [12] concluded that an individuals' dietary preferences were established by copying the foraging preferences of the unrelated individuals who reared them.

Additionally, Sheppard, Marshall and colleagues [12] investigated copying fidelity by looking at how closely isotopic signatures matched escorts in pups with a single escort compared to those with multiple escorts. Information can be culturally transmitted through one-to-one transmission between individuals or by many-to-one transmission with several animals passing on information to a pup. These different modes of transmission have implications for the diversity of behaviors adopted by members of a group. Previously, it was found that behavioral diversity in banded mongooses is driven by intragroup competition [15]. Thus, the authors hypothesized that foraging preference in pups with a single escort would more closely resemble that escorts' preferences, while pups with multiple escorts would exhibit 'blending inheritance', showing a more diverse set of foraging preferences. Indeed, they found that pups with only one escort had isotopic signatures that more closely resembled their escorts' than pups with multiple escorts. Most pups have only a single escort, suggesting some fitness benefit to this strategy. Pups participating in this one-to-one transmission may miss out on eating a greater variety of food, but different foraging niches occupied by group members alleviates the intragroup competition they face [15].

Thus, rearing experience — rather than genetic similarity — is responsible for diet preferences in banded mongoose. And rearing experience is not maternal, but rather comes from a non-relative. In addition, if more than a single non-relative rears a pup, the pup's foraging preferences are blended from the preferences of each escort.

Environmental and maternal predispositions may not always be decoupled in complex social systems, but this unique system provides a clear case study showing that it is possible for young to learn what to eat from non-relatives. The new study by Sheppard, Marshall and colleagues [12] provides a strong case for cultural transmission in animals and sends an important message: non-relatives may influence juveniles in learning some of their most important lessons — what is safe to eat. In addition, cultural transmission promotes a mix of preferences that reduces intra-group foraging competition, allowing groups to be larger with enhanced individual fitness. Finally, this study shows that stable isotope analysis can quantify the nutritional effects of cultural transmission, providing a new technique to measure transmission that can be used in other species, including those where tracking transmission with social observations may be difficult.

Figure 1. Mongoose food guide.
A banded mongoose pup beside its escort. Photo: Feargus Cooney.

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Motor Control: Three-Dimensional Metric of Head Movements in the Mouse Brain

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Many forms of human and animal behavior involve head movements. A new study reveals the neural code for three-dimensional head movements in the midbrain of freely moving mice.

As I am typing these words, my head and eyes are constantly moving in different directions to follow the letters on the monitor. Occasionally, I am turning my head down to look at the keyboard or sideways to prepare a reach towards my coffee mug. In fact, most of our interactions with the world involve orienting movements towards different points of interest in three-dimensional space. Orienting behaviors are crucial for all animals in multiple contexts, such as exploration or in response to attractive or aversive stimuli. However, little is known about how three-dimensional orienting movements are encoded in the brain of freely moving animals. An important step has now been made by Wilson *et al.* [1], who report in this issue of *Current Biology* their new study of the neural representation of three-dimensional head movements in freely moving mice.

In 1870, Adamuk [2] reported that electrical stimulation of the superior colliculus induces eye movements. Research conducted a century later, primarily in head-fixed monkeys, revealed that neurons in this brain region encode a metric for fast eye movements called saccades. Specifically, neurons in the deep subdivision of the superior colliculus were shown to respond preferentially to a particular saccade vector — defined by direction and size of the resulting eye displacement, irrespective of the initial eye position [3]. These neurons produced a vigorous burst of activity shortly before eye-movement initiation. Microstimulations of different parts of the superior colliculus resulted in saccade vectors that varied systematically according to the site of stimulation [4]. Furthermore, neurons recorded at corresponding locations during natural eye movements showed preferences to saccade vectors matching those evoked by microstimulations [5], indicating that this brain region contains a topographic map of eye movements.

In addition to eye movements, in a variety of species, microstimulation of the superior colliculus has been shown also to induce movements of the head and other body parts [6]. These observations suggest a role of the superior colliculus in orienting movements in general. In primates, orienting responses typically involve combined eye and head movements [7], aimed at centering points of interest in space on the fovea — the part