Modelling Social Learning in Monkeys

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The application of modelling to social learning in monkey populations has been a neglected topic. Recently, however, a number of statistical, simulation and analytical approaches have been developed to help examine social learning processes, putative traditions, the use of social learning strategies and the diffusion dynamics of socially transmitted information. Here, I review some of the recent advances and show how they influence and combine with empirical studies of social learning.

Keywords: cultural transmission, modelling, social learning, traditions.

Quantifying Social Learning Processes

In the laboratory, paired demonstrator-observer designs are used primarily to investigate whether animals are *capable* of specific forms of social learning (Galef 1988). Laboratory experimental have also been used to investigate the diffusion dynamics of learned behaviour through populations in controlled conditions (Lefebvre & Palameta 1988; Whiten et al. 2005). The results of such experiments do not tell us much about social learning in the wild and often lack ecological validity in terms of the behaviour being learned. They have the potential, however, to provide quantitative data that can be used in the parameters for mathematical models of social learning.

For instance, Kendal et al. (2007) presented captive groups of callitrichid monkeys with novel extractive foraging tasks. By measuring the proximity of each monkey to the task and noting any food extractions, they quantified the effects of two social learning processes, 'stimulus enhancement' and 'observational learning', and two asocial processes, 'intrinsic movement to the task' and 'asocial learning of the task' on the adoption of a novel foraging behavior. The values of these processes from the observed data were fed into a set of models for the spread of a novel behaviour. Model selection was used to discern that the model best-fit to the monkey diffusion data only required asocial processes. Nonetheless, quantification of the processes provided statistical evidence for a small positive effect of stimulus enhancement, where a demonstrator manipulating the task attracts an observer to move to the task, but not for observational learning at the task.

Derived parameter values can also be used in competing models to predict the shapes of diffusion curves. Theoretical models predict that the diffusion of cultural traits will typically exhibit a sigmoidal ('S' shaped) pattern over time (Boyd & Richerson 1985; Cavalli-Sforza & Feldman 1981), while asocial learning has been expected to result in a linear, non-acceleratory, or at least non-sigmoidal increase in frequency (Lefebvre 1995). In the absence of parameter values to feed into diffusion models, the observed shape of a diffusion curve is unlikely to be reliable, as more recent models predict that under certain conditions asocial learning can generate acceleratory curves while social learning can generate deceleratory curves (Laland & Kendal 2003; Reader 2004). Many competing sets of assumptions can generate very similar diffusion curves using different parameter values. Thus, if parameter values can be estimated, it may be possible to select between competing hypotheses.

Population-Level Homogeneity of Behaviour

While social learning experiments in the laboratory may provide estimates of the limitations of social learning behaviour, an understanding of social learning will be incomplete without analysis of natural populations. Field translocation experiments have been performed to identify traditions in the wild. For instance, Helfman and Shultz (1984) translocated French grunts *Haemulon flavolineatum* between populations and found that fish placed into established populations adopted the same schooling sites and migration routes as the residents. Control fish however, that were introduced into regions from which all residents had been removed, did not adopt the behaviour of former residents.

In monkeys, however, this type of approach would be impractical and often unethical. The identification of traditions in natural monkey populations will often rely on observational data without recourse to manipulating groups of animals. The ethnographic method is one such approach, identifying behavioural variation between populations that cannot be accounted for by local ecology or genetic variation. Whiten et al. (1999) identified 39 different behaviour patterns across populations of chimpanzees (*Pan troglodytes*) in Africa, including tool usage, grooming and courtship behaviours, that were common in some communities but absent in others. Critics of the method have pointed out that ecological explanations may have been discounted erroneously and that some populations have been separated for sufficient time for genetic variation to contribute to the observed behavioural variation (Laland and Janik 2006). Unfortunately, the method excludes cases where selection has resulted in covariance between cultural and (i) ecological factors, because culture is a source of adaptive behaviour, and and/or (ii) genetic factors enabling animals to learn about and exploit environmental resources because animal learning is influenced by evolved predispositions (Laland & Janik 2006; Laland et al. In press).

An alternative, the ‘option-bias’ method, is being developed to identify traditions in the wild, and like the ethnographic approach, assumes that social learning results in within-population homogeneity of behaviour (R. Kendal et al. In prep.). The option-bias method, however, does not require comparison between populations, as instead, the observed level of homogeneity is compared against a distribution of expected homogeneity-levels generated by stochastic simulation that assumes asocial but not social learning. Thus, the simulated distribution represents the probability that populations of monkeys behaving independently would exhibit the observed level of homogeneity in their option choices. Social learning can be inferred if the observed level of homogeneity lies above the critical level (alpha = 0.05) in the tail of the simulated distribution. Kendal et al. applied the method to data collected from groups of callitrichid monkeys provided with novel extractive-foraging tasks, with each task exhibiting two equivalent means (or options) of obtaining a food reward (using different coloured doors to access food). The analysis distinguished social learning in cases where the monkeys were presented with a particularly difficult task; here the acquisition of asocial information is likely to have been costly in terms of time and effort. The method does not assess any genetic influence on behaviour and requires an a priori estimate of the maximum probability of acquiring the behavioural variant through asocial learning (something that could be estimated in the field or taken from laboratory experiments). Unlike the ethnographic method, however, a putative cultural variant in each population can be assessed independently from other populations and can be used to examine variants that covary with the local ecology.

Social Learning and Patterns of Association

Another approach to identify social learning is to look for cases of ‘directed social learning’, that is, non-random paths of information transmission through a population (Coussi Korbel & Fragaszy, 1995). Often, social structure may influence the spread of information, influencing whether innovations spread at all, and if so, the rate of spread relative to rate of change in the environment. In a changing environment, information becomes more likely to become obsolete with time, so the efficacy of socially transmitted information depends on an animal’s location in the chain of acquisition, which may consequently affect the propensity for the animal to use information that is learned socially.

Most approaches start by compiling a matrix of association metrics between all pairs of individuals as a measure of the opportunity for information transmission; if social learning is directed it may often be as a function of the level of association and thus the opportunity to observe the demonstration of a novel behaviour. If social learning is vertically transmitted (parent to offspring), information may be directed according to genealogy. Laland and Kendal (2003) show that a correlation between the coefficient of association and the order of information acquisition can provide evidence to distinguish directed social learning from asocial learning, while cases of acquisition by offspring before parents may often render a genetic account implausible (unless there are developmental constraints on the adoption of the new behaviour). Furthermore, the concordance of the behaviour between parents and offspring can help dissociate cases of vertical transmission (from parents to offspring) from oblique (from non-parents, between parent and offspring generations) and horizontal transmission (within-generation). More sophisticated approaches are currently under development by Laland et al. (In prep.), using a path analysis approach, to predict the relative influence of genetic, environmental and cultural effects on the behavioural phenotype.

Whitehead (In press) suggests using partial regression to test how much inter-individual variation in behaviour is caused by ‘social similarity’, over and above any effects of ecological and/or genetic similarity. Here, social similarity is a measure of the opportunity for social transmission of information, typically measured by some form of association index. The inter-individual variation in behaviour, scored as behavioural similarity between each pair of individuals, is non-independent, so Whitehead addresses the significance of the partial regression coefficient by bootstrapping a distribution of partial regression coefficients, where the similarity scores of the independent variables are randomized across individuals. Social learning, or more precisely, the effect of the social similarity, is invoked if the original partial regression coefficient lies beyond the critical point in the upper tail of the bootstrapped distribution (e.g. $P < 0.05$).

Boogert et al (In press) present a randomization approach to examine whether the order to solve extractive foraging tasks in captive groups of starlings is a function of the level of association between individuals. They compared the association scores between individuals, summed along a linear chain in the order of task acquisition, and compared this ‘path strength metric’ against a distribution of random path strength metrics, generated from randomly ordered chains of acquisition. Directed social learning would be in evidence if the observed path strength metric lay in the upper tail of the distribution; that is, if the sum of associations in the chain of acquisition were significantly larger than expected in a population where each observer’s choice of demonstrator was independent of their strength of association. As naïve individuals could potentially learn from any informed individual and not just the adjacent informed individual in the chain of acquisition, they also repeated the analysis assuming a nonlinear chain of acquisition, where the association strength for each individual is the average across all individuals that had already learned the task. Although they did not find evidence for directed social learning, this method should be appropriate for future investigations of directed social learning.

Voelkl and Noë (submitted manuscript) use the association metrics taken from a population of rhesus monkeys (*Macaca mulatta*) to determine the strength of connections, or edges, between individuals, or nodes, in a social network. They simulated the spread of information across this network and compared the rate of spread and the average path length with that of stylised artificial network structures. Although they did not analyse the structure of the rhesus network directly, they explored how diffusion dynamics can be a function of network structure. Further investigation using this approach will surely yield insight on constraints affecting the spread of information as it can exploit the substantial body of theory on small-world networks (Watts 1999). The approach should also help us understand the relationship between directed social learning and social hierarchy.

Couzin and Krause (2003) used agent based models to show that the non-random assortment of individuals within a population can occur without any capacity for individual recognition, as individuals naturally ‘self-sort’ to form close associations with those of similar behavioural or motivational states. This process is likely to provide a structured pathway for the non-random spread of information across a group. It has been shown in fish that the identity of leaders and followers can be predicted by state dependent factors such as hunger (Reader and Laland 2000). Rands et al. (2003) use a dynamic programming game model to show that if it pays not to forage alone, the foraging behaviour of two individuals can become highly synchronised, from which a difference in energetic state between the two foragers can emerge. The identity of a leader and follower in the pair of individuals is determined by each adopting the ESS (evolutionarily stable strategy) rule of thumb that is 'to forage if either their own reserves have fallen below a certain threshold value, or if their partner chooses to forage'.

Social Learning Biases

Social learning may also be directed as a function of biased attention on the part of the observer, including direct bias, indirect bias and conformity. Much of the theory concerns the evolutionary consequences of social learning biases in humans (Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985). Direct bias occurs when an observer chooses to copy a behaviour that is demonstrated to be particularly successful. If there is noisy feedback about the success of other individuals, however, game-theoretical modelling has found that the most effective strategy is to copy in proportion to the observed payoff that results from the demonstrator's performance (Schlag 1998). In contrast, occurs when an individual copies a behavioural trait exhibited by a demonstrator who is deemed successful (e.g. foraging success) regardless of whether the demonstrator's 'success' was due to that behaviour. Indirect bias may, however, result in erroneous copying of ineffective behaviour. The most intuitive examples are in humans, where advertising companies invoke indirect bias to enhance sales of for example brands of razor, sunglasses or perfume by showing, often falsely, that they are used by particularly successful sportsmen, singers or actors; the adopted behaviour itself, can become a marker for prestige (Henrich and Gil-White 2001).

Studies of direct and indirect bias in animals are rare and evidence for these psychological dispositions is sparse. Wilkinson (1992), however, found evidence of copying successful individuals in nursing colonies of evening bats (*Nycticeius humeralis*); adult females that had been unsuccessful in foraging tended to follow successful individuals, and females that followed successful individuals from the nursing colony were subsequently more successful than females that departed alone (Galef and Laland 2005). Also, in domestic fowl (*Gallus gallus*), high-status individuals are more effective demonstrators than are low-status individuals as flock members are more likely to pay attention to the former than the latter (Nicol and Pope 1999). Henrich and Gil-White (1999) however, would argue that this is not prestige bias, as dominant individuals may attract high levels of attention for reasons other than prestige (i.e. held in high esteem), such as the threat of aggression. Furthermore, they argue that prestige bias might be rare in non-humans, in part, because it requires the capacity for direct transmission of information, for instance, through imitation. Direct transmission ensures that the benefit derived by the copier is a function of the utility of the demonstrator's information, and may be a prerequisite to the evolution of prestige bias. In monkey populations, indirect forms of social learning may be prevalent, such as stimulus enhancement, where a demonstrator attracts the attention of an observer to a task. Once at proximity to the task, the observer may then acquire the solution to the task through asocial learning.

Conformist bias can maintain within-group homogeneity and between group differences and thus may lead to the persistence of between-population variation in behaviour (Boyd & Richerson 1985; Henrich and Boyd 1998). Henrich and Boyd (1998) used a numerical approach to show that the propensities for social learning and for conformity bias may coevolve. Recent theoretical studies however, have not found this to be the case (Eriksson et al. 2007; Wakano and Aoki 2007). There is scant evidence for conformity in animals besides experimental evidence in fish and chimpanzees (Day et al. 2001; Whiten et al. 2005). Nonetheless, one might anticipate conformity in fission-fusion monkey populations, where in a variable environment, it might pay for immigrants to copy locally common patterns of behaviours.

Laland et al. (In prep.) are currently using game theory and individual-based models to examine the evolution of rules-of-thumb (or 'social learning strategies') that animals may use to assess when and from whom to learn socially (Laland 2004; Kendal et al. 2005). The game theory develops the classic producer-scrounger paradigm to consider the producing and scrounging of information rather than food. The individual-based models allow the examination of spatially explicit effects such as local clustering of types of learning strategists. The models are complemented with experimental approaches applied to fish and monkeys. The results should give a comparative insight into the evolutionary processes affecting the use of social learning strategies.

Local Interactions and Collective Behaviour

Individual-based models have also been used to examine the effects of individual decision rules on group spatial dynamics. Couzin (2007) describes how the formation of spatial patterns may facilitate the spread of information through a group; in particular, an individual's 'effective range' of perception can be larger than their actual sensory range as a result of combined local interactions within the group. For instance, a fish might detect a predator sooner due to the behaviour of shoal members rather than seeing the predator themselves. The scaling from actual to effective sensory range is non-linear: too small a range limits group cohesion and limits the spread of information through the group, while too large a range risks misdirecting individuals as they obtain information from distant models that may not be relevant. These results follow the same principles that underpin the evolution of social learning in general, where an intermediate scale of environmental variation is likely to favour social learning. For example, birds at the head of a migrating flock may experience a new thermal that is absent at the back of the group. Here, too long a sensory range may result in the tail-end birds adopting an inappropriate change in course by copying the lead birds.

To date, this theory has been developed with large animal groups in mind, such as insects, birds, bats and humans. In principle, the theory could also be applied to monkeys. For example, a predator alarm call may result in monkeys escaping by copying the route of their neighbours. If there is variation in the optimal escape route depending on variation in the location of the monkeys, too small or too large a sensory range may result in potentially fatal errors in the escape route taken. The optimal level of group cohesion is likely to be context dependent and allows individuals to acquire information that otherwise would elude them.

Conclusions

It is striking how little integration there has been between theoreticians and primatologists. Given the depth of knowledge about life histories, social systems and the local ecology of monkey populations, it would be entirely reasonable to develop models to help identify traditions, examine psychological dispositions underlying social learning, and make predictions concerning the use of social learning and the dynamics of socially transmitted information. In the phylogenetic tree, the origin of human culture lies far deeper than the common ancestor of apes and developing mathematical models of social learning specifically for monkey species will help to write an important chapter in this story.

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