

ANIMAL INNOVATION

Edited by

SIMON M. READER

*Department of Biology
McGill University
Montréal
Canada*

and

KEVIN N. LALAND

*Centre for Social Learning and Cognitive Evolution
School of Biology
University of St Andrews
Scotland
UK*

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SOCIAL LEARNING: PROMOTER OR INHIBITOR OF INNOVATION?

BENNETT G. GALEF, JR.

Introduction

During the 130-year history of the scientific study of animal behaviour, there have been two periods of relatively intense interest in the role of social learning in behavioural development. The first of these episodes occurred in the latter part of the nineteenth century at a time when instinct and imitation were considered to be the main sources of adaptive behaviour in animals. The second began some 30 years ago with the publication of Ward and Zahavi's (1973) classic paper on information centres, and continues to the present day. Below, I discuss contrasting views of the interaction of social learning and innovation characteristic of these two periods.

Social learning as a conservative force

At the end of the nineteenth century, social learning was seen as a way in which the normal behaviours of a population of animals were conserved and transmitted intact from one generation to the next. Consequently, social learning was viewed primarily as interfering with acquisition of novel patterns of behaviour.

I quote from the work of but three of the several nineteenth century behavioural scientists with an interest in the role of imitation in behavioural development. First, a paragraph from a wonderful essay by Alfred Russell Wallace (1870) entitled 'The philosophy of birds' nests.' In this brief paper, Wallace argues that constancy across generations in the structure of nests built by various avian species, like constancy across generations in the shape of human habitations, results from social learning.

'No one' Wallace asserts, 'imputes [the] stationary condition of domestic architecture among... savage tribes to instinct, but to simple imitation from one generation to another, and the absence of any sufficiently powerful stimulus to change or improvement. When once a particular mode of building has become confirmed by habit and by hereditary custom, it will be long retained, even when its utility has been lost through changed conditions, or through migration to a different region... These characteristics of the abode of savage man will be found exactly paralleled by the nests of birds' (Wallace, 1870, p. 212-5).

C. L. Morgan, writing in 1896, expressed a similar view, 'The conservative tendency of imitation, bringing the newly born members of the animal community into line with the average behaviour of the species is probably its most important office. The young bird or mammal... is born into a community where certain behaviour is constantly exhibited before its eyes. Through imitation it falls in with the traditional habits...' (Morgan, 1896, p. 183-4). Or, from an earlier monograph by the same author, 'Where the young animal is surrounded during the early plastic and imitative period of life by its own kith and kin, imitation will undoubtedly have a conservative tendency. The education of young animals by their parents has also a conservative tendency' (Morgan, 1890, p. 455).

Like Morgan, James Baldwin (1895, p. 298), the philosophically minded social psychologist, felt that the role of imitation in acquisition of novel behaviours had been over-emphasised, that 'many of the most "innate" powers of the animals are brought out, perfected and constantly kept efficient, by imitation of their own species.' Thus, imitation was to be viewed as playing an important, if sometimes underestimated, role in conservation of species-typical behaviours.

Of course others, for example Darwin's protege in matters behavioural, George Romanes (1882), saw imitation (especially of human behaviour by animals) as a source of behavioural innovations. Still, the prevailing view of imitation was that it played an essentially conservative role in behavioural development.

Social learning as a progressive force

During the past 30 years, animal behaviourists have more often been concerned with the role of social learning in diffusing novel or innovative patterns of behaviour through a population than with its possible role in maintaining existing patterns of behaviour. The list of innovative behaviours exhibited by animals that have been attributed to social learning of one kind or another is long indeed. It ranges from sweet-potato-washing by Japanese macaques on Koshima Island (Kawai, 1965) and termite fishing by chimpanzees at Gombe (Goodall, 1986) to pinecone stripping by roof rats in Israel (Terkel, 1996) and diving for molluscs among Norway rats living along the Po River in Italy (Gandolfi and Parisi, 1973).

Why such different views of social learning?

Several possible reasons for the change in perspective on the role of social learning come to mind. First, at the end of the nineteenth century, those engaged in the first scientific studies of animal behaviour were struggling to explain the observation that all the members of any given species tend to engage in similar patterns of behaviour. Today's understanding of behavioural consistency within a species rests largely on work carried out in mid-twentieth century by a large group of psychologists and biologists (e.g. Tinbergen, Lorenz, Lehrman, Kuo, etc.), and that work largely ignored the possibility that social learning might contribute to development of species-typical behaviours.

Results of Kasper-Hauser experiments convinced ethologists that behavioural transmission across generations was relatively unimportant in the development of instincts. Lehrman's (1953) reinterpretation of the results of isolation-rearing studies, focussed as it was on the importance of the interaction of individual and environment in behavioural

development, did little to undermine that conclusion. In the late 1800s, on the contrary, discussions on contributions of experience to development of species-typical behaviours focussed on social learning, particularly imitation, rather than on individual trial and error.

Second, scientists working in the late 1890s did not have access to the myriad field observations collected during the last 50 years indicating that, especially in primates, there are systematic differences in the behaviour of allopatric populations of a single species. Now that existence of such population- or locale-specific patterns of behaviour has been clearly established, these animal traditions require explanation, and social learning provides an obvious potential source of differences in the behaviour of allopatric populations of a species.

Third, scientists working in the 1890s had not been through the nature–nurture controversy of the 1960s that so clearly revealed the difficulty of determining causes of similarities in behaviour, and the comparative ease with which analyses of sources of differences in behaviour can be carried out. With the general shift in emphasis from study of sources of constancy to study of sources of variability, social learning was increasingly used to explain the latter rather than the former.

Last, we live in an era when many behavioural scientists, particularly primatologists, seek evidence of human-like performance in animals. Diffusion of technical innovations through human populations is part of the everyday experience of those of us fortunate enough to live in the twenty-first century. If, as anthropomorphic approaches to the study of behaviour require, behavioural capacities of animals in general and of primates in particular are fundamentally like those of humankind, then primates would be expected to transmit behavioural novelty.

Such increased acceptance of anthropomorphism as a heuristic (if not as an explanation) may be a necessary response to the rigid Behaviorism of the first half of the twentieth century. In any case, when anthropomorphic speculations are acceptable, the role of social learning in behavioural development is likely to be viewed differently than it was late in the nineteenth century, when naturalists were intent on rejecting the excessive anthropomorphism that characterised the work of their predecessors (Galef, 1996c).

Is there a resolution?

So, who got it right? Is social learning in animals a force for conservation of the old ways or a force for change, spreading innovative behaviours through populations? Or, are both views correct?

At least part of the answer to such questions lies in results of experiments undertaken to determine just how information is transmitted socially from one individual to another. Understanding how animals learn socially and how social learning interacts with both individual learning and unlearned predispositions of animals should provide some insight into the role of social learning in both promoting and inhibiting the spread of behavioural innovations.

Food choices of wild and laboratory rats as model systems

My students and I have used the feeding behaviour of both a common laboratory animal, the domesticated Norway rat (*Rattus norvegicus*), and of its wild progenitor, as model

systems in which to study: (1) behavioural mechanisms supporting social learning and (2) interactions of socially learned behaviours with other influences on behavioural development. Results of such studies of social feeding in Norway rats, described very briefly below (and reviewed more extensively in Galef, 1976, 1982, 1988, 1996a,b), suggest that social learning is inherently neither progressive nor conservative in its impact on behaviour. Rather, social learning acts in concert with an animal's behavioural proclivities and individual experiences, sometimes to maintain old habits in new recruits to a social group, sometimes to diffuse novel patterns of behaviour through a population.

Social learning as a conservative force in the food choices of Norway rats

Experiments with wild rats

Many years ago, my co-workers and I (Galef and Clark, 1971a) took wild Norway rats, first and second generation descendants of animals that we had trapped on garbage dumps in southern Ontario, and established them in small groups in 1×2 m enclosures. Using taste-aversion learning, we taught all the members of each of our colonies to eat only one of the two foods that we made available to each colony for 3 h each day. Our wild rats learned rapidly to avoid eating the adulterated diet placed in their cages each day and continued, for months, to avoid that diet even when later offered uncontaminated samples of it.

We then waited impatiently until young ones were born to colony members, grew to weaning age and began to eat solid food. By watching on closed-circuit television throughout daily 3-h feeding periods, we could observe and record every mouthful of food that the weaning juveniles in each enclosure ate.

We found, invariably, that the young members of each colony ate only the food that the adults of their colony were eating, and never even sampled the alternative food that adult members of their colony had learned to avoid. For weeks, the young wild rats remained faithful to the food preference we had taught to the adult members of their colony even though both adults and young were presented only with uncontaminated samples of both diets (Figures 6.1(a) and (b)).

Such avoidance of bait by young rats after adult members of their colony have been poisoned on it and learned to avoid eating it is no mere laboratory artefact. Applied ecologists trying to exterminate pest populations of wild Norway rats have reported, as we found in captive animals, that if members of an adult population learn to avoid ingesting a poison bait, their young ones will also avoid all contact with that bait for some time (Steiniger, 1950).

The reason for the socially induced conservatism in food choice seen in wild Norway rats is easy to understand. Wild rats, unlike their domesticated conspecifics, are extremely hesitant to eat any food that they have not previously eaten. For example, in the laboratory, wild Norway rats that are used to eating one food, and are then offered access only to an unfamiliar food, will often starve themselves for days before starting to eat the unfamiliar food, even if the unfamiliar food is highly nutritious and palatable (Galef, 1970). Domesticated rats placed in a similar situation will begin eating the unfamiliar food in a matter of minutes or hours.

Results of our experiments have shown that young wild rats living with older conspecifics are biased in a variety of different ways to begin eating the same food that the

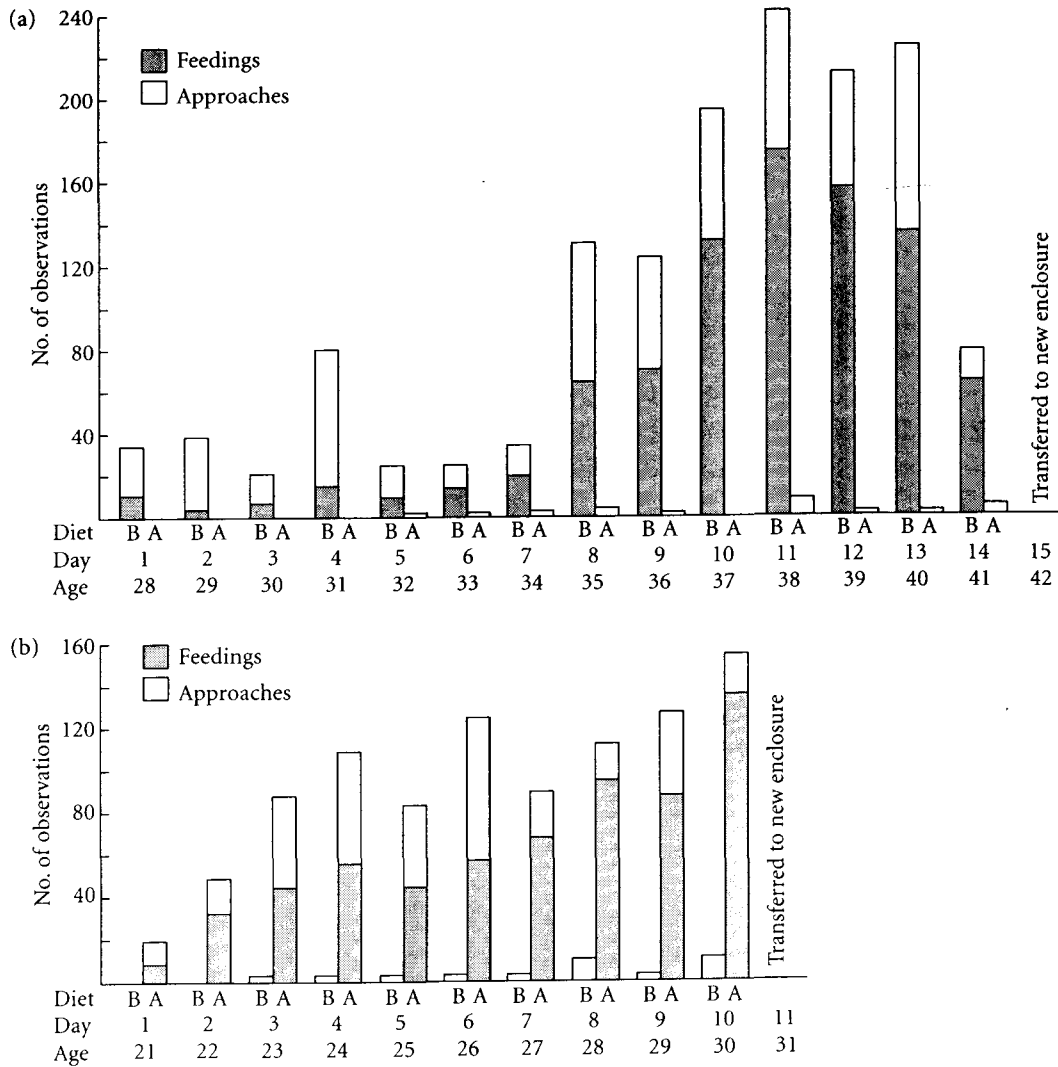


Figure 6.1 Number of observed approaches to and feedings from food bowls containing Diets A and B by weanling wild rat pups the adults of whose colonies had been trained to avoid ingesting: (a) Diet A or (b) Diet B. Reprinted from Galef and Clark (1971a) with permission. Copyright © 1971 by the American Psychological Association.

adults of their colony are eating (Galef, 1996b): (1) Young rats detect the flavour of their mother's diet in her milk and, when weaning, prefer foods having a flavour they experienced while suckling (Galef and Henderson, 1972; Galef and Sherry, 1973). (2) When seeking their first meals of solid food outside the nest, weanling rats approach adults feeding at a distance from the nest site and begin to feed close to those adults, often crawling up under an adult's belly and starting to eat under its chin (Galef and Clark, 1971a, b). (3) Young rats prefer to eat both foods and at feeding sites that have been scent-marked by adults of their species (Galef and Heiber, 1976; Galef and Beck, 1985; Laland and Plotkin, 1993). (4) Rats both young and old can detect the odour of a food on the breath of a conspecific and show enhanced preferences for foods experienced in that way (Galef and Wigmore, 1983;

Galef, 1996b). (5) Young rats show enhanced preferences for foods that they have previously stolen directly from the mouths of conspecifics (Galef *et al.* 2001), and (6) young rats follow scent trails that adults deposit when travelling from feeding sites back to their nest (Galef and Buckley, 1996).

Once weaning wild rats have been biased by interaction with adults of their colony (or with their peers) to begin eating one food rather than available alternatives, the young ones will ignore those alternatives because of their inherent reluctance to ingest unfamiliar substances. Greenberg (Chapter 8) discusses the role of neophobia, and its converse 'neophilia', in development of novel behaviours. Here we will be more concerned with the role of neophobia in maintenance of behaviours once they have been introduced into a population.

We have used comparative methods to test directly the hypothesis that the conservative nature of social influences on the food choices of young wild rats depends on an interaction between the social biasing of initial food choices and the reluctance of wild rats to ingest unfamiliar potential foods. As mentioned earlier, members of domesticated strains of Norway rat are far more willing to eat unfamiliar foods than are wild Norway rats. Consequently, although weaning domesticated rats, like weaning wild rats, might initially eat the same food that adults of their colony are eating, we predicted that domesticated rats should soon sample available foods other than the food to which adults of their colony have introduced them.

Our findings supported these predictions. Domesticated rats, like their wild forebears, initially eat the same food that adults of their colony are eating, but unlike wild rats domesticated rats soon begin first to sample and then to eat, available alternatives (Figure 6.2; Galef and Clark, 1971a). Thus, the 'neophobia' of young wild rats (their tendency to avoid

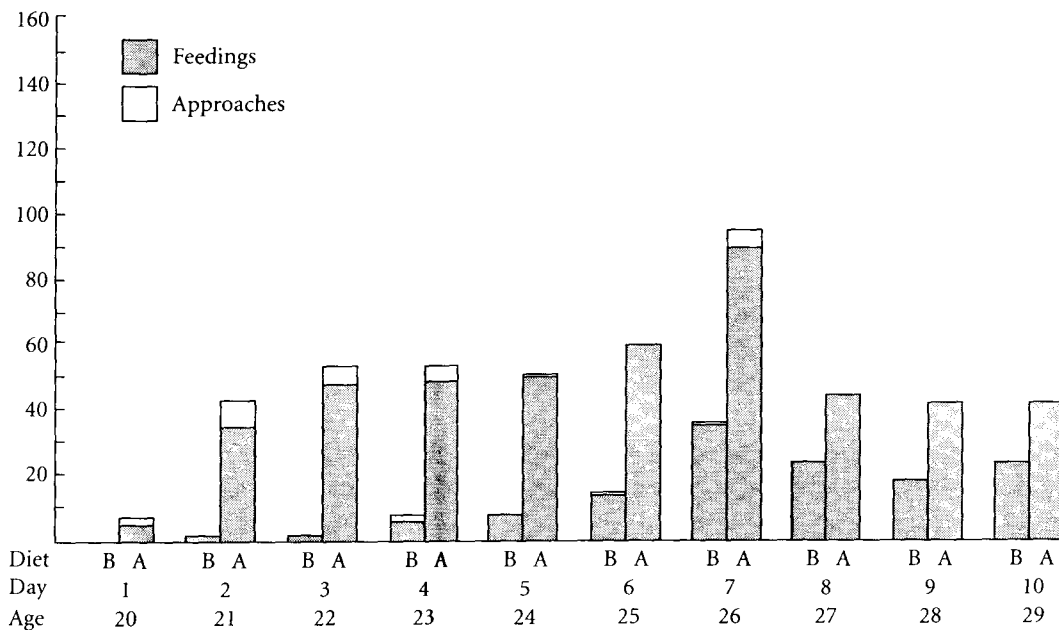


Figure 6.2 Number of observed approaches to and feedings from food bowls containing Diets A and B by weaning domestic rat pups the adults of whose colony had been trained to avoid ingesting the more palatable Diet B. Adapted from Galef and Clark (1971a) with permission. Copyright © 1971 by the American Psychological Association.

