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Potent Social Learning and Conformity Shape a Wild Primate's Foraging Decisions

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Conformity to local behavioral norms reflects the pervading role of culture in human life. Laboratory experiments have begun to suggest a role for conformity in animal social learning, but evidence from the wild remains circumstantial. Here, we show experimentally that wild vervet monkeys will abandon personal foraging preferences in favor of group norms new to them. Groups first learned to avoid the bitter-tasting alternative of two foods. Presentations of these options untreated months later revealed that all new infants naïve to the foods adopted maternal preferences. Males who migrated between groups where the alternative food was eaten switched to the new local norm. Such powerful effects of social learning represent a more potent force than hitherto recognized in shaping group differences among wild animals.

Ever since pioneering studies on the diffusion of a new sweet-potato washing habit in Japanese macaques (*1*) and milk-bottle opening in great tits (*2*), accumulating field studies have suggested that the cultural transmission of behavior through social learning provides many animals with a "second inheritance system" (*3*). This system complements genetic inheritance and individual learning in shaping behavioral repertoires (*4*, *5*). The scope and impact of this second system are important to delineate because exploiting the existing knowledge of others can potentially support efficient adaptation to local circumstances (*6*). It can also generate locally differentiated behavioral traditions, and indeed, much of the evidence for a role for animal culture in the wild derives from identifying local variations consistent with the existence of such traditions (*7–9*). However, owing to their observational nature, these studies lack the experimental rigor to confirm whether putative cultural variations are socially learned. Experiments with captive populations, by contrast, have seeded different groups with models trained to act in different ways, such as opening an "artificial fruit" using either of two alternative techniques, then documenting the differential diffusion of these variants across groups (*10*) and even between them (*11*).

These paradigms have now produced a substantial corpus of laboratory studies documenting cultural transmission in taxa as diverse as insects (*12*), fish (*13*), and apes (*11*, *14*). Such experiments in the wild remain scarce (*10*, *15–19*), however, because in natural populations, it is typically impractical to isolate individuals for differential training as models. The few field studies that have attempted to approximate this approach have generally produced evidence for weaker transmission of the seeded alternatives (*15–18*) than counterparts in captive populations (*10*, *11*, *20*, *21*).

Here we introduce a different methodological approach, which has demonstrated two potent effects of social learning in the wild. Instead of seeding behavioral variants in single models, we seeded variants in four whole groups of wild vervet monkeys, *Chlorocebus aethiops*, totaling 109 individuals (*22*) (table S1 and fig. S1). We then investigated how two classes of individuals naïve to the local group norm—infants and immigrant males—responded to the particular local preferences they were exposed to. To create initial preferences, we provisioned groups with two adjacent trays of maize corn, one with corn dyed blue, the other pink (Fig. 1). One of these (pink in two groups, blue in two others) was made highly distasteful so that after three monthly training sessions, the distasteful alternative was rarely eaten or even tried (table S2 and figs. S3 and S4). After a period of more than 4 months in which a new cohort of identifiable infants matured sufficiently to take solid foods, we again offered the two colored foods with no distasteful treatments and tested (i) whether the naïve infants would copy their mother's preference for the locally favored color over the now equally palatable alternative, and (ii) whether males migrating from a group trained to prefer one color to a second group where the alternative color was preferred would be influenced by the latter.

When the corn provisions were offered again after 4 to 6 months, a preference for the earlier palatable alternative was maintained across five test trials spanning 2 months, despite both colors now being palatable. Some of the previously distasteful food was tried and consumed (Fig. 2 and

Fig. 1. Experimental setup illustrating preferential foraging. Maize corn dyed either pink or blue was provided intermittently in two adjacent containers. Photograph shows infant sitting on the color earlier made distasteful to its mother, as it eats the color currently preferred by its mother and the rest of the group.

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table S3B), but typically only by lower-ranking individuals when they were unable to access the preferred color (table S4), with the result that at least 73% of the corn eaten in any trial was of the trained color (Fig. 2). This persistence of the induced preference over our five trials is important because new subjects joined the experiments up to trial 5.

Of 27 infants naïve to the corn provisions, 26 first ate the locally preferred color eaten by their mother, ignoring the directly adjacent alternative color (some even sat on the nonpreferred color corn, to eat the favored one: Fig. 1). Just one infant's first choice was of the alternative-colored food. Its mother was of low rank and took a small amount of the nonpreferred food while higher-ranked individuals were monopolizing the preferred food. Accordingly, 27 of 27 infants first took the food they witnessed their mothers eat (for 26 of them, the one they would also see most eaten in their group). This represents a highly significant bias that unambiguously demonstrates copying of the local preference (binomial test, $P < 0.0001$), despite the immediate availability of the alternative option. All 23 of such infants who were later recorded eating when their mothers were not at the box continued to match her preference, confirming that their preferred food choice was a result of social learning.

Fifteen males immigrated into the study groups during the experiment (Fig. 3 and fig. S2). Ten were known to us and fortuitously moved to a group that preferred the alternative colored food to that eaten in their original group (Fig. 3 and fig. S2). The first choice of seven of these males, on approaching the food provisions after observing others feeding there, was for the locally preferred option new to them, contrasting markedly with the 11 resident males, none of whom chose their formerly distasteful option (choices 7 of 10 versus 0 of 11: Fisher's exact test, $P = 0.001$, Fig. 3). When each of the 10 migrants first fed with no monkey higher ranking than themselves present, their preference for the locally consumed color was even more pronounced (choices 9 of 10 versus 0 of 11: Fisher's exact test, $P < 0.0001$). The single male (Lekker) who continued to eat the same color as in his original group was unique in immediately taking the top rank in his new group, a factor that may have influenced his behavior. Five additional males migrated into our groups from unknown origins and so were naïve to both colors of corn. The first choice of all of these when no higher-ranking monkey was present was for the local norm. Conservatively testing the preference of all 15 migrant males for the local preference against a random choice confirms a significant positive bias (i.e., 14 of 15: binomial test, $P = 0.001$). Additional tests extending to later feeding on the different options are in the supplementary text and converge with the results above in demonstrating conformity in the migrants' foraging decisions.

Our demonstration of such strong conformity in wild primates has important implications for our conceptions of what is unique in human cultural transmission (*23–27*) as well as in evolutionary biology more broadly, concerning the roles of cultural versus genetic inheritance and individual learning in shaping adaptations. First, our results reveal a potent role for social learning in both infants and migrating adult primates, which for the latter group extends to social conformity, defined in human studies by the flexible subjugation of prior personal knowledge to the observed habits of a majority of the relevant new community (*28*) (see supplementary text for more on definitions of conformity) (Fig. 3). Laboratory studies have begun to suggest a role for such conformity in taxa ranging from *Drosophila* to chimpanzees (*12*, *14*, *29–31*), but in the wild such evidence has remained minimal and circumstantial (*32–34*).

Theoretical work has suggested that reliance on such social information at the expense of personal information can be adaptive because it exploits the fruits of other individuals' prior experience (*6*, *23*, *27*). The actions of both the naïve infants and migrating males whom we studied is consistent with such a "copy when uncertain" strategy. The fitness of foraging decisions made by wild primates like those we studied will be governed by a host of complex factors that are inherently unknown to foragers, ranging from dietary constituents to plant toxins and competing needs such as predator vigilance: Exploiting the prior discoveries of local experts may be an optimal strategy, overriding opposing knowledge gained in a different habitat such as one's original group.

A second implication of our results is methodological. We have simulated the effect on social learning of already well-established traditions by initially creating habits in whole groups, then recording the responses of infants and migrants naïve to these habits. This has revealed very strong effects, contrasting with the relatively weak or nonexistent effects of seeding alternative behavior patterns in single individuals, found in other recent field experiments (*15–18*). Our new approach thus could be applied more widely to other taxa in the wild, as well as in captive studies.

The final implication arises from the combination of the two already outlined. If copying the majority is indeed a more widespread strategy

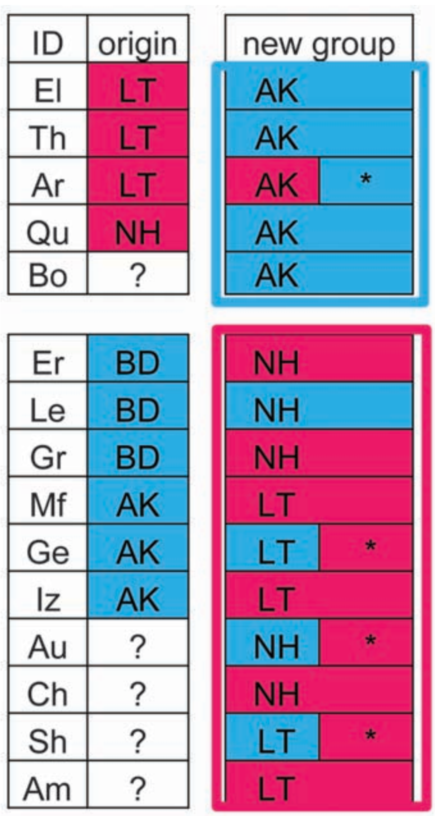

Fig. 3. Males abandon food preference learned in home group in favor of local preference in new, adopted group. Columns show food color preference of each male in original group (origin) and contrasting first choice of food color in adopted new group (framing lines represent preference in adopted group). Asterisk (*) denotes choice of color eaten first once not outranked by residents of adopted group. ID, male identity code.

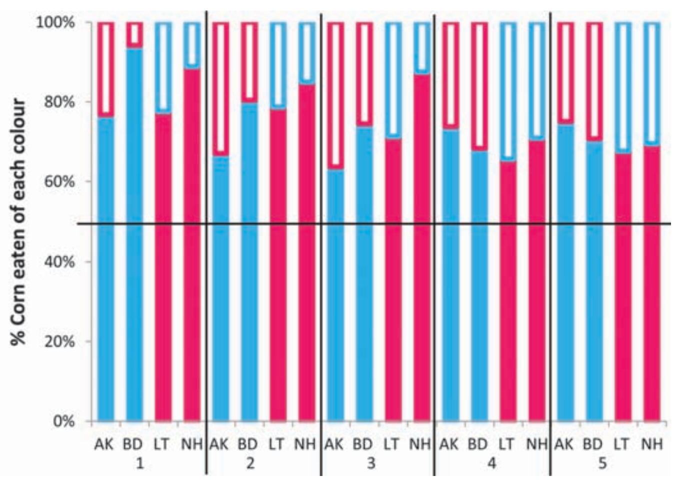

Fig. 2. Local food preference norms of four groups. Percentage of each color of food eaten in each group across the five test trials separated, respectively, by intervals of 1, 1, 2, and 4 weeks. Pink, pink dye; blue, blue dye. Full color bars, food color always palatable; white color bars, food color made unpalatable 4 to 6 months earlier. Letter codes represent the four groups (AK, Ankhase; BD, Baie Dankie; LT, Lemon Tree; NH, Noha).

among wild, nonhuman animals than previously appreciated, the initial establishment of behavioral innovations may be a fragile process, in comparison to the transmission of already-common behaviors. If so, this argues not only for the extension of our group-training approach, but also for systematic comparisons between such experiments and those that instead seed new behaviors in individuals, in order to understand why some innovations are short-lived whereas others spread to become new traditions.

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Supplementary Materials

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Network-Based Diffusion Analysis Reveals Cultural Transmission of Lobtail Feeding in Humpback Whales

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We used network-based diffusion analysis to reveal the cultural spread of a naturally occurring foraging innovation, lobtail feeding, through a population of humpback whales (*Megaptera novaeangliae*) over a period of 27 years. Support for models with a social transmission component was 6 to 23 orders of magnitude greater than for models without. The spatial and temporal distribution of sand lance, a prey species, was also important in predicting the rate of acquisition. Our results, coupled with existing knowledge about song traditions, show that this species can maintain multiple independently evolving traditions in its populations. These insights strengthen the case that cetaceans represent a peak in the evolution of nonhuman culture, independent of the primate lineage.

Debate about traditions and culture in nonhumans has been fueled by claims of evidence for culture, broadly defined as shared behavior propagated by social learning (*1*), in a variety of species (*2–5*), including cetaceans (*6*). Quantifying cultural transmission in any wild population is difficult, however, because field studies are rarely sufficient to allow for the complete elimination of alternative genetic or ecological explanations (*1*, *7–9*). These problems are exacerbated by the limitations on visibility and accessibility inherent in studying marine mammals, but the group continues to attract interest due, for example, to the strong evidence for cultural transmission of vocal patterns (*10*, *11*). Only a handful of cetacean species have lent themselves to the types of data collection necessary to address questions of cultural transmission (*6*), and the evidence remains, for the most part, controversial (*1*).

In the Gulf of Maine, bubble-feeding is a common foraging technique used by humpback whales (*Megaptera novaeangliae*), which is characterized by bubble production 20 to 25 m below the surface, underneath and around a prey school, followed by a lunge through those bubbles (*12*, *13*). Although this general technique has been documented in other humpback populations (*14*), in 1980 one whale in the Gulf of Maine was observed performing an innovative modification to this feeding technique that is now known as lobtail feeding (*13*, *15*). Lobtail feeding consists of striking the water's surface one to four times with the ventral side of the fluke, followed by a bubble-feeding sequence. An accelerating rate of diffusion of this behavior, indicated by a sharp increase in the proportional use of lobtail feeding in the years 1981–1989 (Fig. 1), led to the suggestion that social transmission was responsible for its spread (*15*). Diffusion rate, however, is not a reliable indicator of social transmission (*16*). Furthermore, it has been suggested that lobtail feeding is a specialization related to foraging on sand lance (*15*), because it is spatially concentrated on Stellwagen Bank (Fig. 1A), where sand lance gather for spawning (*17*). In the years immediately preceding the behavior's emergence, the stock of herring, another important prey species, crashed (*18*), suggesting a role for ecological factors. Because such factors are a common influence on innovation and social learning, these hypotheses are not necessarily mutually exclusive, but it is difficult to measure the relative influence of social and ecological factors on the spread of behavior (*1*, *9*). Network-based diffusion analysis (NBDA) (*9*, *19*, *20*), a new method related to network influence models in the social sciences, offers one way forward [see also (*5, 21*)]. We used NBDA to analyze the spread of the lobtail feeding innovation among humpback whales summering in the Gulf of Maine.

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