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Social Dynamics: Knowledgeable Lemurs Gain Status

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A new study shows both that socially well-connected lemurs are more likely to acquire new behavioral innovations, and that individuals displaying such useful new knowledge gain in status. Such positive feedback loops may help explain resilient cultural transmission in animals.

Recent years have seen a productive integration between two fields of enquiry in the life sciences: the study of animal culture, and the investigation of social networks. Animal culture, the study of information transmission via social learning, is the more mature science, with roots back in the middle of the last century [1]. In recent times it has become a burgeoning field, demonstrating social learning and the transmission of functionally important behaviors, from foraging to migration to communication, in a wide range of vertebrate and invertebrate species [1]. The study of animal social networks has a younger pedigree, largely developing over the last two decades, driven by the construction of a range of sophisticated numerical and statistical tools to analyse social relationships [2,3].

A productive integration between these two fields has identified cultural transmission in communities of wild animals by tracking the diffusion of behavioral innovations across social networks. Examples include the spread of 'lobtail feeding' through a population of over 600 humpback whales over 25 years [4] and the diffusion of a new form of tool use among a community of chimpanzees in a matter of days [5]. Another approach has been to examine the implications of network structures for cultural transmission, as in the finding that squirrel monkeys that are socially well connected (have high 'network centrality', in the jargon) are more likely to pick up new experimentally seeded foraging innovations and acquire the particular technique so seeded in their group [6]. A study of ring-tailed lemurs (*Lemur catta*) published in this issue of *Current Biology* [7] reports a similar effect but adds an important new discovery of the converse causal effect, namely that individuals who are in the vanguard of adopting a new innovation are likely to become more socially central (they received more affiliative initiatives, for example). The bi-directional causality these results imply has a number of significant implications for our understanding of sociality and cultural transmission in animals, discussed further below.

The lemurs studied by Kulahci *et al.* [7] belong to two groups that are the descendants of animals introduced to St Catherine's Island off the coast of Georgia, USA, in 1984. They are the only free-ranging groups of ring-tails outside the species' homeland of Madagascar. To study the social diffusion of an innovation, the experimenters introduced a novel foraging task that involved extracting a single grape (to avoid scrounging effects) from a drawer in a small plastic box (Figure 1). Before this was introduced to each group, individuals' positions in the social network were established from observations of who approached whom, and who groomed whom. These observations provided measures of the number ('degree') and frequency ('strength') of each individual's connections with others. These were further split according to whether actions were initiated by the individual towards

others, or instead directed by others towards them.

The first lemurs to solve the task in each group were juveniles (suggesting a 'curiosity bias' in the young, commonly observed in studies of primates and other animals). Subsequently other group members successful in the task (22 of the 38 lemurs in the two groups) observed the success of others (typically watching several others, and multiple successes) before their own first success. Analyses revealed that it was individuals' tendency to initiate interactions with others, in particular approaching them, that predicted successful acquisition of the task, and not others' tendencies to approach them. This echoes similar recent findings of social centrality predicting the social learning of innovations in both squirrel monkeys [6] and ravens [8].

The frequency of an individual's solving the task predicted the frequency with which they were observed, in line with other recent studies showing primates' readiness to access valuable social information [9]. To investigate the possibility that such effects might in turn influence an individual's network position, the authors compared network centrality measures before and after the experiment with the artificial foraging task. It was found that the most frequently observed individuals gained in centrality; in particular, they received more affiliative behaviour (approaching, grooming) after the experiment than before it. Interestingly there was no effect on their tendency to direct such behavior to others. The effect was one-way: they became more attractive to others. This was not because others could directly scrounge, because in the 'after' condition the foraging box was no longer present. The effect echoes one shown earlier by Eduard Stammbach, a student of one of the founders of primate social cognition studies, Hans Kummer, wherein high ranking longtailed macaques came to gradually lessen their initial tendency to displace low ranking individuals who had been trained how to gain plentiful food from a foraging device. Some high-rankers came to groom the new expert more even outside the foraging sessions [10]. However the new lemur study is the first to show

Figure 1. A lemur pulls a drawer to extract a food reward from a novel artificial foraging device.
Group mates were more likely to approach and groom individuals who successfully learned the skill, even after this foraging option was no long available (photo: Ipek Kulahci).

bidirectional effects operating within the same social system, with the acquisition of a new skill enhancing social centrality, and more central individuals most likely to acquire new skills by social learning.

The authors emphasise that the enhancement of affiliative responses was recorded after the experiment, so was not driven by short-term scrounging motivations. Instead, they suggest that their lemurs "may be preferentially associating and interacting with knowledgeable conspecifics for the long-term benefits of such social connections". Such a view of primate sociality is consistent with a recent, growing and exciting body of findings from long-term field studies, that extend to positive effects of relationship-building on fitness, indexed by reproductive success [11,12]. However, we should regard the reference here to "knowledgeable" conspecifics with some circumspection. It is true that the lemurs who succeed on the task and thence receive more affiliative advances must be knowledgeable about the foraging techniqes required; but this is not to say that what the other lemurs perceive and respond to is the knowledge states of others, as such. That would constitute 'mindreading' (aka 'theory of mind'), a capacity demonstrated in some primates [13] but an untested possibility in the present study. More parsimonious interpretations include that groupmates were responding to the enhanced foraging skill and/or success of the individuals concerned (although it is of course an interesting further research question as to whether they go beyond this to recognise underlying cognitive characteristics such as knowledgeability, or a capacity for acquiring valuable innovations).

In humans, individuals with such characteristics have been described as becoming 'prestigious' and figures from whom cultural traits are preferentially copied [14]. These authors postulate a difference between merely copying 'dominant' (high rank) individuals, for

which there is some evidence in primates (e.g. [11]), and copying the prestigious, who are instead 'freely deferred to' because of such characteristics as their expertise. It is asserted that "having evolved alongside cultural learning in the human lineage, prestige was a latecomer to our status psychology. We humans also possess a dominance psychology, which was inherited from our primate ancestors and is thus much older than prestige" (p.120 in [15]). However, the effects recorded by Kulahci *et al.* were unrelated to dominance status and instead attributable to the skill and success of those who attracted deference in the form of enhanced affiliate approaches. This appears to undercut the strong distinction made by Henrich, insofar as 'freely given deference' may have more ancient roots in animal sociality. Prestige may be better viewed as a supervening variable indexing what may be multiple ways in which groupmates show regard for the prestigious, which may include deference earned by expertise and other characteristics, including high agonistic dominance.

Kulahci *et al.* focus their discussion on social dynamics, but their results may also have significant implications for the nature of animal cultures, in particular their resilience. Authors focused on human culture and what distinguishes it from that of other animals emphasise its cumulative nature and argue that this is made possible, uniquely in our species, by capacities for high fidelity transmission via such processes as imitation and teaching [15,16]. This sounds plausible yet there are some serious problems with such ideas (one might almost call them present day dogmas). One challenge comes from other authorities on human culture, who argue that processes like imitation are unable in themselves to sustain resilient cultural transmission and change [17,18]: Morin [18], for example, points out that cultural diffusion experiments, typically heralded to demonstrate transmission, in fact typically display progressive loss of the arbitrary cultural differences experimentally seeded. Another challenge is presented by demonstrations of resilient longevity in animal traditions, notably over 4,300 years of chimpanzee tool-based nut-cracking in West Africa, revealed by archaeological excavations [19]. One can point to few instances of human material culture transmitted so faithfully across this period! How is such resilience maintained?

One obvious answer, seemingly neglected in these debates, is that behaviors like nut-cracking provide major benefits, likely to reinforce their long-term resilience. Another factor may be a disposition to conform, following the rule of thumb to copy what a majority of one's group have come to routinely do [20]. Now, the results of the lemur study suggest a further factor in the form of the feedback loops revealed, with traditions maintained by a self-reinforcing core of socially and culturally central individuals.

We now need to know how widespread such effects are in different animal taxa, especially amongst wild animals living in their natural environments of evolutionary adaptedness.

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