

Animal Traditions: Experimental Evidence of Learning by Imitation in an Unlikely Animal

A new field study provides the first experimental evidence of learning by imitation in a free-living animal and demonstrates that social learning can maintain two behavioral traditions in a single population.

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The possibility that non-human animals living in natural environments have ‘culture’ has been of great recent interest [1]. However, the absence of successful experimental demonstrations of enduring effects of social learning in the development of behavioral repertoires of free-living animals has been a serious problem for those trying to understand the role of tradition in animal life. The field experiment conducted by Corsin Müller and Michael Cant in Queen Elizabeth National Park, Uganda, and reported in this issue of *Current Biology* [2], is a major step forward in solving that problem.

Müller and Cant’s [2] field experiment took advantage of the habit of young banded mongooses (*Mungos mungo*) to form one-on-one associations with older, non-breeding males (escorts). Juveniles are no more closely related to their escorts than they are to other group members, and each juvenile does much of its foraging in the immediate vicinity of its escort (Figure 1). Consequently, juveniles have ample opportunity to observe escorts overcome any defenses of potential prey.

Müller and Cant’s [2] experimental work complements the impressive bodies of data field researchers have amassed in recent decades suggesting that social transmission of behaviors from one group member to another results in differences in the behavioral repertoires of independent groups of free-living animals [3–5]. For example, chimpanzees living to the east of the N’Zo-Sassandra River in the Ivory Coast use stone hammers and anvils to crack nuts, whereas most chimpanzees living to the west

of the river do not, even though all have access to nuts and to stones to use as hammers and anvils [6].

As the nut-cracking example suggests, in the past, evidence of traditions in animals has rested on the ‘ethnographic’ method or ‘method of contrasts’ in which detailed catalogues of the behavioral repertoires of sub-populations of a species, most often a primate [3–5] or cetacean [7,8], are compared. If a behavior is observed in many members of one social group and in no members of another, and there are no obvious differences in the ecology in which those groups live and no reason to believe that the groups differ genetically, then the behavior is provisionally accepted as traditional [4].

However, because the ethnographic method rests solely on observation, it provides only indirect evidence that differences in the behavioral repertoires of sub-populations of a species result from the social transmission of behaviors between individuals. For example, differences in aggressiveness of ant species chimpanzees capture using plant stems as tools result in differences in the techniques that chimpanzees use to capture ants [9,10]. More generally, the possibility always exists that any potentially traditional behavior identified using the ethnographic method reflects some as-yet undiscovered differences in either the environments that groups occupy or in their genetic compositions, rather than social transmission within groups [11,12]. Experimental evidence of social transmission of potentially traditional behaviors in a free-living population provides the best way to establish that any purportedly traditional behavior is, in fact, traditional.

Although a number of previous experimental studies have demonstrated social learning in free-living animals, evidence of stable behavioral traditions resulting from such social learning has been limited to the song dialects of birds [13], and no experiment with free-living animals has provided convincing evidence of learning by imitation in the transmission of behavior between individuals in natural environments. Even in the laboratory, imitation in the sense of ‘learning to do an act from seeing it done’ [14] has proven surprisingly difficult to demonstrate convincingly, and awaited introduction of the ‘two-action’ method [15] that provides the current ‘gold standard’ in laboratory investigations of imitation in both animals and children. The two-action method involves two steps: first, allowing a naïve subject to observe a demonstrator direct one of two readily distinguished actions towards an object and obtain a reward; and second, subsequently testing each subject to determine whether it interacts with the object in the same way as did its demonstrator.

Among the many foods exploited by adult mongooses are several, such as birds’ eggs, that have hard exteriors. Adult mongooses crack open such prey in either of two ways: by holding the item with their front paws and biting it; or by throwing the item against a rock or other hard object. Müller and Cant [2] began by presenting adult escorts, in the absence of their juvenile companions, with an artificial egg containing odiferous food. Some adults used only the biting method to open these artificial eggs, whereas other adults most frequently threw artificial eggs against hard objects to open them.

Pups in two experimental conditions were then allowed to watch while their adult escorts repeatedly used either the biting or



Figure 1. A juvenile banded mongoose closely following its adult escort as they forage in Queen Elizabeth National Park, Uganda (Photo: Corsin A. Müller).

throwing technique to open artificial eggs and feed from them. Two to four months after the last of these observation trials, the now-independent juveniles were each presented on ten occasions with an artificial egg. Amazingly, juveniles preferred to use the technique that they had observed their escorts use several months earlier and most continued to prefer that technique when tested months later in adulthood.

These data [2] provide both the first successful experimental induction of a traditional behavior in a free-living population of animals and the first evidence from a field setting of what has been labeled 'contextual imitation', defined as learning by observation when a behavior already in an individual's repertoire should be performed (as distinct from 'production imitation' learning by observation to perform a novel act) [16]. The findings are important for several reasons. First, as indicated above, the primary field evidence of tradition in free-living animals, derived from the ethnographic studies, has been discovery of homogeneity within and heterogeneity between the behavioral repertoires of groups. The new data [2] strongly suggest that behavioral heterogeneity rather than homogeneity can be maintained within a social group by parallel social transmission of behaviors. Second, Müller and Cant's [2]

observations provide evidence consistent with a growing body of data indicating the importance of association patterns in directing diffusion of socially learned behaviors in animal groups [17–19]. And third, the data are the first to provide strong evidence of contextual imitation in the social transmission of behavior in a free-living population.

The experiment reported by Müller and Cant [2] is, of course, not perfect; both escort mongooses and their young companions were free to assign themselves to experimental conditions. Consequently, it remains possible that for unknown reasons, young mongooses with a proclivity to use a particular method to open artificial eggs chose, as escorts, adult males with a similar proclivity. However, finding a species in which juveniles associate exclusively with unrelated adults is, in itself, of immense potential value, providing opportunities for further investigations of social learning in free-living mammals conducted with the same level of scientific rigor as similar experiments carried out in the laboratory.

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