Effects of social and asocial learning on longevity of food-preference traditions

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Abstract. The influence of both social and asocial factors on the stability of a socially learned tradition of food preference was explored in colonies of domesticated Norway rats, *Rattus norvegicus*. We trained members of 'founding colonies' of rats to avoid eating a distinctively flavoured food and then introduced them into enclosures where they were offered a choice between the food they had learned to avoid and a familiar, safe food. We then monitored the food preferences of these colonies while we gradually replaced founding members with naive subjects. Traditions of food preference were more stable across generations of replacements: (1) in colonies that had food available 2 h/day than in colonies that had food available 24 h/day (experiment 1), (2) when replacement subjects each resided in their respective colonies for 2 days rather than for 4 days before themselves being replaced (experiments 2 and 3) and (3) when founding members of colonies had learned to avoid a relatively palatable diet (experiment 4). The results of the first four experiments were consistent with the view that opportunities to learn asocially to eat a food other than that preferred by one's fellows reduced the stability of a food preference as it was transmitted across generations. We also found that introducing a naive individual into a tradition-bearing colony reduced its rate of acquiring a food preference other than that of the colony it joined (experiment 5). The interactive effects of social and asocial learning on the stability of food preference traditions in Norway rats was discussed.

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In elaborating his intriguing and widely cited analogy between cultural and biological evolution, Dawkins (1976) compared effects of three characteristics of 'memes' (the cultural analogues of genes), their longevity, fecundity and copying fidelity, on the probability of survival of memes in a population. Dawkins suggested that 'The longevity of any one copy of a meme is probably relatively unimportant . . . fecundity is much more important than longevity' (page 208).

In reaching the conclusion that fecundity is more important than longevity in promoting success of alternative memes, Dawkins considered examples involving the spread of traditions through human populations where transmission of memes depends largely on language. Because non-human animals lack the ability to communicate linguistically, they can acquire memes only by observing the behaviour of others. And because

social learning in animals depends on observation of overt behaviour, the duration of expression of a socially acquired behaviour (its longevity in an individual's behavioural repertoire) will have a profound effect on its probability of being transmitted to others (its fecundity).

In both animals and humans, direct experience of the costs and benefits of engaging in a behaviour (what Heyes 1994 labelled 'asocial learning') alters the probability that a behaviour will be repeated. Consequently, asocial learning about behavioural alternatives should directly affect the longevity of a behaviour in an individual's repertoire and, thus, the probability of its spread and maintenance in a population of animals.

In a recent paper, Galef & Allen (1995, experiment 3) described a laboratory situation that they suggested might be used to investigate factors influencing the stability of traditions of food preference in colonies of Norway rats, *Rattus norvegicus*. Galef & Allen trained individual rats to avoid eating one of two distinctively flavoured

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foods. They then placed groups of four rats trained to avoid the same food in enclosures where both foods were available for 2 h/day. Galef & Allen then monitored the food choices of such colonies as they replaced the members of each colony, one per day, with naive rats that were, in turn, replaced with additional naive rats. They found that the food choices of members of the fourth generation of subjects introduced into colonies had food preferences concordant with those taught to the founding members of their respective colonies.

We initiated the present series of experiments to extend the work of Galef & Allen (1995) by examining effects of several ecologically meaningful variables (e.g. colony size, rate of immigration into colonies and temporal patterns of foraging on the stability across generations of a tradition of food preference in colonies of Norway rats. The effects of our manipulations on rates of asocial learning were much greater than were the effects of our manipulations of transmission processes per se. Consequently, our results provided information primarily concerning effects of asocial learning on the stability of a traditional behaviour.

GENERAL METHODS

Subjects

We used as subjects experimentally naive, 42- to 50-day-old (adolescent), female, Long-Evans rats born in the vivarium of the McMaster University Psychology Department (Hamilton, Ontario, Canada) to breeding stock acquired from Charles River Canada (St. Constant, Quebec). We used only young, female rats because such rats are less likely than are either sexually mature rats or male rats to behave aggressively when they first encounter unfamiliar conspecifics.

We housed all subjects, from weaning to initiation of testing, in same-sex groups of three or four in shoe-box cages, measuring $35 \times 30 \times 15$ cm, that we maintained in a temperature- and humidity-controlled colony room illuminated on a 12:12h light:dark cycle. Until the start of experiments, all subjects had ad libitum access to water and pelleted Purina Rodent Laboratory Chow #5001 (Ralston-Purina, Woodstock, Ontario).
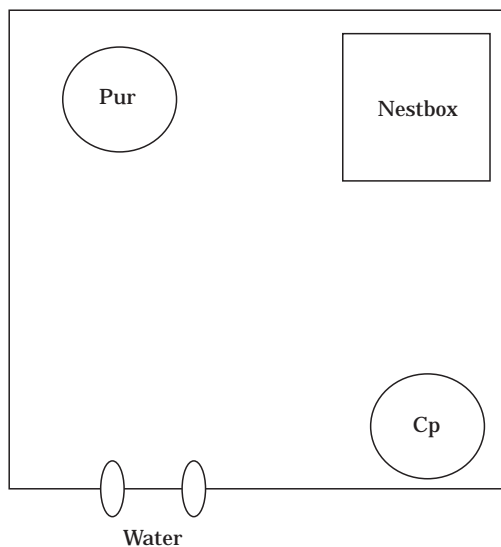
Figure 1. Overhead schematic of enclosures used in experiments.

Diets

We composed a diet (diet Cp) that was unfamiliar to our subjects by adding 3 g of cayenne pepper (McCormick Canada, London, Ontario) to 1 kg of a nutritionally adequate base diet (Normal Protein Test Diet (Rat), Catalogue No. 170590; Teklad, Madison, Wisconsin). The main constituents of diet Cp are casein (26.0%), corn starch (59.8%) and vegetable oil (8.0%); diet Cp is roughly equipalatable with the powdered form of Purina Rodent Laboratory Chow #5001, the subjects' maintenance diet (Galef & Allen 1995).

Apparatus

During experiments, we housed each colony in an enclosure, measuring $1 \times 1 \times 0.3$ m, that we constructed of angle iron and hardware cloth. The galvanized, sheet-metal floor of each enclosure was covered with a thin layer of wood shavings and each enclosure contained a single nesting box, two water bottles and two food cups (Fig. 1).

Procedure

We intended our procedure to mimic a natural situation in which naive rats are gradually recruited, through either birth or immigration, into a numerically stable colony whose members

have all learned from individual experience to avoid eating a toxic potential food to be found in the vicinity of their home burrow.

Training founding colony members

To train subjects that we assigned to act as members of 'founding colonies' to avoid eating diet Cp, we introduced them into individual cages and deprived them of food for 23 h/day for 2 consecutive days. During the remaining 1 h of each day, we offered each of these subjects a food cup containing a powdered form of their normal maintenance diet, Purina Rodent Laboratory Chow #5001 (diet Pur).

To produce a learned aversion to diet Cp, following a third 23-h period of food deprivation, we provided each subject, for 1 h, with access to a food cup containing diet Cp. At the end of this 1-h feeding period, we removed the food cup from each subject's cage and injected her intraperitoneally with 2% of body weight, 1% wt/vol lithium chloride solution. One per cent lithium chloride solution is roughly isotonic with plasma.

We then waited 1 h to permit the effects of the lithium chloride to abate fully before we gave each subject an 8–9 g pellet of diet Pur. We then left her undisturbed for 23 h.

Twenty-four hours following injection, we again offered each subject, for 1 h, a weighed cup of diet Cp and then injected any subject that ate more than 0.2 g of diet Cp during the 1-h feeding period (1–3 subjects/experiment) a second time with 2% of body weight 1% wt/vol lithium chloride solution. We then waited 1 h, marked the tails of all subjects with indelible ink to identify them as founding colony members and provided each with an 8–9 g pellet of diet Pur.

Experimental procedure

Twenty-four hours after founder rats' second exposure to diet Cp, we placed them in groups (that varied in number) in floor enclosures each containing two weighed food bowls, one of diet Cp and the other of diet Pur.

At the end of this feeding period (the duration of which varied between experiments) we: (1) removed both food bowls from each enclosure and weighed them, (2) randomly selected a member of the founding colony in each enclosure and removed her from both the colony enclosure and

the experiment and (3) introduced a randomly selected, individually marked, experimentally naive, replacement subject into each colony enclosure. We repeated this procedure at regular intervals (that varied between experiments), first replacing the members of each founding colony with naive subjects, and, after we had replaced all founding colony members, replacing the replacement subject in each colony enclosure that had been there longest.

EXPERIMENT 1: EFFECTS OF DURATION OF FOOD AVAILABILITY ON MAINTENANCE OF A TRADITION OF FOOD PREFERENCE

The first experiment in the present series was undertaken to examine the effects of variation in circadian patterns of foraging that have been observed in wild Norway rats (Chitty 1954; Berdoy 1994), on the stability of a tradition of food preference in our laboratory colonies.

Galef & Allen (1995) provided evidence consistent with the view that the number of hours per day that foods are available to the members of a rat colony markedly affects the stability of a tradition of food preference in that colony. Because Galef & Allen's evidence of effects of duration of food availability on the stability of colonies' traditions of food preference involved a comparison across experiments, we began the present series of studies by directly comparing the stability of traditions of food preference in rat colonies that had food available for either 2 or 24 h/day.

Methods

Subjects

We used 144, 42-day-old rats as subjects. We trained 48 subjects, four of which we assigned to each of 12 founding colonies, to avoid eating diet Cp. Seventy-two of the remaining subjects served as replacements for members of founding colonies, and the final 24 served as subjects in a control condition.

Procedure

For 7 consecutive days, we offered members of six colonies a choice between diet Cp and diet Pur for 2 h/day (2-h group). We offered the remaining
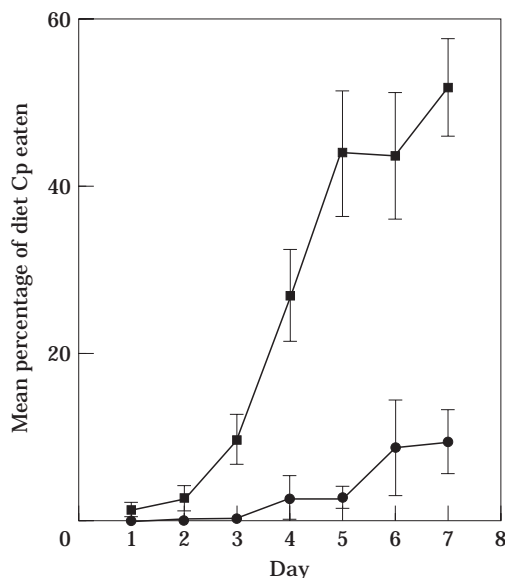
Figure 2. Mean ± SE percentage of diet Cp eaten by colonies assigned to 2-h (●) and 24-h (■) conditions.

six colonies the same choice of foods ad libitum (24-h group). We introduced one of the 72 replacement subjects into each enclosure every 24 h.

The 24 subjects assigned to the control condition were trained as were members of founding colonies, then placed in six groups of four in six enclosures and offered a choice between diet Cp and diet Pur for 24 h/day for 7 days. We did not replace any members of founding colonies that we had assigned to the control condition.

Results and Discussion

The members of each founding colony in the experimental condition showed a strong aversion to diet Cp, the diet that they had eaten immediately before we injected them with lithium-chloride solution (Fig. 2, day 1), and colonies assigned to the control condition ate an average of 0.3–3.1% diet Cp on each of the 7 days of the experiment.

As we had expected on the basis of the results of Galef & Allen (1995), during the 7 days of the experiment, subjects in experimental colonies that had access to food for 24 h/day ate significantly more diet Cp than did subjects in experimental colonies that had access to food for only 2 h/day (Fig 2, days 2–7; Mann–Whitney U-test: $U=0$, $P<0.001$).

There are at least two explanations for the greater stability of the socially transmitted preference for diet Cp observed in rat colonies assigned to the 2-h group than in colonies assigned to the 24-h group. First, subjects in the 2-h group had to feed more or less simultaneously, if they were to feed at all, but members of colonies assigned to the 24-h group did not need to feed with other colony members. Consequently, opportunities for social learning of a preference for diet Cp may have been greater in colonies that had food available for 2 h/day than in colonies that had food available for 24 h/day. Second, as Galef & Allen (1995) proposed, members of colonies with ad libitum access to food had more time than did members of colonies that fed for only 2 h/day to sample diet Cp and evaluate the consequences of its ingestion. If, as seems likely, the probability that subjects would learn about the benefits (and lack of cost) of eating diet Cp increased with increasing opportunity to sample diet Cp, then one would expect subjects in colonies assigned to the 24-h condition to learn that diet Cp was safe and to abandon their preference for diet Pur more rapidly than subjects in colonies assigned to the 2-h/day condition. On this hypothesis, reduced longevity of the socially induced preference for Diet Cp in replacement subjects, not reduced copying fidelity, would be a major cause of the relatively brief life span of the traditional preference for diet Pur in colonies with ad libitum access to diets Cp and Pur.

Of course, once replacement subjects began to eat diet Cp, they could induce founding members of their colony to eat diet Cp, the diet that founding members had learned asocially to avoid eating (Galef 1986). Any founding colony members that ate diet Cp would, of course, learn that it was nutritious rather than toxic, and the breakdown of the tradition of preference for diet Cp would be expected to spread rapidly through a colony. As data from control colonies indicated, the aversion learned to diet Cp by members of founding colonies was sufficiently robust to keep them from eating that diet during the experiment, unless their aversion to diet Cp was affected by interactions with replacement subjects that ate diet Cp.

EXPERIMENT 2: EFFECTS OF COLONY SIZE ON MAINTENANCE OF A TRADITION OF FOOD PREFERENCE

It seems reasonable to expect that, as the number of individuals in a population that bear a behavioural tradition increases, the probability that a new recruit to that population will acquire that tradition would also increase.

In the present experiment, we examined the effect of the size of a founding colony on the stability of a tradition of food preference in that colony.

Methods

Subjects

We used 160 rats as subjects. Twenty of these subjects were members of 10 founding colonies of two subjects each, and 32 subjects were members of eight founding colonies of four subjects each. We used the remaining 108 subjects as replacements that we introduced one per day for 6 days into each of the 18 founding colonies.

Apparatus and procedure

We used both the apparatus described in General Methods and the procedures described there to train members of all 18 founding colonies to avoid eating diet Cp. We then used the procedures described in General Methods to examine the stability of the tradition of eating diet Cp in colonies that consisted of either two or four members that we offered a choice between diets Cp and Pur for 2 h/day.

We replaced one member of each colony on each of days 2–6, so colonies of two subjects went through three complete generations of replacement subjects during the 7 days of the experiment, and colonies of four subjects were in the midst of their second generation of replacement subjects when the experiment ended.

Results and Discussion

As in experiment 1, we successfully induced avoidance of diet Cp in all members of founding colonies; on day 1 of the experiment, no member of any founding colony ate any diet Cp (Fig. 3, day 1).
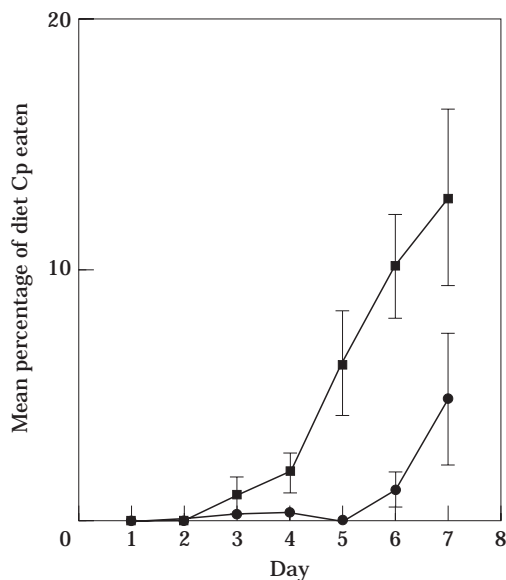
Figure 3. Mean ± SE percentage of diet Cp eaten by colonies with two (●) and four (■) members.

Unexpectedly, during the 7 days of the experiment, members of colonies of four subjects ate significantly more diet Cp than did members of colonies of two subjects ($U=6$, $P<0.002$), despite the fact that, in colonies of two subjects, the tradition of eating diet Cp had passed through three complete generations, while in colonies of four subjects the tradition of eating diet Cp had passed through only one complete generation.

Because effects of failures in copying fidelity should increase with the number of times a traditional behaviour is transmitted between individuals, and the number of such transmission episodes should be highly correlated with the number of generations through which a traditional behaviour is transmitted, it is unlikely that the instability of the tradition of choosing diet Pur in colonies of four subjects (relative to colonies of two subjects) reflected failures in copying fidelity.

The colonies of two and four subjects that we used in experiment 2 differed not only in the number of subjects in each colony, but also in the number of days that each replacement subject spent in a colony enclosure before it was replaced. We removed each replacement subject that we introduced into a colony of two subjects after only 2 days, while each replacement subject introduced

into a colony of four subjects spent 4 days as a colony member before we removed her. The additional time available for replacement subjects introduced into colonies of four subjects to sample diets Pur and Cp provides a plausible explanation of the reduced stability of preference for diet Cp in such colonies.

The uninteresting possibility is that greater competition at the food bowl containing diet Pur among members of colonies of four subjects than among members of colonies of two subjects was responsible for the relative instability of the traditional preference in colonies of four subjects. This possibility is fairly well excluded by the results of both experiment 1 and experiment 3. In experiment 1, subjects assigned to the 2-h group were forced to feed more or less simultaneously, yet showed a more stable tradition of food preference than did subjects assigned to the 24-h group that were able to avoid feeding simultaneously. In experiment 3 (below), all subjects ate for only 2 h/day, yet those in one group had a very stable preference for diet Cp.

EXPERIMENT 3: EFFECTS OF RATE OF REPLACEMENT OF COLONY MEMBERS ON STABILITY OF A TRADITION OF FOOD PREFERENCE

In the present experiment, we examined the influence of rate of replacement of subjects in a colony on maintenance of a tradition of preference for diet Cp in that colony.

Methods

Subjects

We used 104 rats as subjects; 32 served as members of 16 founder colonies (each of two subjects), and the remaining 72 subjects served as replacement subjects that we introduced into colony enclosures.

Procedure

The procedure was identical to that used with founding colonies of two subjects in experiment 2 except that, in experiment 3, we varied the rate at which we introduced replacement subjects into colonies. As in experiment 2, we replaced one of
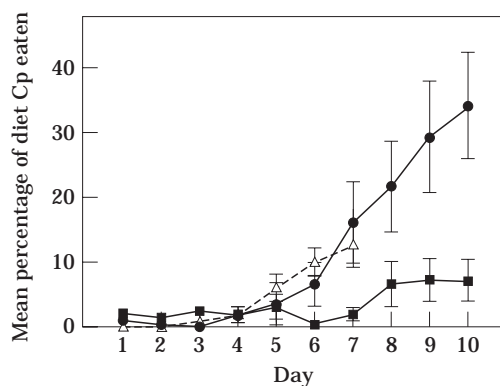
Figure 4. Mean ± SE percentage of diet Cp eaten by colonies assigned to every-day (■) and every-other-day replacement groups (●). Data from the four-member group of experiment 2 (△) are included for comparison.

the two colony founders in each colony after determining the food choices of colony founders on day 1. In the present experiment, however, on day 2 and thereafter, we introduced replacement subjects into each of eight enclosures every day (every-day replacement group) and into each of the remaining eight enclosures every other day (every-other-day replacement group). Consequently, each replacement subject in the every-day replacement group spent 2 days as a member of the colony into which we introduced her (as had replacement subjects introduced into colonies of two subjects in experiment 2), and each replacement subject in the every-other-day replacement group spent 4 days as a member of the colony into which we introduced her (as had replacement subjects introduced into colonies of four subjects in experiment 2).

Results and Discussion

The number of days that replacement subjects spent in a colony had a profound effect on the stability of a tradition of food preference in that colony. Subjects in colonies assigned to the every-other-day replacement group ingested significantly more diet Cp than did subjects assigned to colonies in the every-day replacement group ($U=10$, $P<0.01$; Fig. 4) despite the fact that during the 10 days of experiment 3, we introduced twice as many generations of replacement subjects into the colonies receiving replacement subjects daily as into the colonies receiving replacement

subjects every other day. Furthermore, subjects in both groups were equally likely to eat at the same time as their fellow group members. Consequently, the results of the present experiment, unlike those of experiment 1, cannot be explained as resulting from either differences in the opportunities for copying or greater competition at the food bowl containing diet Pur in one group than in another.

The behaviour of subjects in experiment 3 assigned to colonies of two subjects that received replacement subjects every other day was almost identical to that of subjects in experiment 2 that we maintained in enclosures containing colonies of four subjects, one of whose members was replaced every day (Fig. 4, dashed line). Thus, when the time that colony members had access to food was held constant and colony size was varied, the stability of a tradition of food preference reflected duration of access to food, not colony size.

Also, once again, the time that subjects had to sample available diets affected maintenance of a traditional pattern of food preference more than did the number of generations through which the preference was transmitted. In general, the longevity of a behaviour in individuals appears to have been more important than copying fidelity in maintaining a traditional pattern of food preference.

EXPERIMENT 4: EVIDENCE OF EFFECTS OF REWARD ON THE STABILITY OF A TRADITION OF FOOD PREFERENCE

The results of experiments 1 to 3 are consistent with the view that the opportunity to experience rewards following expression of a pattern of behaviour other than that traditional in a group influences the probability that a new recruit to the group will continue to show the traditional behaviour. None of the first three experiments, however, provided direct evidence of effects of rewards following alternative behaviours on the longevity of a socially learned behaviour.

In the present experiment, we examined the effect of increasing the magnitude of reward consequent upon eating a food different from that eaten by the founding members of colonies on the stability of a traditional food preference.
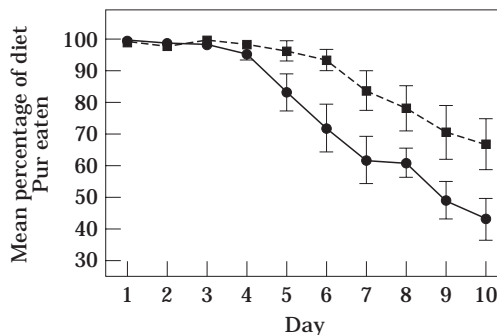
Figure 5. Mean $\pm$ SE percentage of diet Pur eaten by subjects choosing between diet NPT and Pur in Experiment 4 (●). Data from the every-day replacement group of experiment 3 are included for comparison (■).

Methods

Subjects

We used as subjects 80 42–50-day-old rats. Sixteen of these subjects served as the founding members of eight colonies, 48 as replacement subjects and the remaining 16 as members of a control group.

Procedure

We used the same procedure in the present experiment that we had used with the every-other-day group in experiment 3, except that we trained founding colony members to avoid eating unadulterated Normal Protein Test Diet (diet NPT) rather than diet NPT flavoured with cayenne pepper (diet Cp), and (2) we offered each colony a choice between diet Pur and diet NPT (rather than between diet Pur and Diet Cp) for 2 h/day. We treated subjects that we assigned to the control condition exactly as we treated members of founding colonies assigned to the experimental condition, except that we did not replace any subjects in founding colonies assigned to the control condition.

Diet NPT, the base diet for diet Cp, is preferred by naive rats roughly 4 to 1 over diet Pur (Galef 1986); diet Pur and diet Cp are roughly equipalatable (Galef & Allen 1995).

Results and Discussion

As we expected, founding colony members trained to avoid eating diet NPT had a profound aversion to that diet (Fig. 5, day 1), and subjects assigned to the control condition ate more than

92.0% diet Pur on each of the 10 days that they participated in the experiment.

By day 5 of the experiment, replacement subjects in the present experiment ate significantly less diet Pur than had subjects assigned to the every-other-day group in experiment 3, whose data are included in Fig. 5 for comparison (U=11, P=0.02). On each day after day 5, colonies choosing between diet NPT and diet Pur ate less diet Pur than did colonies choosing between diet Pur and diet Cp (Fig. 5, days 6–10; all Us<10, all Ps<0.02).

When we increased the rewards provided by the alternative to a socially transmitted pattern of food choice by increasing the palatability of the alternative food available, the stability of the socially transmitted pattern of food choice decreased even though colony size, rate of replacement of colony members and colony feeding schedule were all held constant. This result, like that of Laland & Plotkin (1993, experiment 2), who found that socially transmitted behaviours are more stable when they reinforce an asocial preference than when they conflict with it, suggests that asocial consequences of engaging in traditional behaviours and their alternatives can profoundly affect the stability of a traditional pattern of behaviour.

EXPERIMENT 5: SOCIAL EFFECTS ON INDIVIDUAL PATTERNS OF FOOD CHOICE

The results of experiments 1–4 indicate that opportunities for asocial learning affect the stability of a tradition of food preference in new recruits to a population and consequently affect the probability of transmission of a socially learned food preference to succeeding generations. On such a view, behavioural traditions are vulnerable to individual acquisition of information that promotes behaviours that deviate from group norms (Galef 1995).

To provide a more balanced picture of the role of asocial and social learning in affecting the duration of a traditional pattern of behaviour in a population, it is perhaps worth considering the converse relationship, the constraints imposed on asocial learning by membership in a group sharing a tradition of behaviour.

In experiment 5, we examined the development of individual rats' food preferences when offered a choice between diet Cp and diet Pur. Comparison of the food choices of rats tested alone with those of rats tested with a companion trained to avoid ingesting diet Cp provides evidence of the effect of social interaction on individual behaviour in the same situation in which we conducted experiments 1–4.

Methods

Subjects

We used 60 42-day-old rats as subjects; 32 of these subjects served as founders of 16 colonies (each of two members), 16 served as subjects to replace one member of each founder colony, and the remaining 12 subjects chose between diets Cp and Pur in the absence of any social influence on their behaviour.

Procedure

We placed each subject on a food-deprivation schedule and fed her diet Pur for 2 h/day for 4 days. Once we had accustomed subjects to feeding on schedule, we introduced them into the enclosures described in General Methods. We placed 12 subjects alone in these enclosures and offered them a choice, for 2 h/day for 3 days, between diet Pur and diet Cp; we placed 16 pairs of subjects trained to avoid eating diet Cp in enclosures and, 24 h later, replaced one of each pair of founder rats with a naive subject.

We allowed pairs of rats, like those rats tested alone, to choose between diets Cp and Pur for 2 h/day for 3 days before we ended the experiment.

Results and Discussion

The comparisons that we wished to make were between the food choices of subjects alone in their cages and those of naive subjects that were members of pairs. Because each pair of subjects contained one founding subject that had been trained to avoid diet Cp, we could not assume that both subjects in each pair ate the same amount of diet Cp. For statistical analysis, we assumed that: (1) all diet Cp eaten during the experiment was eaten by the replacement subject in each pair, and (2) both members of each pair ate equal amounts of food during the 3-day test period (this second
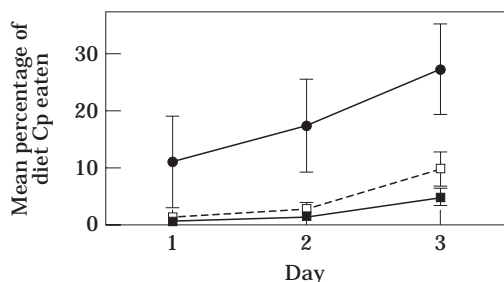
Figure 6. Mean ± SE percentage of diet Cp eaten by subjects feeding either alone (●) or in pairs (■) in experiment 5. Estimate of mean percentage of diet Cp eaten by naive subjects tested in pairs used in statistical comparisons (□).

assumption was consistent with the observation that, during the critical 3 days of the experiment, pairs of subjects ate an average ± SE of $56.0 ± 0.6$ g, exactly twice the $28.0 ± 0.7$ g that single subjects ate). Consequently, on each day, we estimated the percentage of diet Cp eaten by each naive subject that was a member of a pair by dividing the amount of diet Cp eaten in an enclosure by half the total amount eaten in that enclosure.

Even making our conservative assumptions concerning the amount of diet Cp eaten by naive subjects tested as members of pairs, we found a significant difference in the mean percentage of diet Cp eaten by subjects tested in pairs and in isolation ($U=46$, $P<0.05$; Fig. 6). Clearly, the food choices of recruits to a population can be affected by the food choices of the members of a colony that they join (for reviews, see Galef 1988, 1996).

GENERAL DISCUSSION

Galef (1995) recently proposed that the most important role of social interactions in behavioural transmission is to introduce traditional patterns of behaviour into the repertoires of newcomers to a population. In Galef's model, the probability that a socially acquired pattern of behaviour would continue to be expressed depended on the relative amounts of reward resulting from engaging in socially learned behaviours and their alternatives. (We recently discovered that Lloyd-Morgan (1896) had anticipated both of these proposals.)

The results of the present series of experiments are largely consistent with that view. In experiments 1–4, manipulations that increased the opportunity for asocial learning about behavioural alternatives decreased the stability of traditions.

As is evident in the results of experiment 5, however, social interaction can do more than simply introduce a behaviour into a naive individual's repertoire. Social interaction can also reduce the probability that a recruit to a population will engage in behaviours other than those that are traditional in the population it joins. Such conservative effects of social learning reduce the probability that new members of a population will engage in behaviour leading to rewards that might result in their abandoning a behaviour that was traditional in the population that they joined. Thus, social learning can play two distinct roles in modifying acquisition of behaviour by recruits to a population, both introducing behavioural novelty into an individual's repertoire and delaying onset of the trial-and-error learning that can lead individuals to acquire patterns of behaviour different from those shown by others of its social group.

Because in all of the experiments described here, asocial learning about the consequences of eating various foods profoundly affected the stability of traditional food preferences, the present paradigm was not as useful as we had hoped it might be for examining factors that directly affect the fidelity of copying processes. Situations in which a traditional behaviour provides the only means of obtaining reward (for example, the social transmission of digging for carrot pieces studied by Laland & Plotkin (1990, 1992)) may provide superior opportunities for examining factors affecting copying fidelity. Such situations may also provide better laboratory analogues of the unusually stable behavioural traditions observed in some free-living populations (e.g. Aisner & Terkel 1992; Zohar & Terkel 1992) than does the tradition of food preference that we examined here. Similarly, traditional behaviours that may have no extrinsic consequences (for example, singing by passerine birds of one set of syllables rather than another: Lynch & Baker 1986; Baker & Jenkins 1987) may be better suited to study of the fidelity of transmission processes than are traditions of food preference that support behaviours with extrinsic costs and benefits.

ACKNOWLEDGMENTS

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