

## The adaptive value of social learning: a reply to Laland

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The portion of the introduction to Galef (1995) to which Laland (1996) objects in his commentary was concerned not, as Laland suggests, with the entire field of formal modelling of social learning, but with two specific models of social learning in animals, one proposed by Rogers (1988), the other by Boyd & Richerson (1988). I did not refer to the other models that Laland references, not because I was unaware of their existence, but because my comments did not apply to them.

Apparently, Laland and I agree about Rogers's (1988) model, but Laland is not pleased with my published interpretation of Boyd & Richerson's model (1988). Since Galef (1995) went to press, I have had extensive correspondence with Laland and a number of discussions with Richerson concerning the appropriate interpretation of Boyd & Richerson (1988). It has become clear that I should not have taken literally Boyd & Richerson's (1988) verbal presentation of their model. Boyd has provided as clear a statement of the problem as any of my correspondents on the issue.

It is true that the models cited [Boyd & Richerson 1988] are presented as if each individual irreversibly adopts a single behavior during its lifetime. However, this is not a mathematical convenience . . . but a rhetorical choice. The models can apply to situations like food preferences by reinterpreting the time scale—the evolutionary step becomes a day or week rather than a generation. All the same results hold, the only thing that changes is the rate at which things happen. Richerson and I made this point in Chapter 3 of our book and even there it is not emphasized. However, in most of our papers we have left the idea unstated, and in doing so we have misled Galef into thinking that our models require that

behaviors are acquired once and for all. [Boyd, personal communication (June 1994) quoted with permission (October 1995).]

As did Laland in his commentary, I interpreted a rhetorical device as a mathematical simplification, which is not what Boyd & Richerson intended. My reading was, in part, the result of an unfortunate coincidence; Boyd and Richerson's 'rhetorical choice' was identical to a premise of Rogers's (1988) model. Consequently, I did not appreciate the congruence between Boyd & Richerson's 1985 and 1988 models, both of which are, as Laland makes clear, guided variation models.

I hope that my failure to understand Boyd & Richerson's (1988) intent does not detract attention from the basic messages in Galef (1995): individual learning and social influence are not independent processes; social learning in animals might best be described as socially biased individual learning, and interaction of social and individual learning processes should lead to maintenance of adaptive behavioural repertoires in individuals and diffusion of adaptive behaviours through populations.

In the second part of his commentary, Laland turns to discussion of the concept of adaptation as it applies to social learning. It is here that he and I may still have some disagreement.

Given Laland's vigorous refutation of my alleged assertion that those involved in constructing mathematical models of social learning in animals sometimes seem to believe that socially learned behaviours will be maintained in the absence of differential reward, I was surprised to find that the point of all three of Laland's discussions of the term 'adaptive' was to identify ways in which 'not adaptive' or 'maladaptive' socially learned behaviours might persist in animals. For example, Laland's first discussion of the term adaptive contains the hypothesis that 'within some range, arbitrary, or nearly arbitrary, socially transmitted traits may persist' (page 639).

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There is, however, no particular reason to expect that an animal will continue to exhibit with abnormally high frequency a behaviour pattern that it learned socially, if the consequences of expressing the socially learned behaviour and alternatives that lead to the same goal are equally rewarding (Heyes 1993). For example, when Norway rats, *Rattus norvegicus*, that had observed a conspecific displace a joystick to the right and other rats that had observed a conspecific displace a joystick to the left were all rewarded regardless of which way they moved the joystick, their initial imitation of the demonstrated direction of displacement of the joystick rapidly extinguished. After a mere 10 responses, rats in both groups of observers displaced their joysticks right and left with equal frequency (Heyes, 1994). Similarly, Mason et al. (1984) found that the longevity of socially acquired preferences for and aversions to yellow food cups in red-winged blackbirds, *Agelaius phoeniceus*, offered a choice between yellow and plain food cups, extinguished after a dozen hour-long tests, the same number of test trials that it took for individually learned preferences and aversions to yellow food cups to extinguish.

Although, as Laland indicates, relatively few published laboratory experiments have examined the persistence of socially learned behaviours in situations where socially learned behaviours and their alternatives have identical consequences, what laboratory evidence there is does not offer support for the generalization that socially learned responses persist under such circumstances.

In the sole laboratory study that Laland references to support his contention (Galef & Allen 1995), transmission across generations of a socially learned food preference was clearly present only when opportunities for individual learning about alternatives to a socially learned behaviour were restricted and stable preferences were, thus, maintained within generations.

Laland points to the observations of Norton-Griffiths (1967) as providing support for the notion that functionally equivalent socially learned variants are preserved in free-living animal populations. This claim, common in the secondary literature but, I believe, not well supported by data, is based on the final two paragraphs of Norton-Griffiths's (1967) classic article on the feeding behaviour of oystercatchers, *Haematopus*

*ostralegus*. Here, Norton-Griffiths summarized unpublished observations from his Ph.D. thesis indicating first, that 'an individual oystercatcher will either hammer mussels or stab them, but will not do both' and, second, 'that young oystercatchers develop the same feeding technique as their parents' (page 423). However, interpretations of Norton-Griffiths's observations, other than those he provides, are plausible, even likely.

Norton-Griffiths (1967) demonstrated in the body of his classic paper that the circumstances when oystercatchers can use hammering and stabbing to open mussels are quite different. Stabbing is useful only when mussels are submerged in water and are holding their shells slightly open; an oystercatcher can stab its bill directly into a mussel shell only when it is ajar. Hammering, on the other hand, is effective when oystercatchers are feeding on mussels that are exposed to air and tightly closed, but hammering can be used only in areas where mussels can be placed on exposed rock or hard sand that serves as an anvil for hammering. Consequently, Norton-Griffiths had to explain not only how each young oystercatcher became a hammerer or stabber, but also how it found feeding grounds where it could use its particular method for opening mussels. According to Norton-Griffiths's interpretation, young hammerers had to find mussel beds near exposed areas of hard sand or rock, and young stabbers had to find mussel beds below the waterline.

Norton-Griffiths (1967, page 423) proposed that 'While the young are developing their feeding technique they are fed by their parents and accompany them onto the mussel beds. In this way they can learn at least one locality which is suitable for their particular feeding technique . . .'

No evidence was provided that young oystercatchers learned their feeding techniques directly from their parents. Perhaps this lacuna is what led Roper (1989, page 574) to suggest that, perhaps, 'a chick merely follows its parents (or foster parents) to their preferred feeding location, and then adopts the feeding technique most appropriate to that location. The feeding technique could either be individually learned by trial and error, or it could be innate.'

Norton-Griffiths's interpretation of his observations depends critically on his assertion that each oystercatcher has only a single feeding technique at its disposal. Yet Goss-Custard & Sutherland (1984) have reported that 26 of 104

(25%) oystercatchers, each observed while it consumed two or more mussels within a 5-min period, both hammered and stabbed. Consequently, Goss-Custard & Sutherland (page 300) warned explicitly against assuming that individual birds invariably use one feeding technique, stating 'that both free-living and captive birds demonstrate that this is not so'.

Apparently, individual oystercatchers have both hammering and stabbing techniques in their feeding repertoires, and there is no evidence that oystercatchers do not simply use whichever technique is appropriate to mussels encountered while feeding. Given the high rate of alternation between feeding techniques observed by Goss-Custard & Sutherland (1984), it does not seem likely that young oystercatchers persist in the pattern of feeding of their parents for very long or even that their parents use a single pattern of feeding for their young to copy.

Thus, the example of behaviour patterns in free-living animals that Laland provides to make the point that 'functionally equivalent variants may be preserved in animal populations by social learning' (page 639) does not convincingly do so.

Laland's second discussion of the use of the term adaptive seems a strange one. Laland proposes, reasonably enough, that the 'proximate' benefits that result from following others (protection from predation, consistent discovery of food, etc.) may be greater than those that result from seeking food independently, even though independent exploration might lead to discovery of richer food sources than would following others to a feeding site. Laland describes this as a situation in which social learning does not confer highest fitness and, therefore, increases absolute but not relative fitness.

There are two problems with this use of the term adaptive. First, on Laland's description of his hypothetical situation, feeding socially provides greater benefits than does seeking food alone, yet Laland wants to describe seeking food socially as a sub-optimal variant. Solitary feeding has higher fitness consequences than does social feeding only if one treats feeding as a trait on which selection acts independently, which does not seem appropriate.

Second, surely we are all agreed that describing a behaviour pattern as adaptive does not imply that it is the best of all imaginable behaviours, as

seems implicit in Laland's usage. 'Adaptive' does not mean 'perfect'. It never has. It never will.

Laland's third discussion of the term adaptive concerns a type of maladaptive traditional behaviour pattern that, as Laland indicates, has not yet been found in animals. Maladaptive traditions are not likely to be found in animals because evolution has shaped the affective responses of individual organisms so that they are unlikely to learn maladaptive behaviours for others to copy. There is, however, no magic to social learning. If, as the Fore of New Guinea tragically failed to discover, a behaviour pattern that produces greater costs than benefits is perceived as providing greater benefits than costs, then neither social nor individual learning will protect the individual against either acquiring or persevering in that behaviour pattern.

Imperfections in learning processes, however, whether social or individual, do not mean that they are not adaptive, just that they are not perfect. Rats succumb by the tens of millions each year to anticoagulant rodenticides mixed with palatable baits. Yet, so far as I know, no one has argued that either ingestion of palatable foods or learning associations between the taste of a food and toxicosis are not adaptive.

It also may be worth stating explicitly that extrapolation from social learning in humans to social learning in animals can be misleading. It has been argued with some success, at least since Wallace (1870), who attributed the glories of classical Greek architecture to the persistence of conventions more appropriate for constructing edifices of wood than of stone, that human traditions can persist despite the availability of more rewarding alternatives. One need not travel to New Guinea to find examples of the persistence of what appear to be maladaptive behaviours in human populations. Seeing members of ultra-orthodox sects dressed in dark fur hats and black suits walking about the streets of Jerusalem in the noonday, summer sun brought this home to me (and, presumably, to those I was watching as well) most forcefully. However, the wealth of such perverse habits in humans is not evidence that they occur in other animals.

Why do humans, but (I would argue) not other animals, persist in expressing socially acquired behaviour patterns that are punished by the physical environment? Because the processes maintaining traditions in humans and other organisms can

be radically different. But that is material for an extended essay.

Laland is, of course, right to call for additional empirical work on factors that might affect the persistence of socially learned behaviour patterns in animals. Still, at the present time, there is little evidence of unusual persistence of socially learned behaviour patterns in species other than our own. Given what is known about rates of extinction of individually learned behaviour patterns when they cease to be differentially rewarded, and the important role that individual learning plays in social learning, there is no reason to assume that behaviour patterns learned socially will persist when they are no longer differentially rewarded any more than will individually learned behaviour patterns.

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