Why behaviour patterns that animals learn socially are locally adaptive

BENNETT G. GALEF, Jr

Department of Psychology, McMaster University, Hamilton, Ontario L8S 4K1, Canada

Abstract. Recent models of the social transmission of behaviour by animals have repeatedly led their authors to the counterintuitive (and counterfactual) conclusion that traditional behaviour patterns in animals are often not locally adaptive. This deduction results from the assumption in such models that frequency of expression of socially learned behaviour patterns is not affected by rewards or punishments contingent upon their expression. An alternative approach to analysis of social learning processes, based on Staddon–Simmelhag's conditioning model, is proposed here. It is assumed that social interactions affect the probability of introduction of novel behaviour patterns into a naive individual's repertoire and that consequences of engaging in a socially learned behaviour determine whether that behaviour continues to be expressed. Review of several recently analysed instances of animal social learning suggests that distinguishing processes that introduce behaviour patterns into the repertoires of individuals from processes that select among behavioural alternatives aids in understanding observed differences in the longevity of various traditional behaviour patterns studied in both laboratory and field. Finally, implications of the present approach for understanding the role of social learning in evolutionary process are discussed.

During their lifetimes, individual animals can acquire behaviour in one of two ways: by individual learning or by social learning. Individual learning refers to behaviour acquired by an animal as the result of its own experience of the rewards and punishments contingent upon engaging in various acts, while social learning refers to those instances in which the acquisition of behaviour is influenced by observation of or interaction with another animal or its products (Heyes 1994). Classic examples of socially learned behaviour include the song dialects of white-crowned sparrows, *Zonotrichia leucophrys* (Marler 1970), sweet-potato washing and wheat placer mining exhibited by macaques on Koshima Island in Japan (Kawamura 1959) and the termite fishing engaged in by chimpanzees in Gombe National Park, Tanzania (Goodall 1973). The numerous behavioural processes supporting social learning in animals have been discussed at length elsewhere (Galef 1988; Whiten & Ham 1992; Heyes 1994) and will not be considered further here.

Both individual and social learning are forms of phenotypic plasticity enabling animals to acquire behaviour that is adaptive in local habitat (Boyd & Richerson 1988). Theoreticians have argued that individual learning and social learning have different patterns of costs and benefits that make one or the other superior in any given environment. For example, Rogers (1988) discussed a hypothetical species, the 'snerdwump', whose members inhabit a variable environment and learn what foods to eat either by individual learning (sampling among available foods and discovering which is the most nutritionally valuable) or by copying the food choices of a member of the previous generation. In environments that are relatively constant across generations, snerdwumps that avoided exposure to poisons by copying the food choices of their elders would prosper, while snerdwumps that lived in environments that fluctuated significantly between generations and learned what to eat by copying members of the previous generation would be unable to discover superior foods that their brethren might identify while learning what to eat by trial and error.

Psychologists studying behavioural traditions in animals have generally assumed that no learned behaviour, whether acquired socially or individually, will be long maintained in an individual's repertoire unless that behaviour is at least as likely to produce rewards as are available alternatives (Galef 1976; Heyes 1993). Furthermore, most students of social learning have assumed implicitly

that because acquisition of rewards (or avoidance of punishment) are, in general, necessary to maintain a learned behaviour in an individual's repertoire, continued expression of a behaviour provides prima-facie evidence of that behaviour's utility. Consequently, it is usually assumed that any socially or individually learned behaviour that an animal continues to exhibit is locally adaptive in the sense that engaging in that behaviour tends to provide efficient access to some local resource of value to the behaving individual.

However, in the last few years, several authors have proposed mathematical models of the diffusion of socially learned behaviour through populations in which it is assumed that maintenance of a socially learned behaviour in an individual's repertoire is not affected by the consequences of that behaviour. Use of models in which frequency of expression of socially learned behaviour patterns is considered to be independent of their outcomes leads to the counterintuitive (and counterfactual) conclusion that socially learned behaviour patterns, unlike behaviour patterns that develop as the result of individual trial-and-error learning, are often locally maladaptive, as would be the food choices of snerdwumps that lived in a fluctuating environment and chose foods to eat by copying the food choices of their forebears.

The assumption that socially learned behaviour is immutable has led some theoreticians to some surprising positions. For example, Rogers (1988, page 822) proposed that 'when all learning is social, no one is monitoring the environment and the information acquired will eventually be worthless'. By starting with some unlikely postulates (in particular, that 'individual learning does not modify or improve behaviours acquired culturally' (1988, page 826)), Rogers arrives at the unlikely conclusion that, to date, there is no satisfactory explanation for the observation that most socially learned behaviour patterns are, in fact, locally adaptive.

Similarly, Boyd & Richerson in a model of animal social learning (quite different from the 'guided variation' model of human culture they developed in 1985), made the simplifying assumptions, that: (1) 'social learning involves the faithful copying of the behavior of other individuals' and (2) 'once an individual has acquired [a behaviour], it does not change' (Boyd & Richerson 1988, pp. 32–33). It follows that an individual living in a variable environment that acquires a locally maladaptive behaviour (by, for example, imitating a model that learned some response when the environment shared by model and social learner was in a different state) is fated both to continue to exhibit that socially learned, locally maladaptive behaviour indefinitely and to serve as an inappropriate model for naive individuals with which it interacts. Consequently, when Boyd & Richerson (1988) conclude that the probability that model and social learner will acquire a behaviour in the same environment is low (e.g. when an environment is highly variable), a population will contain a relatively high proportion of individuals that exhibit locally maladaptive behaviour patterns ('models exhibiting locally adaptive behaviors might become uncommon'), social learning will become increasingly likely to result in diffusion of locally maladaptive behaviour through a population, and selection against social learners should increase.

Dawkin's (1989) discussion of 'memes' (units of imitation that play a role in cultural evolution analogous to that played by genes in biological evolution), like the later quantitative models of social learning proposed by Rogers (1988) and by Boyd & Richerson (1988) allows cultural evolution of maladaptive behaviour by animals living in variable environments.

Dawkins explains differential survival of memes in a population 'meme pool' in terms of differences in the 'psychological appeal' of competing memes. Obviously, if memes are selected on the basis of a psychological appeal which evolved in response to ancestral environments, then the probability of spread of different memes through a population need not be correlated with the current local utility of the overt behaviour for which those memes code. Explanation of the apparent adaptedness of socially learned behaviour in variable environments remains problematic, as both Rogers (1988) and Boyd & Richerson (1988) concluded that it is. However, discussing selection of memes in terms of differences in their psychological appeal, as Dawkins does, is not the only possible approach to understanding meme selection. In fact, explaining differential survival of memes in terms of differences among memes in psychological appeal is not a compelling extrapolation from the analogy between genes and memes.

Explaining the differential survival of memes in terms of variation in the psychological appeal of

memes is analogous to explaining differential survival of genes as a result of natural selection acting directly on genes themselves. Yet, in orthodox neo-Darwinian theory, natural selection is presumed to act directly not on genes, but on their phenotypic expression.

If differential survival of memes results from selection acting not, as Dawkins proposed, directly on memes but, instead, on the phenotypic expression of memes (the behaviour for which the memes code), then memes that code for behaviour patterns producing relatively large or frequent rewards (i.e. behaviour patterns that are locally adaptive) should be more likely to spread through a population than memes that code for behaviour patterns producing lesser rewards. This is because (1) animals can learn by imitation (or other social learning processes) only those behaviour patterns that others actually perform and (2) animals continue to perform only those behaviour patterns that are relatively highly rewarded. In brief, if selection acts directly on the phenotypic expression of memes, rather than on memes themselves, then socially transmitted behaviour should be neither more nor less locally adaptive than behaviour learned by individual trial and error.

An Alternative View

William James (1890, page 390) proposed more than a century ago that 'it is obvious that every instinctive act, in an animal with memory, must cease to be ''blind'' after being once repeated, and must be accompanied with foresight of its ''end'' '. I will argue similarly here that, as animals with memories are sensitive to consequences of 'instinctive acts', so too are they sensitive to consequences of socially learned behaviour patterns.

On such a view, durable traditions in animals are not a result of social learning per se. Rather, socially acquired behaviour patterns are maintained in individuals, spread through populations and become traditional only when their expression receives consistent environmental support. Consequently, understanding both the spread and maintenance of traditions in populations of animals requires attention to consequences of socially learned behaviour as well as to their origins.

As Heyes (1994; see also Heyes 1993) aptly stated, 'Available evidence suggests that . . . behaviours acquired through imitation are no more likely than those acquired through any other form of learning to be retained if they are punished, if alternative behaviours are rewarded equally, or if alternative behaviours are preferentially rewarded'. The implication is that, if an individual continues to exhibit some learned pattern of behaviour when in a particular situation, it is because in that situation the individual experiences more favourable consequences following performance of that behaviour than following performance of alternative behaviour patterns in its repertoire (Morgan 1900; Galef 1988).

A Model of Animal Learning

Some years ago, Staddon & Simmelhag (1971) developed a model of individual learning in animals which is also useful in discussing animal social learning. The Staddon & Simmelhag learning model, based on an analogy with neo-Darwinian evolutionary theory, allows incorporation of social influences into discussions of individual learning in a totally natural fashion. Furthermore, because understanding the spread of adaptive behaviour through populations is a goal common to studies of both biological evolution and social learning, the parallels between neo-Darwinian evolutionary theory and Staddon & Simmelhag's learning model are particularly useful in discussion of the origins and maintenance of animal traditions.

In the Staddon–Simmelhag model, as in neo-Darwinian theory, an explicit distinction is made between processes generating phenotypic variability and subsequent processes selecting and maintaining some phenotypic variants at the expense of others: principles of behavioural variation determine which behaviour an animal will exhibit when introduced into a situation, and principles of behavioural selection then operate to determine which behaviour patterns that an animal exhibits are maintained in its repertoire.

Principles of behavioural variation

Staddon & Simmelhag (1971) discuss six principles of variation, each influencing production of behaviour in novel situations. I will describe here only those two most relevant to social learning. First, particular environmental stimuli often directly elicit patterns of behaviour. Consequently, details of the environment into which an animal is introduced can influence directly the

relative probability that it will exhibit various elements of its behavioural repertoire. Second, orienting responses, such as exploration, play and curiosity, elicited by environmental cues, can either expose an organism to stimuli it might otherwise not experience or alter the order in which an organism encounters stimuli.

The relevance of these two principles of variation to social learning is obvious. Social stimuli in an environment can act either directly to elicit behaviour, as in either imitation (Thorndike 1898) or social facilitation (Zajonc 1965), or indirectly, as in local or stimulus enhancement (Spence 1937; Thorpe 1963), either by increasing the probability that a subject will respond to stimuli it might otherwise ignore or by influencing the order in which a subject encounters stimuli.

Principles of behavioural selection

The Staddon–Simmelhag model is relatively unusual among learning models in that Staddon & Simmelhag propose that the rewards or 'reinforcements' that an animal receives following activity in a novel situation do not stamp in or strengthen behaviour patterns that directly precede their occurrence. Instead, absence of reinforcement is presumed to eliminate any behaviour patterns that are relatively poorly correlated with reinforcement, much as natural selection weeds out phenotypes that reproduce relatively poorly.

For the present discussion, it is not important whether one accepts a response strengthening or response selecting view of the action of reinforcement in individual learning. What is important is that in discussing learning, as in discussing evolution, principles governing production of novel phenotypes should be conceived of as both separate and potentially different from principles governing maintenance either of behaviour patterns in individuals' repertoires (in learning) or of phenotypes in populations (in evolution).

Separating processes of variation from processes of selection in the social learning of behaviour highlights an interesting parallel between understanding of organic evolution in mid-19th century and current understanding of animal learning. In the 19th century, Darwin could describe accurately the factors that caused a heritable phenotypic variant to increase in frequency in a population, but had little useful information about the source of such variants. Today we have

considerable knowledge of the effects of rewards and punishments on the frequency of occurrence of behaviour patterns established in an individual's behavioural repertoire. However, we lack depth of understanding of the ways in which new behaviour patterns are introduced into that repertoire.

Of course, similarities between an evolutionary model and a learning model are no indication of the utility of the latter. The usefulness of any model depends both on the ease with which it can be used to discuss known examples of relevant phenomena and the ability of the model to predict the outcome of future observations and experiments.

Examples of social learning

In the present section, I discuss several examples of social learning of locally adaptive behaviour patterns that have been subject to extensive investigation during the last decade. Particular examples were chosen both for their recency of publication and because each demonstrates both the utility of treating the generation and maintenance of socially learned behaviour as distinct processes and the lack of contact with behavioural reality of models in which it is assumed that the probabilities of expression and, consequently, of diffusion of socially learned behaviour patterns are not affected by their consequences.

Pine seed eating by roof rats in Israel. Aisner & Terkel (1992) have described populations of roof rats, *Rattus rattus*, living in the pine forests of Israel, that survive on a diet consisting entirely of water and seeds that the rats extract from pine cones (Zohar & Terkel 1991; Aisner & Terkel 1992). Extraction of pine seed has been a stable tradition in these forest-dwelling rats for many generations, and there is every reason to expect persistence of this singular habit (and of roof rats in this unusual habitat) until more specialized exploiters of pine seeds invade the pine forests of Israel and supplant their current inhabitants.

Laboratory studies of the development of the energetically efficient spiral pattern of removing scales from pine cones, necessary for realizing a net energy gain from stripping pine cones and ingesting pine seeds, have shown that only those young rats reared by dams that strip scales from

pine cones learn the efficient method of scale removal that allows survival on a diet consisting solely of pine cones and water. Experience of young rats in completing the stripping of scales from pine cones that had been appropriately started, either by accomplished adult rats or by humans imitating their behaviour, is sufficient to permit young rats to develop the efficient spiral pattern of scale removal.

Although the spiral pattern of pine cone opening is clearly introduced into the behavioural repertoire of juveniles socially, maintenance of the behaviour in forest-dwelling populations is most easily understood as a consequence of feedback from the non-social environment. Because pine cones provide greater rewards to rats that use the efficient spiral pattern of scale removal than to rats that fail to do so, adult, forest-dwelling roof rats in each generation continue to perform the efficient behaviour and provide the necessary stimuli for social learning by members of the next generation. Thus, one would expect the adaptive pattern of behaviour to be maintained throughout the life of individuals and transmitted from generation to generation, not because of the social origins of pine cone opening, but because of the strong and consistent environmental support for efficient behaviour.

Digging for carrots by Norway rats. Maintenance of a socially learned behaviour across generations has also been demonstrated in a laboratory situation that provides patterns of reward similar to those experienced in nature by rats living in pine forests. The similarity in behavioural longevity of an adaptive behaviour is observed despite marked differences in the social learning processes involved in behavioural transmission.

Laland & Plotkin (1990, 1992) trained 'demonstrator' Norway rats, *Rattus norvegicus*, to dig up small pieces of carrot that had been buried under 5 cm of peat; they then allowed naive 'observer' rats to watch through a wire mesh partition for 10 min while a trained demonstrator recovered and ate carrot pieces buried on its side of the partition. After watching demonstrators, observer rats dug up twice as many carrot pieces during subsequent 10-min test periods as did naive control rats that had been fed carrots from a dish but had been denied the opportunity to watch demonstrator rats dig for carrots.

Rats that had served as observers and, therefore, exhibited high frequencies of digging behaviour, were used by Laland & Plotkin (1992) as demonstrators for naive observers, and such chaining of demonstrators and observers was sustained for eight successive generations with only a slight decrease in the rate of carrot recovery by observers.

On the view proposed here, the important features of the situation that produced stability of the socially transmitted behaviour were the reinforcement contingencies in the situation. The sole rewards in both training and test situations were buried carrot pieces. Consequently, once an individual recovered a carrot piece by digging, digging was selected (or maintained) by the reward that carrot pieces provided.

On such a view, social interaction increased the rate of digging in observer rats simply by inducing them to start digging, while acquisition of carrot pieces maintained digging behaviour. In fact, during testing, subjects that had watched demonstrator rats dig up carrots took an average of only 2·4 min to recover the first piece of carrot, while subjects that had not been allowed to watch demonstrators dig up carrots took an average of 7·7 min to begin to do so.

Food-well exploitation by feral pigeons. It is useful to contrast the longevity of socially learned pine cone opening and carrot recovery, with the much shorter life span of another socially transmitted appetitive behaviour, this one studied in feral pigeons, *Columbia livia*. Giraldeau and his co-workers (Giraldeau & Lefebvre 1986, 1987; Giraldeau & Templeton 1991) have found that 'observer' pigeons tested individually after watching trained conspecific demonstrators peck open paper-covered food wells and recover seed, rapidly learned to open food wells themselves, while pigeons denied the opportunity to watch conspecifics open food wells acquired the behaviour much more slowly.

When observer pigeons were tested in flocks rather than individually, some pigeons ('producers') continued to open food wells, while others stopped exhibiting this socially learned behaviour and, instead, regularly 'scrounged' food from the wells that producers in their flock had opened.

When the producer pigeons were removed from such a flock, scroungers in that flock began to

open food wells for themselves. Later in the experimental protocol, when the original producers were returned to a flock, the scroungers that had turned to producing food once again began to scrounge food (Giraldeau & Lefebvre 1986). Clearly, expression of socially learned opening of food wells depended on the absence of alternative sources of reward in the test situation, and the longevity of the socially learned response was determined by the rewards available in the test situation, not by the social origins of the learned response.

Is learning of bird song an exception to the rule?

There is a range of models of song development in birds. Some contain learning principles quite different from those used to account for other instances of animal learning, others treat song learning as similar to other types of learned behaviour. Both types of model are discussed below.

White-crowned sparrows. Marler (1976) interpreted the results of his classic series of experiments on song learning by white-crowned sparrows as demonstrating that young sparrows learn song dialect as a result of exposure during the first 50 days of life to the song of adult conspecifics (Marler 1970). Some months later, when a young sparrow begins to sing, acoustic feedback from its own early attempts at song allows the young bird to match its song to a stored representation of the conspecific song that it heard prior to fledging. Because, in Marler's model, the representation of adult sparrow song that a juvenile sparrow stores results in an immutable template, there is no way for the juvenile to modify its song production in response to the consequences (if any) of singing the song that it heard early in life.

If Marler's analysis is correct, then social processes involved in song learning would result in a pattern of behaviour that is impervious to modification by experience. Consequently, if an individual's song were fitness enhancing, it would be so only because its song was modelled on the song of a reproductively successful individual, and the fitness of any individual's song would depend on environmental stability rather than environmental feedback. Marler's interpretation of song learning in sparrows is compatible with the

models proposed by Rogers (1988) and by Boyd & Richerson (1988). Perhaps irreversible learning mechanisms, like those that Marler suggested support song learning by white-crowned sparrows, are the origin of models that treat socially learned behaviour as impervious to modification by individual experience. However, results of recent studies of song development in white-crowned sparrows, using live rather than taped tutors to provide stimuli to juveniles (see Petrinovich 1988 for review), seem to require substantial revision of Marler's interpretation of the mechanisms of song learning by sparrows (Logan 1992). Songs of young white-crowned sparrows can be modified by acoustic stimuli experienced by birds after they reach 50 days of age, and social stimuli in addition to acoustic ones appear to be important in guiding development of white-crowned sparrow song (Baptista & Petrinovich 1984, 1986; Petrinovich & Baptista 1987; Petrinovich 1988). Until the uncertainties regarding song learning by white-crowned sparrows are resolved, Marler's (1970) analysis of song learning by white-crowned sparrows cannot be used as a basis for general models of social learning processes.

Swamp sparrows. In a recent discussion of the development of song dialect by swamp sparrows, *Melospiza georgiana*, Marler (1991) proposed an alternative to the memory-based model of song learning which he has used for decades to analyse song learning in white-crowned sparrows. This 'action-based' model of song learning is consistent with the general view of social learning proposed here.

Male swamp sparrows, while establishing their first territory, produce more song themes than they will use in subsequent years. During the first breeding season, the probability that a song type will be maintained in an individual swamp sparrow's repertoire is affected by the countersinging of its male neighbours. Songs that match those of neighbours are most effective in eliciting countersinging, and males tend to continue to sing those songs from their socially learned repertoires that provide a close match to the songs of their neighbours. They gradually delete songs from their repertoires that fail to elicit countersinging by their neighbours.

If eliciting a song from a conspecific is, in fact, rewarding to a young male swamp sparrow (and this would be an easy matter to determine

experimentally), then action-based song learning provides a fine example of the type of contribution of social learning to the development of adaptive behavioural repertoires proposed here.

Brown-headed cowbirds. Development of sub-specific song variants by brown-headed cowbirds, *Molothrus ater*, like development of song dialects by swamp sparrows, is consistent with the view of the relationship of social and individual learning that is presented here.

Functionally relevant geographical variations in cowbird song are learned socially. Rearing juvenile males from one geographical area with adult males from another results in juveniles that produce the song variant of their adult male tutors (King et al. 1981).

The variant sung by males (either adult or juvenile) is affected by the responses of females to their songs. Those songs of males that are most likely to elicit copulatory postures in females during the breeding season are responded to by females outside the breeding season with a 'wing stroke' display. Male cowbirds normally sing their various song types one after another without repetition. However, after a wing stroke, they repeat the song type that elicited the wing stroke three or four times in succession, violating one of the basic rules of blackbird song production (King & West 1983).

Thus, in response to the behaviour of females, males learn to sing the dialect that will be most effective in securing copulations (King & West 1983).

Within variants, the precise form of the songs that male cowbirds sing is influenced by social interaction with conspecific males. Those songs that are most potent in eliciting copulatory postures from females are also most effective in eliciting attacks by conspecific males (West et al. 1981), and each male responds to the rewards and punishments it receives for singing potent song. Consequently, only dominant males maintain the most potent song types in their song repertoires (West et al. 1981).

In summary, male brown-headed cowbirds learn song variants socially from other males, yet the continued production of these socially learned songs depends on the responses made to those songs by conspecifics of both sexes. Development of song in cowbirds is an excellent example, not of the isolation of socially learned behaviour from its consequences, but of social learning introducing variants into a behavioural repertoire and rewards and punishments selecting the adaptive elements from that socially learned repertoire.

Summary

Availability of behavioural alternatives leading to reward, not the nature of the learning process involved in acquisition of behaviour determine when and for how long socially learned behaviour is expressed. Digging for carrot pieces by rats and pecking at food wells by pigeons are socially transmitted in similar fashion, yet the longevity of these socially transmitted behaviour patterns varies dramatically. Removal of scales from pine cones and digging for pieces of carrot are transmitted in markedly different ways, yet both patterns of behaviour are sustained in individuals and in populations by patterns of reinforcement produced by interaction with the environment. Attention to the rewards and punishments that follow from the exercise of behaviour patterns, not to their origins, is the key to understanding both the longevity of behaviour patterns and the apparent adaptedness of socially learned behaviour in non-human animals.

A prediction

There are surprisingly few experiments described in the literature in which subjects learn some behaviour socially and maintenance of the socially learned behaviour is examined when behaviour patterns other than the socially learned one are also rewarded.

Absence of such evidence is useful in that it allows a strong and as yet untested prediction to be made from the Staddon–Simmelhag model: the duration of expression of a learned behaviour by individuals will be determined by the relative frequency with which rewards follow its expression, not by the nature of the learning process that introduced the behaviour into an individual's repertoire.

Food choice by red-winged blackbirds. Mason & Reidinger's (1981, 1982) studies of social and individual learning of food preferences and aversions by red-winged blackbirds, *Agelaius phoeniceus*, provide one of the few instances in which longevity of a behaviour has been compared

directly in individuals that learned a behaviour either socially or individually (Mason et al. 1984).

After four preference learning trials or one aversion learning trial, in which members of independent groups of subjects were either directly trained to feed from or to avoid yellow food cups, or were allowed to watch the direct preference or avoidance training of others, all subjects were offered a choice between yellow and green food cups for 1 h/day for 12 consecutive days. Both individually and socially learned preferences for yellow containers extinguished in approximately 7 days and both individually and socially learned aversions to yellow containers extinguished in about 12 days. Reinforcement contingencies, rather than origins, appeared to determine the longevity of learned responses.

DISCUSSION

It is proposed here that social interactions affect the development of behaviour in animals by altering the probability of introduction of behavioural variants into an individual's repertoire and thus affecting the probability that individual learning will proceed in one direction rather than in another. Once a pattern of behaviour is introduced into an individual's behavioural repertoire, the duration of its survival there reflects not its source in trial-and-error learning, imitation, local enhancement or some other process, but its consequences relative to the consequences of available behavioural alternatives. Stable, socially learned behaviour patterns in animals that do not garner disproportionate rewards from the environment (i.e. socially learned behaviour patterns that are not locally adaptive), should be rare and ephemeral, rather than common and persistent as the models proposed by Rogers (1988), Boyd & Richerson (1988) and Dawkins (1989) allow. These models all require the existence of behavioural processes that sustain maladaptive socially learned behaviour patterns in a population and reduce the reproductive success of those that learn them. Although hypothetical examples of the disadvantage of social learning in fluctuating or heterogeneous environments can be fabricated without difficulty, as Rogers (1988) did with his snerdwumps, the absence of real-world examples of maladaptive socially learned behaviour in the hundreds of papers and monographs on social

learning in animals raises questions about the utility of models that suggest such examples should be fairly common.

On the present view, in contrast to that of Rogers and others, social learning and individual learning are not treated as independent processes. Rather, individual learning and social influence play complementary roles in behavioural development, social learning might best be described as socially biased individual learning, and social learning should lead to adaptive behavioural repertoires in individuals and diffusion of adaptive behaviour through populations.

Of course, I am not the first to suggest that social processes and individual processes are both involved in the development of socially learned behaviour. In a recent theoretical review, Laland et al. (1993, page 262) suggest that 'acquisition of a socially learned behaviour can be thought of as resulting from a mix of individual experience and social interaction, and its position on this [social/individual learning] dimension is dependent on the relative weighting given to cues derived from individual experience and social interaction'. Although Laland et al. acknowledge the conjoint influence of social interactions and individual learning in the development of animal traditions, their model is both quite different from and, I believe, considerably less useful than that proposed here.

A 'weighted-mix' approach to analysis of animal social learning invites sterile arguments about just where on the individual learning/social learning continuum particular socially learned behaviour patterns fall. Such arguments are particularly likely to be unproductive because it is useless to conceive of a behaviour (for example, pine cone opening by black rats) as 60% individually learned and 40% socially learned (or the converse). Both socially derived stimulus inputs and individual experience of the consequences of action are necessary components of expression of pine cone opening by young roof rats. Consequently, pine cone opening is 100% socially learned as well as 100% individually learned, and there is no locus on an individual/social learning dimension that describes the behaviour in a meaningful way.

In a second paper, Laland (1992) has explored the interaction between tradition and genetic evolution in animals. In Laland's model, the spread and maintenance of a socially learned behaviour in a population depends on: (1) the fidelity with

which that behaviour is transmitted between individuals, (2) the longevity of the behaviour in an individual that acquires it and (3) the fecundity of the behaviour, the probability than an individual will transmit the behaviour to other individuals. Laland's calculations suggest that, for a significant genetic response to a socially transmitted behaviour to occur, the socially transmitted behaviour would have to be very stable.

It follows from the view presented here that, although the fidelity and fecundity of socially learned behaviour patterns may vary with the social learning process underlying their transmission (for example, observers that learned by imitation might, as Heyes (1994) has suggested, be more likely to faithfully copy a model's behaviour than would observers that learned by local enhancement), the longevity of a behaviour in an individual's repertoire, and hence its probability of spreading through a population, will depend on the environment the population occupies and selection among differential rewards garnered by behaviour patterns expressed in that environment.

On the present model, there is no a priori reason to believe that the longevity of a behaviour should vary as a function of the learning process that resulted in its introduction into an individual's repertoire. Only in those environments where a socially learned behaviour results in greater frequency or magnitude of reward than individually learned alternatives will the socially learned behaviour continue to be expressed and available for transmission from one individual or generation to the next. Consequently, models of the role of social learning in evolution must, as Laland's (1992) model does not, incorporate parameters reflecting the results of individual interaction with the environment, if those models are to distinguish those patterns of socially learned behaviour that have the potential to influence the course of evolution from those that do not.

In summary, on the view presented here, social learning, which serves to introduce elements into the behavioural repertoire of individuals, and individual learning, which can produce adaptive modifications in behavioural expression in response to the consequences of engaging in socially learned behaviour, are both integral to the spread and maintenance of traditions in animal populations. Understanding animal traditions and their role in evolution will, therefore, require attention not only to social interactions, but also to the frequency and magnitude of the rewards and punishments that socially learned behaviour garner relative to the rewards and punishments following expression of other elements in the behavioural repertoires of members of animal populations.

ACKNOWLEDGMENTS

REFERENCES

Aisner, R. & Terkel, J. 1992. Ontogeny of pine cone opening behaviour in the black rat, *Rattus rattus. Anim. Behav.*, **44,** 327–336.

Baptista, L. F. & Petrinovich, L. 1984. Social interaction, sensitive phases and the song template hypothesis in the white-crowned sparrow. *Anim. Behav.*, **32,** 172–181.

Baptista, L. F. & Petrinovich, L. 1986. Song development in the white-crowned sparrow: social factors and sex differences. *Anim. Behav.*, **34,** 1359–1371.

Boyd, R. & Richerson, P. J. 1985. *Culture and the Evolutionary Process.* Chicago: University of Chicago Press.

Boyd, R. & Richerson, P. J. 1988. An evolutionary model of social learning: the effects of spatial and temporal variation. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by T. R. Zentall & B. G. Galef, Jr), pp. 29–48. Hillsdale, New Jersey: Lawrence Erlbaum.

Dawkins, R. 1989. *The Selfish Gene.* Oxford: Oxford University Press.

Galef, B. G., Jr. 1976. Social transmission of acquired behavior: a discussion of tradition and social learning in vertebrates. In: *Advances in the Study of Behavior, Vol. 6* (Ed. by J. S. Rosenblatt, R. A. Hinde, E. Shaw & C. Beer), pp. 77–100. New York: Academic Press.

Galef, B. G., Jr. 1988. Imitation in animals: history, definition and interpretation of data from the psychological laboratory. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by T. R. Zentall & B. G. Galef, Jr), pp. 29–48. Hillsdale, New Jersey: Lawrence Erlbaum.

Giraldeau, L. A. & Lefebvre, L. 1986. Exchangeable producer and scrounger roles in a captive flock of feral pigeons: a case for the skill pool effect. *Anim. Behav.*, **34,** 797–803.

Giraldeau, L. A. & Lefebvre, L. 1987. Scrounging prevents cultural transmission of food-finding behaviour in pigeons. *Anim. Behav.*, **35,** 387–394.

Giraldeau, L. A. & Templeton, J. J. 1991. Food scrounging and diffusion of foraging skills in pigeons, *Columbia livia*: the importance of tutor and observer rewards. *Ethology*, **89,** 63–72.

Goodall, J. 1973. Cultural elements in a chimpanzee community. In: *Precultural Primate Behavior: Symposia of the Fourth International Congress of Primatology* (Ed. by W. Montagna), pp. 144–184. Basel: Karger.

Heyes, C. M. 1993. Imitation, culture and cognition. *Anim. Behav.*, **46,** 99–110.

Heyes, C. M. 1994. Imitation and culture: longevity, fecundity and fidelity in social transmission. In: *Behavioral Aspects of Feeding* (Ed. by B. G. Galef, Jr, M. Mainardi & P. Valsecchi), pp. 271–278. Chur, Switzerland: Harwood Academic.

Heyes, C. M. 1994. Social learning in animals: categories and mechanisms. *Biol. Rev.*, **69,** 207–231.

James, W. 1890. *Principles of Psychology, Vol. 2*. New York: Henry Holt.

Kawamura, S. 1959. The process of sub-culture propogation among Japanese macaques. *Primates*, **2,** 43–45.

King, A. P. & West, M. J. 1983. Epigenisis of cowbird song: a joint endeavor of males and females. *Nature, Lond.*, **305,** 704–706.

King, A. P., West, M. J. & Eastzer, D. H. 1981. Song structure and song development as potential contributors to reproductive isolation in cowbirds (*Molothrus later*). *J. comp. physiol. Psychol.*, **94,** 1028–1039.

Laland, K. N. 1992. A theoretical investigation of the role of social transmission in evolution. *Ethol. Sociobiol.*, **13,** 87–113.

Laland, K. N. & Plotkin, H. C. 1990. Social learning and social transmission of foraging information in Norway rats (*Rattus norvegicus*). *Anim. Learn. Behav.*, **18,** 246–251.

Laland, K. N. & Plotkin, H. C. 1992. Further experimental analysis of the social learning and transmission of foraging information amongst Norway rats. *Behav. Proc.*, **27,** 53–64.

Laland, K. N., Richerson, P. J. & Boyd, R. 1993. Animal social learning: towards a new theoretical approach. In: *Perspectives in Ethology, Vol. 10* (Ed. by P. P. G. Bateson, P. H. Klopfer & N. S. Thompson), pp. 249–277. New York: Plenum Press.

Logan, C. A. 1992. Developmental analysis in behavioral systems: the case of bird song. *Ann. N.Y. Acad. Sci.*, **662,** 102–117.

Marler, P. 1970. A comparative approach to vocal learning: song development in white-crowned sparrows. *J. comp. physiol. Psychol.*, **71,** 1–25.

Marler, P. 1976. Sensory templates in species-specific behavior. In: *Simple Networks and Behavior* (Ed. by J. C. Fentress), pp. 314–319. Sunderland, Massachusetts: Sinauer.

Marler, P. 1991. Song-learning behavior: the interface with neuroethology. *Trends Neurosci.*, **14,** 199–206.

Mason, J. R., Artz, A. H. & Reidinger, R. F. 1984. Comparative assessment of food preferences and aversions acquired by blackbirds via observational learning. *Auk*, **101,** 796–803.

Mason, J. R. & Reidinger, R. F. 1981. Effects of social facilitation and observational learning on feeding behavior of the red-winged blackbird (*Agelaius phoeniceus*). *Auk*, **98,** 778–784.

Mason, J. R. & Reidinger, R. F. 1982. Observational learning of food aversions in red-winged blackbirds (*Agelaius phoeniceus*). *Auk*, **99,** 548–554.

Morgan, C. L. 1900. *Animal Behaviour*. London: Arnold.

Petrinovich, L. 1988. The role of social factors in white-crowned sparrow song development. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by T. R. Zentall & B. G. Galef, Jr), pp. 255–278. Hillsdale, New Jersey: Lawrence Erlbaum.

Petrinovich, L. & Baptista, L. F. 1987. Song development in the white-crowned sparrow: modification of learned song. *Anim. Behav.*, **35,** 961–974.

Rogers, A. R. 1988. Does biology constrain culture? *Am. Anthropol.*, **90,** 819–831.

Spence, K. W. 1937. Experimental studies of learning and higher mental processes in infra-human primates. *Psychol. Bull.*, **34,** 806–850.

Staddon, J. E. R. & Simmelhag, V. L. 1971. The 'superstition' experiment: a reexamination of its implications for the principle of adaptive behavior. *Psychol. Rev.*, **78,** 3–43.

Thorndike, E. L. 1898. Animal intelligence: an experimental study of the associative process in animals. *Psychol. Monogr.*, **2** (No. 8).

Thorpe, W. H. 1963. *Learning and Instinct in Animals.* London: Methuen.

West, M. J. & King, A. P. 1988. Female visual displays affect the development of male song in the cowbird. *Nature, Lond.*, **334,** 244–246.

West, M. J., King, A. P. & Eastzer, D. H. 1981. The cowbird: reflections on development from an unlikely source. *Am. Scient.*, **29,** 57–66.

Whiten, A. & Ham, R. 1992. On the nature and evolution of imitation in the animal kingdom: reappraisal of a century of research. In: *Advances in the Study of Behavior, Vol. 21* (Ed. by P. J. B. Slater, J. S. Rosenblatt, C. Beer & M. Milinski), pp. 239–283. New York: Academic Press.

Zajonc, R. B. 1965. Social facilitation. *Science*, **149,** 269–274.

Zohar, O. & Terkel, J. 1991. Acquisition of pine cone stripping behaviour in black rats (*Rattus rattus*). *Int. J. comp. Psychol.*, **5,** 1–6.