Animal Behaviour 79 (2010) 1353–1362

Contents lists available at ScienceDirect

Animal Behaviour

journal homepage: www.elsevier.com/locate/anbehav

One cultural parent makes no culture

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ARTICLE INFO

Article history:
Received 22 September 2009
Initial acceptance 30 November 2009
Final acceptance 9 March 2010
Available online 13 April 2010
MS. number: 09-00619R

Keywords:
culture
primates
social learning
tradition
uniparental transmission

The ability to acquire knowledge and skills from others is widespread in animals and is commonly thought to be responsible for the behavioural traditions observed in many species. However, in spite of the extensive literature on theoretical analyses and empirical studies of social learning, little attention has been given to whether individuals acquire knowledge from a single individual or multiple models. Researchers commonly refer to instances of sons learning from fathers, or daughters from mothers, while theoreticians have constructed models of uniparental transmission, with little consideration of whether such restricted modes of transmission are actually feasible. We used mathematical models to demonstrate that the conditions under which learning from a single cultural parent can lead to stable culture are surprisingly restricted (the same reasoning applies to a single social-learning event). Conversely, we demonstrate how learning from more than one cultural parent can establish culture, and find that cultural traits will reach a nonzero equilibrium in the population provided the product of the fidelity of social learning and the number of cultural parents exceeds 1. We discuss the implications of the analysis for interpreting various findings in the animal social-learning literature, as well as the unique features of human culture.

The capacity to learn from others is a characteristic feature of human existence, and cultural transmission is widely thought to be responsible for the extraordinary demographic and ecological success of our species (Boyd & Richerson 1985). Humans acquire valuable skills and knowledge from others, and build on this reservoir of shared culture in a cumulative fashion (Cavalli-Sforza et al. 1982; Boyd & Richerson 1985; Ghirlanda & Enquist 2007). Other animals also benefit from social learning, which allows them to acquire solutions to survival problems such as 'what to eat?' or 'how to evade predators?' rapidly and efficiently (Galef & Laland 2005). The number of examples of animal social learning increases steadily, with interest fuelled by high-profile reports of inter- and intrapopulation variation in the behavioural repertoires of animal populations, and spawning claims of shared culture in apes (Whiten et al. 1999; van Schaik et al. 2003), monkeys (Perry et al. 2003) and cetaceans (Rendell & Whitehead 2001; Krützen et al. 2005). Other researchers have documented vocal dialects in the songs of numerous species of birds (Catchpole & Slater 2008) and traditional behaviour in fishes (Warner 1988, 1990). Such claims are reinforced by many reports of the spread of novel behaviour in natural animal populations, where previously unseen behaviour rapidly increases in frequency in a population, too rapidly to be plausibly attributed to population genetic or demographic factors (Lefebvre & Palameta 1988). Animal social learning appear to be widespread among vertebrates, and present in many invertebrates too (Leadbeater & Chittka 2007), and to underpin a broad variety of behavioural traditions in animals.

One feature of the now extensive literature on animal, including human, social learning is that little attention has been given to whether individuals acquire knowledge from a single individual or multiple models. Researchers commonly refer to instances of sons learning from fathers, or daughters from mothers, with little consideration of whether this is actually feasible. Particularly in the primatological and cetacean literatures, it is often assumed that social learning from mothers to offspring plays an important role in maintaining shared culture (Boesch 1991, 1993; Coussi-Korbel & Fragaszy 1995; Reader 1999; Mann & Sargeant 2003). In a meta-analysis of studies of primate social learning, Reader (1999) found that mother to offspring learning is overrepresented in the literature, given the null expectations for particular age classes. Reader observed more instances of social learning reported in nonadults,

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0003-3472/$38.00
doi:10.1016/j.anbehav.2010.03.009

and fewer in adults, than would be expected by chance given the age distribution of individuals among the species tested. Similarly, adults are overrepresented as information transmitters. A large proportion of adult-to-nonadult cases (33/46) were reports of infants learning from their mothers, spanning 12 species. A well-known case is Boesch's (1993) claim that common chimpanzee, *Pan troglodytes*, infants learn to crack nuts from their mothers. Reader noted, however, that it is difficult to be certain that transmission from mother to infant or indeed any form of learning has genuinely occurred, on the basis of field observations alone. Other researchers (e.g. Coussi-Korbel & Fragaszy 1995) have suggested mother – offspring transmission is common in particular kinds (despotic) of primate society. In bottlenose dolphins, *Tursiops aduncus*, Mann & Sargeant (2003) noted that daughters acquire a repertoire of foraging behaviours that resembles their mother's, after spending long periods of time together. Birdsong is another case where people have reported males learning from fathers (e.g. bullfinches, *Pyrrhula pyrrhula*: Nicolai 1959; zebra finches, *Taeniopygia guttata*: Immelmann 1969; Darwin's finches, Geospizinae: Grant 1984; Millington & Price 1985; and marsh tits, *Poecile palustris*, Rost 1987). However, evidence that the father is the only cultural role model is frequently lacking. Far more commonly, young males copy their neighbours (Catchpole & Slater 1995). In summary, in the animal literature, reports of uniparental transmission exist but are comparatively rare, as they are in the human literature too (Shennan & Steele 1999), and far more commonly claims of biparental transmission or learning from multiple nonrelatives are reported (Boyd & Richerson 1985).

Our aim in this paper is to gain a theoretical understanding of how the number of cultural models affects the social learning and cultural transmission of knowledge and skills between generations. By definition cultural traits are learned, which means that they are not present at birth and may or may not be learned during an individual's lifetime. This means that every cultural trait can be described as absent or present in a given individual (i.e. has the individual learned how to fish for termites?). The same applies to humans, where the fact that individuals may vary in what vehicle they drive, which religion they follow or which food they cook does not preclude categorizing the traits as present or absent: that is, individuals may or may not acquire a religious belief, learn to drive a car or learn to cook yams, and one can quantify the numbers of religious people or car drivers in a population. This reasoning applies to all cultural traits. While there is extensive mathematical theory investigating the differential adoption of cultural variants (Cavalli-Sforza & Feldman 1981; Boyd & Richerson 1985), there is comparatively little on how much culture will be present in a population, and which factors affect this. In this paper we explore how the mode of transmission impacts on the stability of a cultural trait. Using simple mathematical models, we consider whether uniparental transmission is actually feasible as an explanation for shared culture in animals. We also ask a related question about the number of learning trials necessary for shared culture, since another feature of the social-learning literature is the assumption that imitation can be extremely rapid (Laland et al. 1993; Hurley & Chater 2005), at the extreme allowing skills to be socially transmitted after a single learning trial. However, the plausibility of single-trial social learning as an explanation for behavioural tradition also remains unexplored. We then investigate whether transgenerational social learning, in various forms, can maintain a shared cultural trait starting from a situation where most individuals in the population possess the trait, and whether it can establish culture in a population starting from the situation where only a small number of individuals have the trait. We also consider the effects of finite population size, fitness differences between traits and additional individual learning of the transmitted trait. Our main theoretical result is that several cultural models and repeated social learning is typically necessary to establish and maintain shared culture.

The paper has four sections: first we demonstrate that random copying of a single cultural parent cannot support culture; second, we establish that access to more than one cultural parent can maintain culture; third, we consider the effects of various kinds of transmission bias; and finally, we explore the circumstances under which cultural homogeneity, that is customary cultural traits shared by the majority of the population, can emerge.

ACCESS TO A SINGLE CULTURAL PARENT

Here we explore under which circumstances culture can be maintained in a population. We begin with the simple case of 'random' or 'unbiased' uniparental cultural transmission, by which we mean the copying of a single randomly chosen individual. This assumption is not as unreasonable as it might first appear. For instance, if we assume copying occurs in proportion to contact with the model, then one might a priori anticipate a large degree of copying from a single biological parent in species with uniparental care. We also consider how the probability of maintenance is affected if the trait has a significant fitness advantage, or if its prevalence in the population is bolstered by an additional individual.

In our model, two things determine whether an individual will learn a cultural trait socially. First, the cultural parent (who may or may not be the same as the biological parent) must possess the trait. Second, social learning must be successful. If q is the probability that the cultural parent has the trait (where $0 \leq q \leq 1$) and p the probability that a single social-learning trial is successful given that the cultural parent has the trait, the probability that the individual picks up the trait from a single social-learning trial is pq. We consider perfect social learning to be unrealistic (thus we assume that $p < 1$). Additional social-learning trials will increase the probability of the individual picking up the trait at some juncture. For simplicity, we assume that the probability of learning the trait is the same for each trial. Thus, after n learning trials with the same cultural parent the probability that the individual has picked up the trait is $(1-(1-p)^n)q$, which increases with n but is always less than q (since $p < 1$ by assumption).

To begin with, we assume that cultural parents are drawn independently at random from the parent population. In this case the probability that the cultural parent has the trait (q) is equal to the proportion of individuals that possess the trait in the parental generation. We want to know how this proportion changes over time. First, consider an infinite population. If the proportion with the trait is x in the parental population and individuals are allowed only one social-learning trial, then the proportion possessing the trait in the next generation is exactly px. It follows that the proportion will always decrease from generation to generation, according to the exponential form

$$x_t = x_0 p^t,$$

where x_0 is the proportion at time $t = 0$ and x_t the proportion at time t.

Qualitatively, this result holds also for repeated trials of social learning with the same cultural parent, although the decline becomes less steep when the number n of trials increases. With the above assumptions, the proportion of individuals with the trait will decline towards zero according to the exponential form

$$x_t = x_0\left(1-(1-p)^n\right)^t. \quad (1)$$

In a finite population, expression (1) describes the behaviour of the expected value of the proportion. It follows that social learning