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Interaction of social and individual learning in food preferences of Norway rats

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We conducted four experiments to examine the effects of individual experience of postingestive consequences of eating foods on the longevity of Norway rats', *Rattus norvegicus*, socially enhanced food preferences. The results of these experiments showed that: (1) waning of a socially enhanced food preference resulted from experience of postingestive consequences of foods, (2) time available each day to sample foods affected the rate at which a socially enhanced food preference waned, (3) the relative value of a food for which enhanced preference had been socially induced and of alternative foods markedly affected the rate at which socially enhanced preferences waned, and (4) experience of a food and its alternatives after social enhancement of a food preference had a significantly greater effect on the rate at which the socially enhanced preference waned than similar exposure to the same foods before social enhancement of a preference. These results are consistent with the view that social learning acts primarily to introduce behaviour into an individual's repertoire and experience of the consequences of engaging in a socially learned behaviour and its alternatives determines the persistence of the socially learned behaviour.

Optimal use of social learning in the development of a behavioural repertoire that is responsive to local conditions often requires an individual to be sensitive to whatever consequences ensue from expressing socially learned behaviours (Boyd & Richerson 1985, 1988; Galef 1995, 1996). Despite a considerable theoretical literature on the important role of interaction between social and asocial sources of information in development of adaptive behavioural repertoires (e.g. Cavalli-Svorza & Feldman 1981; Boyd & Richerson 1985, 1988; Laland et al. 1993), there has, to date, been relatively little experimental work examining effects of asocial learning on social learning (but see Mason et al. 1984; Heyes et al. 1993).

Our laboratory has been using social influences on food choices of Norway rats, *Rattus norvegicus*, as a model system in which to explore effects of experience of consequences on the longevity of socially learned behaviours (Galef & Allen 1995; Galef & Whiskin 1998). In our basic experimental paradigm (Galef & Wigmore 1983), a naïve rat (an observer) interacts briefly with a conspecific (a demonstrator) that has been fed one of two isocaloric foods. After demonstrators and observers interact, the observers are allowed to choose between the two foods, and invariably show an enhanced preference for whichever food their respective demonstrators ate.

Although such social effects on food choice are surprisingly robust (Galef et al. 1984; Galef 1989), with the opportunity for continued evaluation of two foods, any socially enhanced preference for one of them gradually disappears, and observer rats eventually come to eat the same proportions of the two foods regardless of which food their demonstrators ate. For example, when observer rats were given a choice between two foods following interaction with demonstrator rats fed one of these foods (cinnamon- or cocoa-flavoured diet) ad libitum, the observers rats' socially induced preferences for their respective demonstrators' diets slowly extinguished during 1 week of continuous testing (Galef & Whiskin 1998).

EXPERIMENT 1

In interpreting results of experiments in which socially enhanced food preferences wane, we have assumed without direct evidence that such extinction of enhanced preference reflects individual experience of the equivalent consequences of ingesting the food for which a preference had been socially enhanced and the alternative (Galef & Allen 1995; Galef & Whiskin 1998). It is, of course, possible that the gradual disappearance of a socially induced food preference does not result from

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observers learning about the relative value of their initially preferred food and its alternatives. The influence of socially acquired information on behaviour might simply wane with the passage of time.

In the present experiment, we first socially induced an enhanced preference for a cinnamon-flavoured food (diet Cin) in two groups of observer rats. Then, 4 days later, we offered members of both groups a choice between diet Cin and a somewhat more palatable, isocaloric cocoa-flavoured food (diet Coc). We gave observers assigned to the delayed-choice condition a choice between diets Cin and Coc for the first time 4 days after social induction of preference for diet Cin, whereas observers assigned to the continuous-choice condition chose between diets Cin and Coc for the 4 days intervening between induction of an enhanced preference and the start of the critical preference test. If waning of socially enhanced preferences for foods results from experience of the consequences of eating those foods and their alternatives, then we would expect observer rats assigned to the delayed-choice condition to eat more diet Cin than observer rats assigned to the continuous-choice condition because the latter had 4 days experience of the consequences of ingesting diets Cin and Coc before the critical test. If, to the contrary, waning of a socially induced food preference results from simple waning of the effects of social interaction on preference, then 4 days after preference induction, subjects assigned to the two conditions should not differ in their preference for diet Cin.

Methods

Subjects

We used as observers 24 42-day-old, experimentally naïve, female Long-Evans rats born in the vivarium of the Psychology Department of McMaster University (Hamilton, Ontario) to breeding stock acquired from Charles River Canada (St Constant, Quebec).

From weaning (on day 21 postpartum) to the start of the experiment (on day 42 postpartum), we housed observer rats in shoe-box cages in groups of three or four littermates and gave them ad libitum access to pellets of Purina Rodent Laboratory Chow 5001 (Ralston-Purina Canada, Woodbridge, Ontario) and water.

We used as demonstrators an additional 24, 50- to 60-day-old, female Long-Evans rats that had served as observers in other experiments.

Before beginning the experiment, we randomly assigned 12 demonstrators and 12 observers to each of the two conditions described in Procedure (below).

Apparatus

During the experiment, we housed observer rats in individual wire-mesh hanging cages that measured $21.5 \times 24 \times 27.5$ cm and demonstrator rats in cages identical to those in which we kept observers, but placed in a rack separated from that holding observers by several feet. (Changes in local enforcement of Canadian guidelines for animal holding facilities have made it impossible for us to house demonstrator rats and observer rats in separate rooms, as we have done previously in similar experiments).

We presented food to all subjects in semicircular, stainless-steel cups (8 cm diameter $\times$ 4 cm deep). To prevent spillage, we filled cups to a depth of 2 cm or less. We monitored spillage by examining trays under cages for spilled food, but found none.

Foods

We composed two distinctively flavoured foods by adding either 2.0 g of Hershey's Pure Cocoa (diet Coc) or 1.0 g of bulk ground cinnamon (diet Cin) to 100 g of powdered Purina Rodent Chow 5001 (diet Pur). A pilot test revealed that a group of 12 experimentally naïve rats that we offered a choice between diet Cin and diet Coc for 24 h ate an average ($\pm$ 1 SE) of $36.3 \pm 5.3\%$ diet Cin.

Procedure

Because our subjects had a palatability-based preference for diet Coc, in experiment 1, we socially enhanced observers' preferences for diet Cin.

Demonstrators. After we placed demonstrator rats in their respective individual cages, we put them on a 23-h schedule of food deprivation. While they were on schedule, we gave them access to diet Pur for 1 h/day for 2 consecutive days.

Twenty-three hours after each demonstrator rat's second scheduled feeding with diet Pur, we introduced a weighed food cup containing diet Cin into its home cage. One hour later, we removed the food cup and ascertained that each demonstrator had eaten more than 3 g of diet Cin. We then introduced each demonstrator into the home cage of an observer and left demonstrator and observer undisturbed for 30 min. At the end of the 30-min period of interaction of observers with demonstrators, we removed each demonstrator from its observer's cage and ended the participation of demonstrators in the experiment.

Observers. During the first 2 days of the experiment (while we habituated demonstrators to their feeding schedule), we provided each observer rat with ad libitum access to pellets of diet Pur. We removed these pellets just before we introduced demonstrator rats into the home cages of observers.

Immediately following removal of demonstrators from the cages of observers, we offered each observer assigned to the continuous-choice condition two weighed food cups, one containing diet Cin and the other diet Coc. Once every 24 h for 5 days an experimenter weighed, refilled and reweighed each of the two food cups in each observer's cage and then calculated the percentage of the total food intake of individual observers during the preceding 24 h that was diet Cin.

We treated observer rats that we had assigned to the delayed-choice condition exactly as we treated observer rats assigned to the continuous-choice condition except that for the first 4 days after we removed demonstrators from cages of observers assigned to the delayed-choice

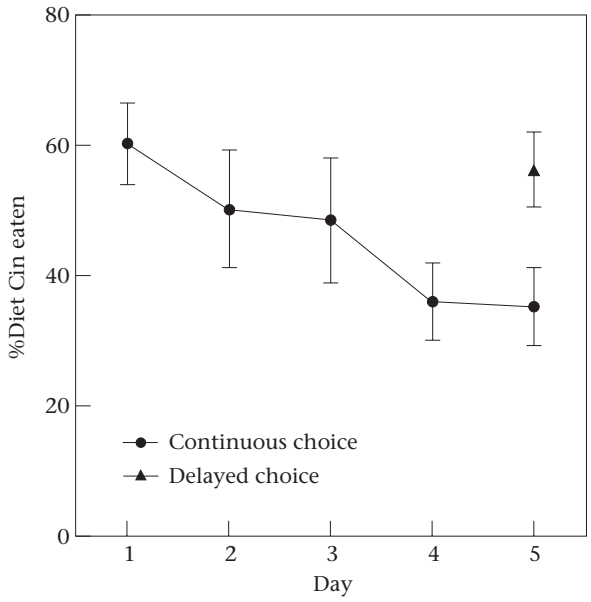

Figure 1. Mean±SE percentage of cinnamon-flavoured diet (diet Cin) eaten by observers assigned to continuous-choice and delayed-choice conditions in experiment 1.

condition we offered the observers two food cups containing diet Pur. On the fifth day of the experiment, each observer assigned to the delayed-choice condition received two weighed food cups, one containing diet Cin and the other diet Coc. Twenty-four hours later, an experimenter weighed the two food cups in each observer's cage and calculated the percentage of its total food intake during the preceding 24 h that was diet Cin.

Results and Discussion

Across the 5 days of the experiment observers assigned to the continuous-choice condition showed a significant decline in the relative amount of diet Cin they ate (repeated measures analysis of variance, ANOVA: $F_{4,11}=4.00$, $P<0.01$; Fig. 1). Furthermore, on day 5 of the experiment, subjects assigned to the delayed-choice condition: (1) ate a significantly greater percentage of diet Cin than subjects assigned to the continuous-choice condition (Student's t test: $t_{22}=2.15$, $P<0.05$; Fig. 1), and (2) ate the same amount of diet Cin as observers assigned to the continuous-choice condition during the first 24 h when they chose between diets Cin and Coc ($t_{22}=0.79$, NS; Fig. 1).

The results of experiment 1 are consistent with the view that the gradual waning of the socially enhanced preference for diet Cin observed in members of the continuous-choice condition resulted from experience over days of the consequences of ingesting diets Cin and Coc, not from a spontaneous waning of the effects of socially acquired information on food preference.

EXPERIMENT 2

It is generally held that to determine the consequences of ingesting each of two or more unfamiliar foods present simultaneously, animals have to eat one food, then wait for some time before eating another. On this view, eating two or more unfamiliar foods in rapid succession would make it impossible for an animal to assess independently the postingestive consequences of eating each food (Zahorik & Houpt 1981; Shettleworth 1984; Beck et al. 1988). Consequently, animals placed on a restricted feeding schedule and forced to eat for only a short time each day should have difficulty sampling among alternative foods in a way that would allow determination of the relative value of the foods.

In the present experiment, we socially enhanced subjects' preference for a cinnamon-flavoured diet in two groups of rats, then offered members of each group cinnamon- and cocoa-flavoured diets. Subjects assigned to the 1-h/day group had access to both diets Cin and Coc for only a single h each day, while subjects assigned to the 24-h/day group had ad libitum access to both diets Cin and Coc.

Methods

Subjects

We used as observers 23 42-day-old, experimentally naïve, female Long-Evans rats from the McMaster colony. At the start of the experiment we assigned 12 of these observers to the 1-h/day condition and the remaining 11 to the 24-h/day condition described in Procedure (see below). Twenty-three additional 60-day-old rats that had served as observers in other experiments served as demonstrators here.

Apparatus and diets

We used the same apparatus and diets that we had used in experiment 1.

Procedure

We treated demonstrators and observers exactly as we had treated demonstrators and observers assigned to the continuous-choice condition of experiment 1 except that after demonstrators and observers interacted, we offered observers assigned to the 1-h/day condition weighed samples of diet Cin and Coc for only 1 h/day for 4 successive days, while we offered observers assigned to the 24-h/day condition ad libitum access to weighed samples of the two diets as we had observers assigned to the continuous-choice condition in experiment 1.

As in experiment 1, the experimenter ascertained that demonstrators had eaten more than 3 g of diet Cin before they interacted with their observers, and once each day, weighed, refilled and reweighed the food cups in each observer's cage before calculating the percentage of each observer's total intake during the preceding 24 h that was diet Cin.

Results and Discussion

Data was lost from one subject when it overturned its food cup.

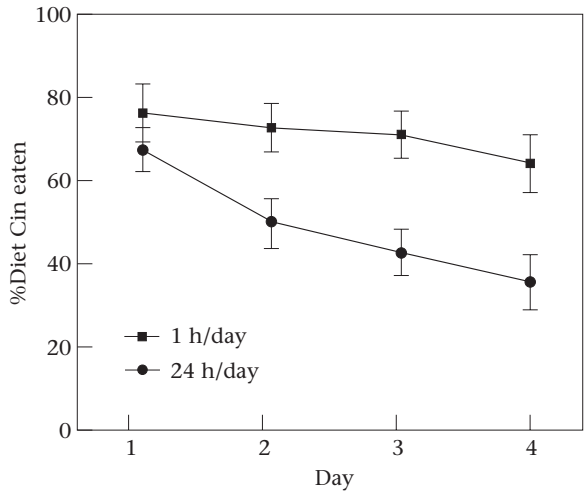

Figure 2. Mean±SE percentage of cinnamon-flavoured diet (diet Cin) eaten by observers assigned to 1-h/day and 24-h/day conditions in experiment 2.

There was a significant effect of group assignment on subjects' intake of diet Cin on day 5 of the experiment (ANOVA: $F_{1,20}$=12.82, P<0.002). This effect was a result of a significant downward linear trend over days in the mean percentage of diet Cin eaten by subjects assigned to the 24-h/day condition ($F_{1,3}$=19.15, P<0.001; Fig. 2), but not by subjects assigned to the 1-h/day condition ($F_{1,3}$=0.79, NS; Fig. 2).

The results of experiment 2 are consistent with the view that, after acquiring a socially induced preference for diet Cin, observers evaluated the relative consequences of ingesting diets Cin and Coc and used the outcome of that evaluation to determine their asymptotic levels of diet Cin intake. The present results are also consistent with the view that feeding schedules affect flavour preferences, a hypothesis we have not tested.

EXPERIMENT 3

Results of both experiments 1 and 2 suggest that rats evaluate the relative postingestive consequences of ingesting diets for which they have a socially induced preference and use information from that evaluation to modify their selection of foods. If so, the magnitude of differences in the consequences of eating a diet for which a preference had been socially enhanced and an alternative diet should affect the duration of the socially enhanced preference for a diet.

In this experiment we socially enhanced a preference for cinnamon-flavoured diet in two groups of rats and then offered subjects assigned to both groups a choice between diets for 4 days. Subjects assigned to the control group chose between the cinnamon-flavoured diet and the cocoa-flavoured diet, while subjects assigned to the sugar-added group chose between the cinnamon-flavoured diet and a cocoa-flavoured diet, the caloric density and palatability of which both had been increased by the addition of sucrose.

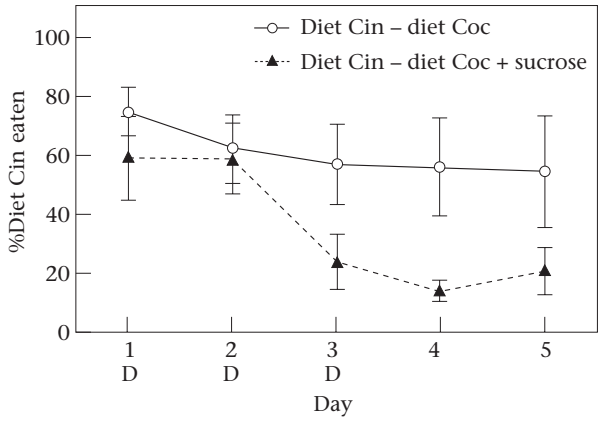

Figure 3. Mean±SE percentage of cinnamon-flavoured diet (diet Cin) eaten by observers assigned to diet Coc and diet Coc+sucrose conditions in experiment 3. D indicates days on which observers interacted with demonstrators fed cinnamon-flavoured diet.

Methods

Subjects

We used as observers 12 42-day-old, experimentally naïve, female Long-Evans rats from the McMaster colony. At the start of the experiment we assigned six of these observers to the sugar-added condition and the remaining six observers to the control condition described in Procedure (see below). Twelve additional 60-day-old rats that had served as observers in other experiments served here as demonstrators.

Apparatus and diets

We used the same apparatus and diets that we had used in experiment 1 as well as diet 'Coc+sucrose' composed by mixing 900 g of diet Coc with 100 g of granulated sugar. In a pilot study, 12 rats offered a choice between diet Cin and diet Coc+sucrose for 24 h ate an average (±1 SE) of 17.4±6.0% diet Cin, while 12 rats offered a choice between diet Cin and diet Coc for 24 h ate an average (±1 SE) of 56.0±7.7% diet Cin. Note that the relative palatabilities of diets Cin and Coc were different in the present experiment than in experiments 1 and 2, which is an unavoidable problem when using natural, rather than artificial, flavorants in experiments.

Procedure

We treated demonstrators and observers much as we had treated demonstrators and observers assigned to the continuous-choice condition in experiment 1 except that: (1) to produce a long-lasting preference for diet Cin (Galef & Whiskin 1998), each observer rat interacted with a demonstrator fed diet Cin for 30 min on each of 3 consecutive days, and (2) each day, after demonstrators and observers interacted, for 4 days, we offered observers assigned to the diet Coc+sucrose condition weighed samples of diet Cin and diet Coc+sucrose, while we offered observers assigned to the control condition access to weighed samples of diets Cin and Coc.

Results and Discussion

Adding sucrose to diet Coc affected the longevity of the socially induced preference for diet Cin (ANOVA: $F_{1,10}$=5.27, P<0.05; Fig. 3). When given a choice between diet Cin and either diet Coc or diet Coc+sucrose, observers that had sugar added to the diet Coc available to them, showed a significant reduction in their intake of diet Cin relative to diet Coc. This result is consistent with that of Laland & Plotkin (1993, experiment 2). Laland & Plotkin (1993) found that, a socially induced preference for cinnamon-flavoured diet was more stable than a socially induced preference for cocoa-flavoured diet, when both preferences were passed along chains of observers. In interpreting their data, Laland & Plotkin (1993) suggested that an interaction of preferences based on the relative, inherent palatabilities of cinnamon and cocoa with socially induced preferences determined the relative stability of the two traditions of food selection in rat populations.

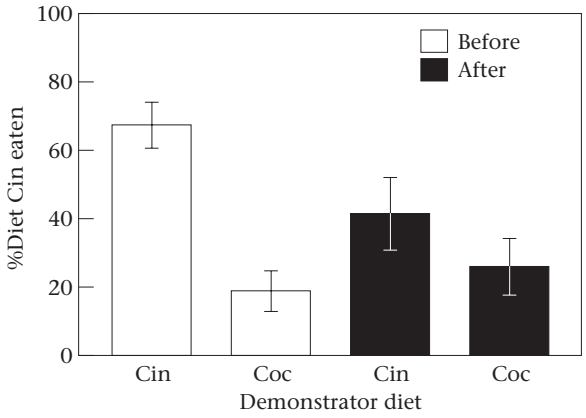

Figure 4. Mean±SE percentage of cinnamon-flavoured diet (diet Cin) eaten by observers in experiment 4 that had individual experience of diet Cin and cocoa-flavoured diet (diet Coc) before or after they were exposed to a demonstrator that had eaten either diet Cin or diet Coc.

EXPERIMENT 4

There are at least two ways in which animals might integrate individually acquired information concerning foods with information concerning the same foods acquired socially. First, animals could maintain in memory information about the relative value of each of the various foods that they had eaten, and could then use that stored information to evaluate any further information concerning one of those foods that they acquired socially. If so, exposure to two foods before social induction of a preference for one of them should affect the amount of social influence on preference for the food experienced in a social context. Alternatively, animals might begin to evaluate a food for which a preference had been socially enhanced only after preference enhancement occurred. If so, exposure to two foods before social enhancement of preference for one of them should not affect the amount of social influence on preference for the food experienced socially.

In the present experiment, we examined social influences on food preferences in two groups of rats offered a choice between cinnamon- and cocoa-flavoured diets. Each observer assigned to the 'before' condition ate both cinnamon- and cocoa-flavoured diets for 4 days before interacting with a demonstrator fed one of them, and then chose between cinnamon- and cocoa-flavoured diet for a fifth day. Each observer assigned to the 'after' condition ate both cinnamon- and cocoa-flavoured diets for 5 consecutive days after interacting with a demonstrator fed either cinnamon- or cocoa-flavoured diet. Thus, each member of both groups of subjects chose between diets Cin and Coc, and each member of both groups interacted with a demonstrator fed either diet Cin or Coc. All that differed between groups was when the interaction with a demonstrator took place.

Methods

Subjects

We used as observers 24 42-day-old, experimentally naïve, female Long-Evans rats from the McMaster colony. At the start of the experiment we randomly assigned 12 of these observers to the 'before' condition and the remaining 12 to the 'after' condition described in Procedure (see below). Twenty-four additional 60-day-old rats that had served as observers in other experiments served here as demonstrators.

Apparatus and diets

We used the same apparatus and diets that we had used in experiments 1 and 2.

Procedure

Each observer assigned to the 'after' condition first interacted with a demonstrator just after the demonstrator had eaten either diet Cin or diet Coc for 30 min. The observers were then offered a choice between diets Cin and Coc for 5 successive days. Observers assigned to the 'before' condition received the same treatment as did observers assigned to the after condition except that observers assigned to the before condition chose between diets Cin and Coc continuously for 4 days before they interacted with their respective demonstrators and then chose between diets Cin and Coc for an additional day after interacting with their respective demonstrators.

Results and Discussion

A two-way ANOVA performed on the percentage of diet Cin eaten by observers on the fifth day of choice between diets Cin and Coc showed a highly significant main effect of diet fed to demonstrators on the food choices of observers during testing ($F_{1,44}$=16.09, P<0.0001; Fig. 4) and no main effect of assignment to before and after conditions on diet choice ($F_{1,44}$=1.29, NS). Most important was the significant interaction between group assignment and diet ($F_{1,44}$=4.42, P<0.04) caused by the greater effect that diets fed to demonstrators had on the food choices of observers assigned to the before condition than on the food choices of observers assigned to the after condition. The implication of these data is that

Norway rats' experience of diets that occurs after social enhancement of a preference for one of them plays a greater role in evaluating those diets than equivalent experience of the same diets that occurs before social enhancement of a preference for one of them takes place.

GENERAL DISCUSSION

The results of the present series of experiments suggest that socially enhanced food preferences and individual experience of the postingestional consequences of eating a food for which preference has been socially enhanced interact in a fairly straight-forward way. Animals' exposure to foods before experiencing social enhancement of preference for them has relatively little effect on subsequent preference enhancement. However, after an animal has experienced social enhancement of preference for a food, it evaluates that food relative to others present in its environment, and over time, an animal's individual experience of the relative values of the foods it consumes comes to determine the mix of foods that it eats.

These findings are consistent with the view of Galef (1995) and Heyes (1993) that social learning acts primarily to introduce patterns of behaviour into an individual's repertoire, while individual experience of the relative consequences of engaging in socially learned behaviour and available alternatives determines the probability of continued expression of socially learned behaviours.

The results indicate that, like individually learned behaviours, socially learned behaviours extinguished in the absence of continued differential reinforcement. One consequence of such extinction would be prevention of the perseverance of socially acquired behaviours in a population when such behaviours no longer lead to greater rewards than available alternative behaviours (Galef 1995, 1996). Such a process would tend to limit longevity in a population of socially learned behaviours transmitted by those that had acquired behaviours in environments different from that experienced by receivers.

The data also suggest that, although it may be convenient to talk in terms of 'socially' and 'individually' acquired behaviours, the dichotomy is not quite so real as the terms imply. As Heyes (1993) has made clear, with the exception of learning by imitation, social learning is not a way of learning directly about actions or behaviours. Rather social learning is learning about stimuli, objects or events in the environment. Thus, given the rarity of learning by imitation in animals, in the vast majority of cases, social learning is most accurately described as social biasing of individual learning. It follows that the frequency of occurrence of socially learned behaviours and their longevity in the behavioural repertoires of individuals, will be strongly influenced by environmental contingencies as are the frequency of occurrence and longevity in the behavioural repertoires of individually learned behaviours (Galef 1995).

In the short term which behaviours an individual is more likely to learn and therefore to express as part of its behavioural repertoire can and will be influenced by social interactions. However, in the final analysis all learning, including 'social learning', is learning by an individual and, therefore, social learning, like asocial learning, will be sensitive to experience of environmental consequences.

Acknowledgments

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