Animal Behaviour 78 (2009) 155–166

Contents lists available at ScienceDirect

Animal Behaviour

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

Cultural inheritance and diversification of diet in variable environments

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ARTICLE INFO

Article history:
Received 8 October 2008
Initial acceptance 12 December 2008
Final acceptance 2 April 2009
Published online 23 May 2009
MS. number: 08-00657R

Keywords:
cumulative cultural change
cultural inheritance
cultural diversification
diet
diet innovation
environmental change
individual-based model
opportunities
self-organization
social learning

Both cultural inheritance and cultural diversification of diets may play an important role in animal evolution. Here we studied how diet innovation and cultural change relate to cultural inheritance in a changing environment. We did this by studying diet cultures in group foragers adapting to environmental change through learning, and the consequences this has for diet differentiation between groups. We used an individual-based model of 'monkeys' that learn what to eat in a rich environment, and we changed resource species that are available in the environment. Relative to social influences on learning that arise spontaneously in groups, we found that more direct social learning, in the sense of observing another individual and copying what it eats, helps groups deal with high levels of environmental variability by generating greater group level incorporation of diet 'innovations' and enhancing cumulative cultural diet improvement. An important factor for the dual role of copying in diet innovation and cultural inheritance is how copying is mediated by foraging opportunities in the environment in the short term. During adaptation to environmental changes, groups diverge in diet. This is caused by differences in learning history and is increased when individuals copy each other, but this depends on migration. Furthermore, when groups live together in the same environment and compete for resources, diet differentiation is enhanced through what appears to be culturally mediated character displacement.

Cultural inheritance, where behaviour is inherited from one generation to the next through socially influenced learning, is a potentially important force in animal evolution, providing an additional means of information inheritance next to genes. The cross-talk between these two levels of inheritance is referred to as gene–culture coevolution (Feldman & Laland 1996). Through a process called niche construction (Laland et al. 2000), individuals shape the cultures they live in, which in turn shape the evolutionary pressures they experience. Across cultures, cultural variation could generate divergent selection pressures. How behavioural changes and innovations generate cultural variation will therefore be important.

At present little is known about the scope of cultural transmission in wild animals, let alone cultural variation and dynamics. Often the only way to establish evidence of cultural inheritance in wild animals is to reveal behavioural variation between groups that is independent of ecological and genetic variation. This allows cultural variation and transmission to be inferred (i.e. as the only remaining explanation; McGrew 1998; van Schaik 2003). As a consequence, cultural variation, and thus cultural inheritance, has been established mainly for behaviour that is relatively independent of ecological variation, such as social customs and foraging techniques (see Whiten et al. 1999; Rendall & Whitehead 2001; Panger et al. 2002; Perry et al. 2003; van Schaik et al. 2003). Unfortunately, for behaviour closely linked to ecological conditions, such as what individuals eat, ecological reasons for intergroup differences generally cannot be excluded (e.g. Chapman & Fedigan 1990).

This does not mean diet differences are not cultural. A cross-fostering study with blue tits, *Cyanistes caeruleus*, and great tits, *Parus major*, shows that young tits can inherit their adoptive species' feeding niche, indicating that a substantial part of a species' feeding niche is culturally inherited (Slagsvold & Wiebe 2007). It is also well known that simple forms of social learning can affect food preferences in rats (*Rattus norvegivus*, *Rattus rattus*) and give rise to 'traditions' across chains of individuals (Galef 2003b). Moreover, we have shown that grouping in itself can be sufficient to generate both diet traditions and cumulative cultural diet improvement (van der Post & Hogeweg 2008). The conditions for diet cultures may therefore be easily met.

However, since environmental variation is a confounding factor for studying cultural variation in diet, both its prevalence and how

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0003-3472/$38.00
doi:10.1016/j.anbehav.2009.04.009

cultures change in relation to ecological variability are still largely unknown. It has been suggested that cognitive abilities help individuals adapt to environmental change through a combination of behavioural innovations and their spread through social learning, and drive cultural change and eventually evolutionary diversification (see Wyles et al. 1983; Lefebvre et al. 2004; Sol et al. 2005). This is supported by various correlations between brain size, innovation rates, social-learning abilities and rates of environmental change in birds and primates (Lefebvre et al. 1997, 2004; Reader & Laland 2002; Reader 2003; Sol et al. 2005). However, mathematical population models, in which social learning is implemented and equated with cultural inheritance, predict that social learning becomes maladaptive when environments change too fast between generations (Rogers 1988; Boyd & Richerson 1988; Feldman et al. 1996; Laland & Kendal 2003). Therefore, while socially learnt innovations may be helpful, socially acquired traditional information may be outdated. This suggests environmental variation may limit the evolution and prevalence of social learning in animals.

In previous work, we have shown that as soon as individuals live in groups, social influences on learning arise as a side-effect and are unavoidable (van der Post & Hogeweg 2006). In particular in patchy environments, groups of individuals learning by trial and error automatically share learning opportunities and converge in learning. Such a social influence on learning by grouping has also been called local enhancement (see Hoppitt & Laland 2008). This spontaneous social influence on learning can give rise to both traditional inheritance and cumulative cultural change (van der Post & Hogeweg 2008). Furthermore, this social influence arises irrespective of its adaptive consequences; it is unavoidable. Therefore, in this case it is not a question of whether social learning and cultural inheritance can evolve given environmental change, but given spontaneous social learning and cultural inheritance, how do groups respond to changing environments?

In addition, in previous work we found that when spontaneous social influences on learning are present, and, on top of that, we implement a more direct form of social learning, where individuals directly observe what other individuals are eating and copy them (which we refer to here as copying), this can enhance information integration in groups and improve diets through collective exploration and enhanced cultural inheritance (D. J. van der Post, B. Ursem & P. Hogeweg, unpublished data). However, it is unclear whether this holds in changing environments and how this impacts cultural inheritance. Moreover, given that groups adapt their diets to changing environments, what consequences does this have for cultural diversification between groups?

We addressed these issues by studying how diet cultures are affected by environmental change. We studied how individuals respond to environmental changes through learnt adaptations in the short term, and the consequences this has for cultural diet differentiation between groups in the long term. In this context, we studied two levels of social influence on learning: (1) spontaneous social influences on learning and (2) copying. Spontaneous social learning is the baseline type of learning in groups learning by trail and error, which arises as a side-effect and cannot be avoided (van der Post & Hogeweg 2006, 2008). On top of this we studied groups in which individuals can also directly observe each other's food choices and copy each other (copying). In both groups with and without copying, cultural inheritance can take place. We used an individual-based model with a rich environment, which makes it possible to study rich behavioural repertoires and cultural variation (see van der Post & Hogeweg 2006). The model was formulated keeping primates in mind, but could be more generally relevant. The model simulates group foragers that learn what to eat and forage selectively on short timescales, and gives rise to cultural inheritance on longer timescales (see van der Post & Hogeweg 2008). We therefore did not implement cultural inheritance, but studied how it arises and is affected by adaptation to environmental change through learning, and what this means for cultural niche differentiation.

METHODS

The individual-based spatial model we used is adapted from van der Post & Hogeweg (2008). In our modelling approach we implemented basic assumptions based on primate groups, namely: (1) developing preferences for resources, (2) foraging selectively, (3) living in groups in a (4) structured spatial environment. In the model, individuals make behavioural decisions according to simple behaviour rules, using local ecological and social information and individual internal state. Foraging and learning are therefore not fixed strategies, but depend on the local ecological and social opportunities that arise and what individuals observe in their environment. We studied the implications of these assumptions for longer-term cultural phenomena by exploring the dynamics generated by the interactions between them.

In previous work we have studied the ecological and social parameter conditions in which spontaneous social influences on learning and cultural inheritance arise (van der Post & Hogeweg 2006, 2008), and in which copying (i.e. directly observing the food choice of another individual and copying it) improves diet learning relative to spontaneous social influences on learning in groups (van der Post et al., unpublished data). Here, we used this background to set the parameter conditions such that we were in a context in which cultural inheritance takes place, and copying improves learning in constant environments. Only in that way could we study the impact of environmental change on both these processes, which we did by varying the type and rate of environmental change and social influences on learning. We therefore focused on patches with multiple resources, where we know cultural variation between groups is well expressed (see van der Post & Hogeweg 2008), and where copying clearly helps to improve diet learning (van der Post et al., unpublished data) and which is also the most natural setting (for more discussion on parameter details see Appendix 1). Below we describe the model in more detail.

Model Description

Environment

The environment is a two-dimensional grid where grid points represent locations where resource items can be found. We implemented 250 resource species with a Gaussian quality (energy) distribution. Resources were distributed in patches, where each patch was assigned a subset of five resources (varied patches), giving 50 patch types. Patches of a given patch type differed in that we only plotted a subset of three of the five assigned resources generating different combinations of resources in patches of a given patch type. Each patch had a radius of 10 grid units and about 13 items per grid location and could be visited several times by groups before they were depleted. We used a grid size of 2800×2800 square units (1 unit is scaled to 1 m) and implemented 4900 patches each consisting of about 4000 resource items. We set our timescale as follows: 1 time step = 1 min, 1 day = 1000 min, and 1 year = 100 days.

Resources were depleted during foraging and were renewed at the beginning of each year. This was simply done by repeating the initial resource distribution pattern and removing any resource units from the previous year. Ecological dynamics were therefore limited to single influxes of all resources at the beginning of each year.