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Diet traditions and cumulative cultural processes as side-effects of grouping

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Social learning and cognitive sophistication are often assumed to be prerequisites for the origins of culture. In contrast, we studied to what extent the most simple social influences on individual learning can support cultural inheritance. We did this using a spatial individual-based model where group foragers have to learn what to eat in a diverse patchy environment, and used simple population dynamics to investigate the potential of 'merely living in groups' to allow for inheritance of diet traditions. Our results show that grouping by itself is a sufficient social influence on individual learning for supporting the inheritance of diet traditions. Unexpectedly, we find that grouping is also sufficient to generate cumulative group-level learning through which groups increase diet quality over the generations. Whether 'traditions' or 'progressive change' dominates depends on foraging selectivity. We show that these cultural phenomena can arise as side-effects of grouping and therefore independently of their adaptive consequences. This suggests that cultural phenomena could be quite general and shows that cumulative cultural processes already occur even for the most simple social influences on learning.

Studies on the origins of culture focus on different social learning mechanisms and the evolution of behavioural inheritance by social learning (e.g. Henrich & McElreath 2003). In general, social learning is thought to evolve because it allows individuals to avoid the costs of individual learning. However, only sophisticated forms of social learning, such as imitation and teaching, are thought to be sufficiently accurate to allow for certain cultural phenomena, such as large traditional repertoires and cumulative cultural evolution (e.g. Boyd & Richerson 1995; Boesch & Tomasello 1998; Castro & Toro 2004).

Theoretical approaches to the evolution of social learning generally focus on the adaptive benefits of social learning relative to the costs of asocial learning. In such cases social learning is found to be adaptive when the environment is constant enough not to make socially learned behaviour obsolete (e.g. Boyd & Richerson 1985; Laland & Kendal 2003), or social cues are more reliable than asocial cues (e.g. Dewar 2003).

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In contrast, we studied cultural phenomena as side-effects of foraging behaviour. We used an opportunity-based approach drawing on the 'ToDo' principle (Hogeweg & Hesper 1985), which focuses on behavioural structuring by local opportunities, rather than behavioural strategies. This approach is sensitive to interactions and feedbacks that can arise, allowing for novel phenomena and self-organizing processes to occur (see Hogeweg & Hesper 1989; te Boekhorst & Hogeweg 1994), and can be referred as process-oriented modelling (Hemelrijk 2002).

Using such an approach, we have previously shown that grouping will spontaneously generate social influences on diet learning in fixed groups of individuals that learn only by trial-and-error (van der Post & Hogeweg 2006). Our results show that, in patchy environments, local sharing of learning opportunities automatically leads to convergence in learning within groups, and diet differences between groups. Important is that this convergent social influence on learning arises spontaneously and is not an evolved strategy, that is, it is a side-effect of grouping in a patchy environment. Such convergent social influences therefore appear generic for group foragers and are relevant for understanding diet differences such as those found between neighbouring groups of capuchin monkeys (Chapman & Fedigan 1990).

However, it is still an open question whether such spontaneously arising convergence in learning can lead to diet inheritance and support diet traditions. The main concern here is whether the convergent social influence on trial-and-error learning is accurate enough to allow for sufficient fidelity of transfer of food preferences. Here, we studied whether this is the case by running simulations in which we mimic transmission chain experiments (cf. Curio et al. 1978; Galef & Allen 1995). Such experimental set-ups are used to study whether a behavioural variant can be transmitted beyond the individuals that first learned and discovered the behaviour. The behavioural transmission is studied over a chain of individuals whereby, in sequence, the most experienced individual is replaced by a naïve individual (see also Laland & Williams 1997). Using such a set-up, we included group dynamics and the influx of naïve individuals in our simulations. We did not add any other feature to our model which could affect the nature of learning, and so explicitly studied the inheritance of diet preferences by trial-and-error learning, with only 'living in groups' as a social influence on learning.

MODEL

We used an individual-based model (adapted from van der Post & Hogeweg 2006) that incorporates an explicit spatial environment in which multiple species of resources can be arranged in different distributions and densities. Individuals were modelled to move and forage in groups through the environment, and learn what to eat. A combination of local ecological and social context, and individual internal state, determines what individuals can do, making foraging dependent on the ecological and social opportunities that arise. Therefore, learning is not a fixed strategy but depends on what individuals observe. The model was built up as follows (see Appendix 1 for a complete list of parameters).

Environment

The environment is a 2 dimensional grid where grid points represent locations where resource items can be found. As a default, we implemented 250 resource types (species) with a Gaussian quality (energy) distribution, which were distributed in patches of a single resource type with a radius of 10 grid units and about 12 items per grid location. Each patch could be visited several times by groups before they were depleted.

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.

We used a grid size of 2800 square units (1 unit is scaled to 1 m) and implemented 4900 patches each consisting of about 4000 resource items. This is a larger grid than in our previous model, but this scales with the longer timescales we implemented here. Timescales are important in

learning processes, especially with respect to convergence through learning. Our timescale was set in rough correspondence to that of primates (see Fig. 1), where 1 time step = 1 min, 1 day = 12 h and 1 year = 365 days. For more details on modelling the environment see van der Post & Hogeweg (2006).

Individuals

We modelled individual behaviour using an event-based formalism, that is, actions take time. The behaviour procedure is given in Fig. 1 and basically ensures that individuals remain in groups, find preferred food and eat, discover new resources, move forward, or do nothing while digesting after eating to satiation (maximum stomach capacity).

Grouping

To achieve grouping, individuals were modelled to remain in close proximity to a sufficient number of other individuals (see Fig. 1). Individuals check how many neighbours are present within a distance of 10 grid units. If they have more than two neighbours, then they are 'safe' and proceed with foraging. Otherwise they move to where they observe the highest density of individuals within 150 grid units. These grouping parameters were chosen to reduce subgroup formation to focus on intergroup processes. Note that individuals do not pay any attention to any behaviour cues of other individuals, that is, whether they are eating or not does not make any difference. It is purely a case of wanting to remain in a group.

Learning

Individuals try every unknown resource (for which they do not yet have a preference) they encounter. Thus, we implemented maximum trail rates such that every individual tries everything. Once eaten, resource quality is assessed by individuals through delayed postdigestive feedbacks (every 100-time steps) and resource preferences are updated according to:

$$p_{ir} := p_{ir} + \left(U \frac{S_{ir}}{S_{it}} (\overline{E_i} - \overline{p_i}) \right) \tag{1}$$

where p_{ir} is individual i's preference for resource r, S_{ir} is the number of items of resource r in its stomach, S_{it} is the total number of items in its stomach, $\overline{E_i}$ is the average energy per resource item it obtains from digestion, and $\overline{p_i}$ is the average preference it has for the items digested. Note that equation (1) is only updated after digestion and only for the digested resources.

Preferences represent an individual's energy estimate for a given resource and $\overline{p_i}$ therefore represents an expected energy feedback from digestion. Moreover, we draw $\overline{E_i}$ from a normal distribution with a mean of $\overline{E_i}$ and a standard deviation of 0.005 to add some environmental noise.

We set U to 0.01, which means that if individuals eat a resource continuously for about 7 days, their preference will be equal to half the actual quality of the resource. This at least appears to be in the order of magnitude of what is