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A new model system for studying behavioural traditions in animals

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Abstract. Laboratory paradigms currently available for study of behavioural traditions in animal populations do not provide sufficient information to permit extrapolation from laboratory findings to more natural situations. By focusing solely on the transmission process, such paradigms fail to provide an opportunity to explore fully the complex determinants of the longevity of behavioural traditions and the probability of diffusion of socially transmitted behaviour patterns through populations. The reliability of a new model system is established that will permit exploration of the effects of (1) individual learning about the environment and (2) social relationships between bearers of tradition and recruits to a population, on maintenance and propagation of traditions of food preference in colonies of Norway rats. 'Founder' colonies of four rats were taught an arbitrary food preference. Individual members of the founder colonies were then slowly replaced with naive subjects. Three generations of replacements after the last founder had been removed from a colony, the arbitrary food preference taught to a colony's founders was still evident. The behavioural mechanism supporting the observed traditional behaviour in rats was identified, as was a possibly important, previously unidentified parameter (the duration of opportunities to learn by sampling alternatives) influencing the stability of behavioural traditions in animals.

In recent papers, Laland (1992) and Laland et al. (1993) have called attention to the fact that although numerous experiments have examined mechanisms of social learning in animals (Zentall & Galef 1988), relatively few experiments have explored parameters that might either influence the longevity of behavioural traditions in groups of animals or determine the rate of spread of such traditions through animal populations.

Although Laland and his co-authors did not speculate as to why mechanisms of social learning have been studied more frequently than have factors affecting the propagation and stability of traditional types of behaviour, surely a major impediment to laboratory study of animal traditions has been the lack of satisfactory model systems in which to carry out such investigations. Without an adequate model system, those interested in the longevity of traditional behaviour patterns in animal populations have had little choice but to study processes that support the transmission of behaviour from one animal to a second and to assume that such information can be extrapolated to predict the fate of behavioural traditions in larger populations. It is, however, an open question whether such extrapolation is valid. Laland et al. (1993) clearly feel that it is not: 'although [experimental studies of animal social learning] have all the advantages of laboratory control and manipulation, they say little about the diffusion of socially learned behaviour through populations or the maintenance of cultural differences between groups' (page 254).

The sole paradigm presently available for laboratory study of traditions in animals (Curio et al. 1978; Laland & Plotkin 1990, 1992) involves teaching a naive subject (a model) some behaviour, then allowing that model to interact briefly with a second naive subject (an observer). As a consequence of interacting with the model, the observer learns the relevant behaviour and can then be used as a model for yet another observer. Such chaining of models and observers is repeated several times.

Although the paradigm used by Laland & Plotkin and by Curio et al. captures some features of the diffusion of a socially learned behaviour through a free-living population of animals, it

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involves a simple iteration of the basic social learning paradigm (in which a naive observer learns a behaviour as a consequence of observing the actions of a trained model). Outside the laboratory, transmission of behaviour from one individual to another does not occur in either a social or ecological vacuum. Propagation of behaviour through populations takes place within complex environmental and social situations, providing animals with opportunities not only for social learning, but also for individual learning about the environment and for social interaction between individuals at times other than those when they are engaged in social transmission of behaviour.

Both the longevity of a behavioural tradition in a population and the probability that a behaviour will spread through a population will depend not only on the fidelity of the transmission process per se (which has been examined in many experimental situations), but also on the social and environmental contexts within which behavioural transmission occurs. Individual learning about the environment in the interval between social acquisition of a behaviour and the opportunity to transmit that behaviour to a naive individual will affect the probability that propagation of the behaviour will occur. The composition of a tradition-bearing population (e.g. its size, the homogeneity of the behaviour of its members, the status of its members relative to that of recruits, the rate of recruitment of members into it) will affect the probability that new recruits will acquire a behaviour that is traditional in the population they join. Consequently, the transmission of behavioural traditions must be studied in situations that permit manipulation of the social and environmental contexts in which social learning occurs.

The absence of such contexts in the paradigms currently used to study animal traditions led us to the present attempt to develop an alternative model that would permit systematic manipulation of social and environmental contexts in investigations of the fidelity, longevity and fecundity (Dawkins 1976) of behavioural traditions in animals. Here, we first demonstrated that we can sustain a tradition of food preference across several generations of subjects in a situation where ecological and social variables can be systematically manipulated. We then analysed the process of social transmission that supports such traditional types of behaviour.

The methods described below were adapted from procedures developed by Jacobs & Campbell (1961) for laboratory study of the stability of arbitrary traditions in human social groups (see also Gerard et al. 1956). Jacobs & Campbell used an optical illusion, the autokinetic movement effect (Adams 1912), to study transmission of an arbitrary behaviour in human subjects in a 'laboratory microculture'. To experience illusory autokinetic movement, a subject views a stationary pinpoint of light in an otherwise totally darkened room. Even subjects who know that the light is stationary report that they perceive it making random excursions of 7–10 cm.

To begin their experiments, Jacobs & Campbell seated, in a row of chairs, four 'confederates' who had been instructed to report seeing the stationary light in demonstrations of the autokinetic movement phenomenon move much further than would an honest observer. A 'real' subject was seated in a fifth chair situated to the immediate left of the row of chairs the confederates occupied. All five participants in the experiment then viewed a stationary light in a darkened room and reported, from right to left along the row of chairs, the distance they had seen the light move. After all five reports had been recorded, the participant in the chair at the right end of the line was excused from the experiment, the remaining four participants each shifted one chair to the right, and a new real subject took the now-vacant chair on the left end of the line. This procedure was repeated many times, and after all four confederates had left the room, succeeding generations of real subjects carried on the tradition of reporting abnormally large excursions of the point of light.

GENERAL METHODS

Subjects

All rats used in this study were experimentally naive, juvenile, female, Long-Evans rats born in the vivarium of the McMaster University Psychology Department (Hamilton, Ontario) to breeding stock acquired from Charles River Canada (St Constant, Quebec).

We used only young female rats as subjects because such rats are less likely than either male rats or sexually mature rats to behave aggressively

when placed together with an unfamiliar conspecific. We expect that the results of experiments on behavioural tradition will be found to vary as a function of the sex, relative ages and relative dominance status of subjects.

Diets

We composed two diets (diet Jh and diet Cp, respectively) by adding either 25 g of Japanese horseradish (Mitoku, Tokyo) or 3 g of cayenne pepper (McCormick Canada, London, Ontario) to 1 kg of a nutritionally adequate base diet, the major ingredients of which were casein and corn starch (normal protein test diet (rat), catalogue no. 170590; Teklad, Madison, Wisconsin). In choice tests, we had found diets Cp and Jh roughly equipalatable and also of approximately the same palatability as Purina rodent laboratory chow no. 5001 (diet Pur), the diet on which all subjects had been reared and maintained before they were used in the experiment. Six young, female, Long-Evans rats from our colony, each offered a choice between diets Cp and Jh for 24 h, ate ($\bar{X} \pm$ SE) 53·1 ± 7·6% diet Cp. An equal number of similar subjects that were offered a choice between diet Pur and diet Cp ate 47·5 ± 9·2% diet Cp, while six similar rats choosing between diet Jh and chow ate 57·6 ± 8·1% diet Jh.

Apparatus

Except as noted otherwise, for the following experiments, founding colony members were trained to eat either diet Jh or diet Cp while maintained in individual, wire-mesh hanging cages measuring 18 × 34 × 19 cm. For the experiment proper, we placed each founding colony of four subjects in an enclosure measuring 1 × 1 × 0·33 m, which we constructed of angle iron and hardware cloth (Fig. 1). The galvanized, sheet-metal floor of each enclosure was covered with a thin layer of wood shavings, and each enclosure contained a single, painted, wooden nestbox (measuring 33 × 33 × 16 cm), two water bottles and two ceramic food bowls (15 cm diameter).

Procedure

Our procedure, adopted from that of Jacobs & Campbell (1961), was intended as a laboratory analogue of a naturally occurring situation in which naive individual are gradually recruited, through either birth or immigration, into a numerically stable population, replacing population members lost through either death or emigration.

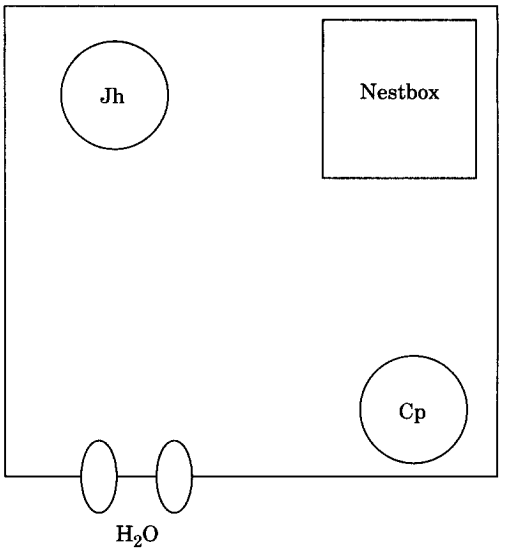

Figure 1. Overhead schematic of floor enclosure (Jh=Japanese horseradish flavoured diet; Cp=cayenne pepper-flavoured diet; H_2O=water bottles).

After we taught all members of a 'founding' population of Norway rats (our confederates) an arbitrary food preference, we replaced them over days with naive recruits (our real subjects), until none of the members of the original population remained. We monitored the food choices of the population throughout the experiment to determine the fate of the traditional behaviour we had established in its founders.

EXPERIMENT 1: TRANSMISSION IN RAT MICROCULTURES

Methods

Subjects

Subjects were 128 42-day-old rats. We assigned 64 of these subjects to 16 founding colonies, each consisting of four rats trained to avoid eating either cayenne pepper-flavoured diet (Cp; 8 founding colonies) or diet flavoured with Japanese

horseradish (Jh; 8 founding colonies). The remaining 64 subjects that we used in experiment 1 served as replacements for original colony members.

Procedure

Training founding colony members. To begin the experiment, we introduced subjects that we had randomly assigned to be founding colony members into individual wire-mesh hanging cages and deprived them of food for 23 h/day for 2 consecutive days. During the remaining hour of each day, we offered each subject a food cup containing powdered diet Pur.

Following a third 23-h period of food deprivation, we gave each subject a food cup containing either diet Jh or diet Cp for 1 h. 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% weight/volume lithium-chloride solution to produce a transient gastro-intestinal upset. We waited 1 h and then gave each subject 8–9 g of diet Pur and left her undisturbed for 23 h.

At the end of the 23-h period following injection, we offered each subject, for 1 h, a weighed food cup containing the diet to which she had learned an aversion on the previous day, and then once again injected any subject eating more than 0·2 g of diet with 2% of body weight, 1% weight/volume lithium chloride. We then waited 1 h, marked the tail of each subject with indelible ink to identify her as a founding colony member and provided her with 8–9 g of diet Pur.

Conduct of the experiment. Twenty-three hours later, we placed groups of four subjects that had been taught to avoid eating diet Jh (which, consequently, would eat only diet Cp) and groups of four subjects that had been taught to avoid eating diet Cp (which, consequently, would eat only diet Jh) in floor enclosures, each of which contained a weighed bowl of diet Cp and a weighed bowl of diet Jh (Fig. 1), and left these colonies undisturbed for 24 h.

At the end of the 24-h period we: (1) removed the food bowls from each enclosure and weighed them, (2) randomly selected a member of each founding colony and removed her from her colony enclosure (and from the experiment) and (3) introduced a randomly selected, experimentally naive replacement subject into each colony enclosure. We repeated this procedure three additional times, at 24-h intervals, until we had replaced all four members of each original colony.

Once we had replaced all four members of each founding colony with naive subjects, we left the newly constituted colonies undisturbed for 4 days, except for daily measurement of the intake by each colony of diets Cp and Jh.

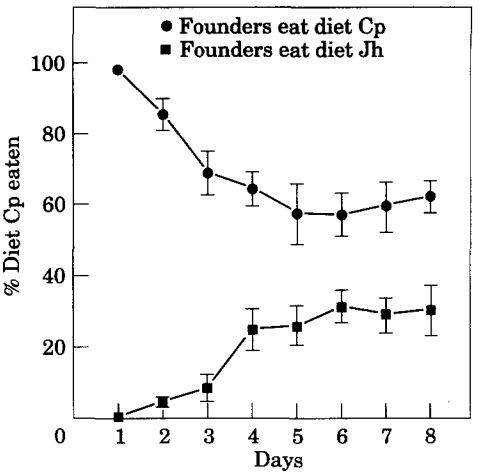

Figure 2. Mean (± SE) amount of diet Cp, as a percentage of total amount eaten by subjects in floor enclosures that housed founding colonies that ate either diet Cp or diet Jh. Day 1: enclosures contained only members of the founding colony; days 2–4: enclosures contained both original colony members and replacement subjects; days 5–8: enclosures contained only replacement subjects.

Results

As we expected, the members of each founding colony exhibited a strong aversion to whichever diet they had eaten immediately before we injected them with lithium-chloride solution and ate only the alternative diet available to them (Fig. 2, day 1).

Following total replacement of the members of original colonies (Fig. 2, days 5–8), the new members of each colony continued to favour whichever diet the members of their founding colony had eaten. Clearly, we have preliminary evidence of a stable tradition of food preference in replacement subjects.

The mean values reported in Fig. 2 suggest that replacement subjects exhibited a weak preference

for the diet that their respective founding colonies had eaten (see Fig. 2, days 5–8). Closer examination of data describing the food preferences of individual colonies revealed that the mean values were not a statistical artefact resulting from some groups of replacement subjects eating only the diet that their founding colony had eaten and other groups of replacement subjects exhibiting equal intakes of the two diets. Rather, by day 8 of the experiment, 14 of the 16 groups of replacement subjects still showed a preference for the diet that the members of their respective founding colonies had been trained to eat (binomial test: $P<0{\cdot}002$) and these preferences were generally modest. For example, on day 8, members of seven of the eight groups of replacement subjects introduced into founding colonies eating diet Cp still showed a preference for diet Cp, and the 3-h intake of diet Cp by these seven groups ranged from 59·4 to 73·5% of their total 24-h intake. Thus, although the tradition we had established in the founders was sustained for at least four days after their departure from each colony, under the conditions of the present experiment, the fidelity of the replacement subjects to the learned diet preference of founders was relatively low.

We do not know how long the socially induced preferences for diets Cp and Jh would have been sustained in the colony, because no one has yet examined the stability of socially learned food preferences in groups of undisturbed animals. In isolated animals, such preferences can last from 2 days (Galef et al. 1985) to 2 weeks or more (Galef 1989) depending on the details of the procedures used to establish them.

EXPERIMENT 2: DO RATS ACQUIRE A TRADITION?

The evidence of a behavioural tradition provided in experiment 1 is less compelling than it may first appear. Because we calculated our sole index of food preference in each colony from the total amounts of diets Cp and Jh eaten during each 24-h period by all four replacement subjects in an enclosure, we could not determine how much of each of the two available foods individual colony members were eating. It is possible, for example, that only those replacement subjects that interacted with two or three members of a founding colony acquired the food preference of that colony, and that those replacement subjects introduced last into each colony enclosure (which never interacted with any original colony members) ate equal amounts of diets Cp and Jh.

Experiment 2 was undertaken to determine whether all four replacement animals introduced into a colony would acquire the food preference of the members of the founding colony in which we placed them.

Methods

Subjects and apparatus

Eighty rats served as subjects; 40 subjects served as members of 10 founding colonies and the remaining 40 served as replacements for founding colony members.

We used the same apparatus as in experiment 1 except that we used a time-lapse, video-cassette recorder and closed-circuit television system to monitor feeding behaviour in each enclosure after all founding colony members had been replaced.

Procedure

The procedure was identical to that used in experiment 1 except that, to reduce the time required to analyse videotapes of feeding behaviour and to run the experiment, we (1) placed food bowls in each enclosure for only 3 h/day (rather than 23 h/day), and (2) ran the experiment for 6 rather than 8 days.

We replaced founding colony members with naive subjects immediately after the 3-h colony feeding period on each day and because we wanted to be able to identify individual replacement subjects within each colony when we viewed their behaviour on closed-circuit television we used as replacement subjects rats that had easily distinguished pelage markings.

We reviewed videotapes of feeding behaviour recorded on day 6 of the experiment to determine the amount of time that each of the four replacement subjects introduced into each colony enclosure spent eating from the food bowls containing diets Cp and Jh. We scored a subject as eating from a bowl from the moment that its nose passed over the edge of that bowl until it removed its nose from the bowl.

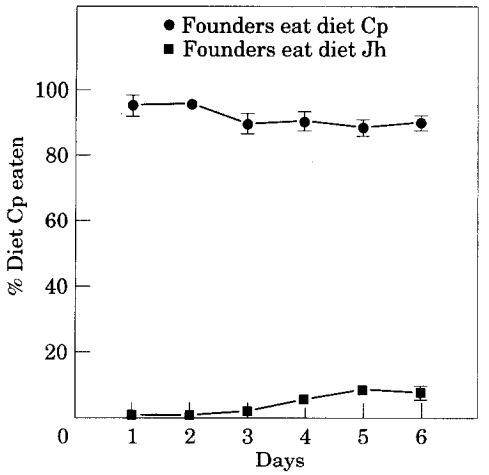

Figure 3. Mean (± SE) amount of diet Cp, as a percentage of total amount eaten by subjects in experiment 2 housed in floor enclosures with founding colonies that ate either diet Cp or diet Jh. Day 1: enclosures contained only members of the originating colony; days 2-4: enclosures contained both original colony members and replacement subjects; days 5–6: enclosures contained only replacement subjects.

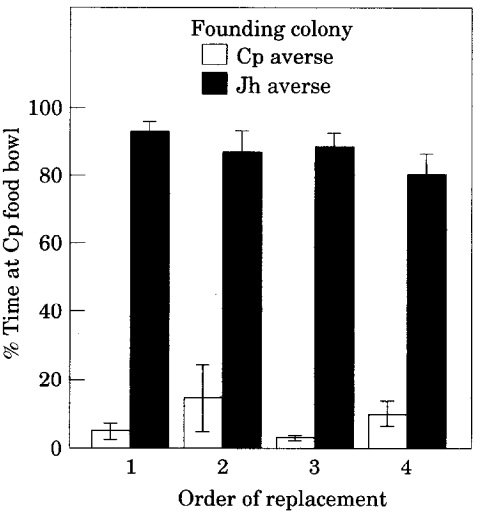

Figure 4. Mean (± SE) amount of time spent by first, second, third and fourth replacement subjects feeding from the bowl containing diet Cp in enclosures that had housed founding colonies that ate either diet Cp or diet Jh.

Results and Discussion

Replacement subjects showed a striking fidelity to the diet that their respective initiating colonies had been trained to eat (Fig. 3). Each of the four replacement subjects, whether the first or last introduced into a colony enclosure, was equally likely to spend time eating the type of food that the members of its founding colony had been trained to eat (Fig. 4; Kruskall–Wallis one-way ANOVA: both $H<7{\cdot}82$, NS).

A correlational analysis of the relationship on day 6 between the total time spent eating from food bowls containing diet Cp by all four replacement subjects in each of the 10 groups and the percentage of their total intake that was diet Cp was highly significant ($r=0{\cdot}99$, $P<0{\cdot}001$). Thus, the relative amount of time spent eating a diet was a reliable indicator of the relative amount of that diet that the subjects ate.

On days 5 and 6, replacement subjects in experiment 2, which had 3 h/day access to bowls of diet Jh and Cp, showed greater fidelity to the diet preferences of their respective founding colonies than did replacement subjects in experiment 1, which had ad libitum access to bowls containing diets Cp and Jh (repeated-measures ANOVA; replacement subjects introduced into founding colonies eating diet Cp: $F_{1,11}=12{\cdot}26$, $P<0{\cdot}005$; replacement subjects introduced into founding colonies eating diet Jh: $F_{1,11}=10{\cdot}57$, $P<0{\cdot}008$).

It may be relevant to note that free-living, wild Norway rats are most active at dawn and dusk, and many individuals feed for only a few hours each day (Barnett 1975; Berdoy & MacDonald 1991; Berdoy 1994). Consequently, our laboratory results are consistent with the view that recruits to a colony of free-living Norway rats should adhere rather closely to the learned food preferences of the members of the colony into which they are recruited.

EXPERIMENT 3: STABILITY OF TRADITIONS

The striking fidelity shown by replacement subjects in experiment 2 to the food preferences of members of their founding colonies is consistent with the notion that rat colonies might be able to sustain traditions of food preference over several generations. It is important, however, to investigate directly the stability of such traditions of food preference across generations of rats. Consequently, in experiment 3, we examined the food

preferences of four generations of replacement subjects introduced into founder colonies of Norway rats trained to eat either diet Cp or diet Jh.

Methods

Subjects and apparatus

Forty female rats, 45–56 days of age, served as the founding colony members for 10 colonies each containing four subjects. An additional 140 subjects from the same source served as replacement subjects. We used the apparatus described previously (Fig. 1).

Procedure

We followed the same procedure as that of experiment 2 except that (1) we marked the tails of both founder colony members and replacement subjects with different colours of indelible ink so that individuals could be readily identified, (2) we replaced one subject in each enclosure each day for 14 consecutive days and (3) each time we removed a replacement subject from an enclosure, we removed the one that had been longest in that enclosure. Consequently, in 14 days, we were able to examine the stability of the tradition of food preference in members of four generations of rats, only the first of which had interacted directly with a member of the founding colony.

Results and Discussion

The differences that we had established in the food preferences of founding colonies were sustained across four generations of replacement subjects (Fig. 5). Although the preference for diet Cp weakened over generations, on the last day of the experiment there was still a significant difference in the food preferences of replacement subjects introduced into colonies whose founders had eaten diet Cp and Jh (Mann–Whitney U-test: $U=0$, $P<0{\cdot}004$). These final replacement subjects had interacted with replacements of replacements of replacements that had interacted with founding colony members.

The deterioration of the tradition of flavour preference was clearly more rapid in colonies with an initial preference for diet Cp than in colonies with an initial preference for diet Jh. All five

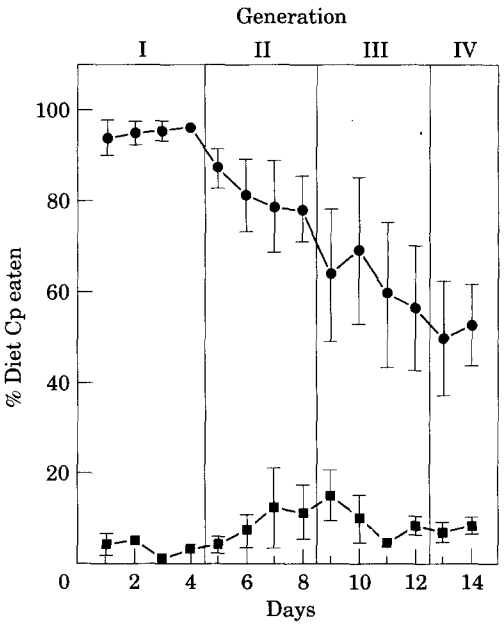

Figure 5. Mean (± SE) amount of diet Cp, as a percentage of total amount eaten by subjects in experiment 3 housed in floor enclosures that contained founding colonies that ate either diet Cp or diet Jh. Day 1: enclosures contained only members of the originating colony: days 2–4, enclosures contained both original colony members and replacement subjects; days 5–14: enclosures contained only replacement subjects.

colonies with an induced preference for diet Cp showed a decline in preference for diet Cp between the second and fourth generation of replacement subjects, whereas only one of the five colonies with an induced preference for diet Jh showed an increase in its mean percentage intake of diet Jh from the second to fourth generation of subjects (Fisher exact probability test: $P<0{\cdot}05$). Without further experimental work, we can only speculate as to the causes of this apparent difference in the stability of socially induced preferences for diets Cp and Jh, which we had equated in palatability before beginning our experiments. It is possible that the two diets differ in their effectiveness as signals for the social induction of food preferences. If so, we have serendipitously discovered a powerful tool for manipulating the fidelity of transmission of preference for a food without varying the reinforcement that a subject receives for ingesting that food. Such a tool would be particularly useful in the paradigm used here to

analyse the role of the fidelity of transmission in determining the longevity of traditions of food preference.

Because our breeding colony ran out of subjects on day 14, we had to terminate the study before the food preferences of the two groups had stabilized. We expect that eventually both would have converged at approximately 50%, but that result remains to be demonstrated.

EXPERIMENT 4: URINE AND FAECES

Taken together, the results of experiments 1, 2 and 3 indicate that it is possible to establish a tradition of food preference in laboratory colonies of Norway rats that can survive for several generations. The final two experiments in this series were undertaken to explore necessary conditions for transmission of food preference from one generation of rats to the next. The results of such studies should permit the integration of the present method for study of traditional food preferences in Norway rats with previous work on their social learning of food preferences (for reviews, see Galef 1977, 1982, 1988, 1994).

Laland & Plotkin (1991, 1993) demonstrated that urine and faeces deposited by Norway rats in and near a food bowl can result in transmission of food preferences between rats. Feeding sites marked with excretory products are more attractive to rats seeking food than are unmarked sites (Galef & Heiber 1976), and rats feeding at a marked site develop a preference for an unfamiliar food that they find there (Laland & Plotkin 1993). We designed experiment 4 to determine whether excretory deposits accumulated in or near a food site were necessary for maintenance of the traditions of food preference exhibited by subjects in experiments 1, 2 and 3 in the present series.

Method

Subjects and apparatus

Thirty-two female rats, 45–56 days of age, served as founding colony members for eight colonies each of four rats. An additional 32 subjects served as replacement subjects. The apparatus was identical to that used previously (Fig. 1).

Procedure

We followed the same procedure as in experiment 2 except as follows. (1) To ensure that the locations of olfactory cues deposited by rats in an enclosure one day were not systematically related to the location of food bowls on the next day, each day we used a random number table to determine in which of eight locations in each enclosure we would place food bowls on each day. (2) To ensure that no excretory deposits placed by rats in food bowls on one day were available to guide subjects' food choices on succeeding days, we placed new samples of food in clean food bowls at the beginning of each 3-h feeding session. (3) To examine the food preferences of individual replacement subjects, rather than videotape subjects' feeding behaviour (as we did in experiment 2), we removed each replacement subject from her enclosure at the end of the 3-h feeding period on day 6, placed her alone in a wire-mesh hanging cage and deprived her of food for 21 h. At the end of the 21-h deprivation period, we offered each subject two weighed food cups, one containing diet Cp and the other containing diet Jh, and allowed her to feed undisturbed for 3 h.

Results and Discussion

Social influences on food choice were sustained despite disruption of excretory cues present in or near food cups between days (Fig. 6). On days 5 and 6, replacement subjects show similar preferences for the diet eaten by members of their originating colony to those shown by subjects in experiments 2 and 3 that had access to residual olfactory cues from preceding days. Thus residual excretory cues deposited by rats while feeding on one day of the experiment are not necessary to guide the food preferences of subjects on the next day.

Of course, colony members might have placed excretory deposits in or around a food bowl they were exploiting during a 3-h feeding period, and those deposits might have influenced the feeding behaviour of other subjects during that feeding period. Thus, although the present results allow us to conclude that the presence of residual excretory deposits are not necessary to maintain a tradition of food preference, they do not allow us to conclude that such deposits are not guiding social learning about food preference within a given day. Experiment 5 presents evidence that excretions deposited in or near a food bowl by founders are not necessary for transmission of food preferences to their replacements.

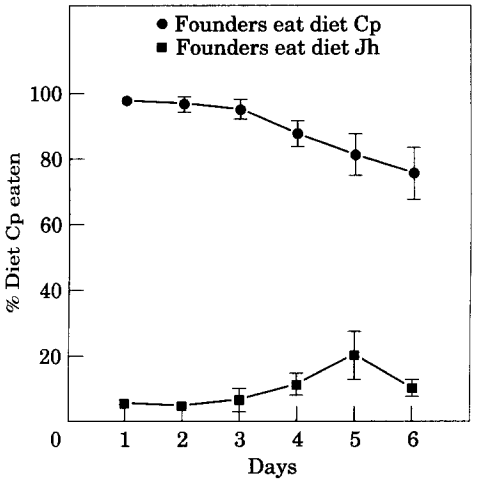

Figure 6. Mean (± SE) amount of diet Cp, as a percentage of total amount eaten by subjects in experiment 4 housed in floor enclosures that contained founding colonies that ate either diet Cp or diet Jh. Day 1: enclosures contained only members of the founding colony; days 2–4: enclosures contained both original colony members and replacement subjects; days 5–6: enclosures contained only replacement subjects.

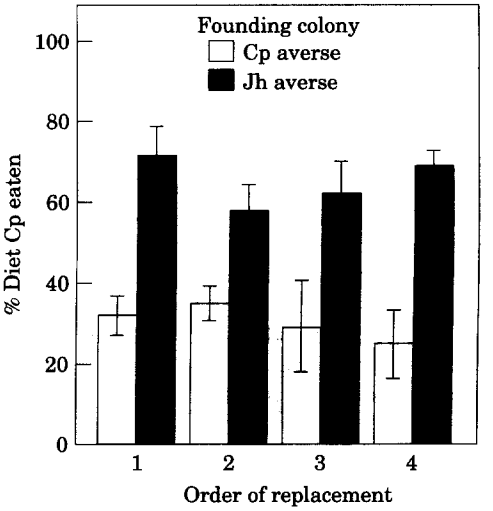

Figure 7. Mean (± SE) amount of diet Cp eaten during individual testing by first, second, third and fourth replacement subjects taken from enclosures that once contained founding colonies that ate either diet Cp or diet Jh.

Our finding that excretory deposits remaining in the environment from one bout of feeding to the next are not necessary for the establishment of traditional patterns of food preference does not contradict Laland & Plotkin's (1991, 1993) finding that excretory deposits are sufficient to support such preferences. Furthermore, differences in the strain, age and sex of subjects between Laland & Plotkin's studies and ours may make them difficult to compare directly. We speculate that the adult, male rat subjects in Laland & Plotkin's studies might have been less likely to assume the nose-to-nose position necessary for direct social induction of a food preference when they encountered an unfamiliar adult male conspecific (Galef & Stein 1985) than were the juvenile, female rat subjects in the present experiments. Adult males might have to use different social cues than juvenile females when selecting substances to ingest.

During the choice test given to replacement subjects after we had removed them to individual cages, all four replacement subjects introduced into an enclosure showed roughly equivalent preferences for the diets eaten by their respective founding colonies (Fig. 7). Replacement subjects thus acquired the food preferences taught to their respective founding colonies with equal probability, irrespective of the order of their introduction into a colony.

EXPERIMENT 5: LOCAL ENHANCEMENT

Informal observation of the behaviour of replacement subjects in experiment 2 suggested that replacement subjects might be attracted to a feeding site by the presence of feeding conspecifics. Previous research in our laboratory has demonstrated that the presence of a rat eating from a bowl enhances the attractiveness of that bowl to its fellows and causes them to eat there (Galef & Clark 1971; Galef 1981). Such local enhancement (Thorpe 1963) may have been responsible for maintaining the traditions of food preference that we observed in experiments 1–4.

On the other hand, the results of numerous experiments have shown that after a naive rat interacts with a conspecific (a demonstrator) that has recently eaten some food, the naive rat exhibits a substantial enhancement of its preference for the food that its demonstrator ate (for reviews, see Galef 1988, 1994). Such direct influence of one rat on the food preferences of another could have

acted, as could local enhancement or residual olfactory cues, to sustain the traditions of food preference demonstrated in experiments 1–4.

In the present experiment, we examined the maintenance of traditional patterns of food preference in colonies of rats when neither local enhancement nor scent marking by members of founding colonies could influence the food choices of their replacement subjects. In experiment 5, only direct communication of information concerning ingested foods between members of a founding colony and their replacements could support the diffusion of a food preference from members of a founding colony to their replacements.

Method

Subjects and apparatus

Twenty-four female rats served as members of eight founding colonies each of three subjects. An additional 24 female rats served as replacement subjects.

Whenever subjects were fed individually, each was housed in wire-mesh hanging cages measuring 18 × 34 × 19 cm. When not housed in individual hanging cages, all subjects were kept in floor enclosures as illustrated in Fig. 1.

Procedure

We housed all 48 subjects individually in wire-mesh hanging cages, placed them on a 21 h/day schedule of food deprivation and fed them powdered diet Pur for 3 h/day for 2 consecutive days. We continued to feed diet Pur for 3 h/day to each rat that served as a replacement subject until we moved her from her hanging cage to a floor enclosure.

Following the third 21-h period of food deprivation, for 3 h, we fed diet Jh to 12 subjects and diet Cp to 12 subjects that were to be assigned to founding colonies.

At the end of this third period of scheduled feeding, we (1) placed eight founding colonies, each consisting of three subjects that had been fed either diet Cp or diet Jh and one subject that had been maintained on diet Pur, in a floor enclosure and (2) left the colonies thus constituted without food for 21 h.

At the end of the 21-h period of interaction between four rats (three original colony members and one replacement subject) in each floor enclosure, we (1) removed the three original members of each colony from their floor enclosure, (2) removed one of the three founding colony members from the experiment, (3) placed the other two founding colony members in individual hanging cages and (4) for 3 h, fed those two subjects the same diet (either diet Jh or diet Cp) that they had eaten on the previous day.

While we fed the founding members of each colony either diet Cp or diet Jh in individual cages, we placed two weighed food bowls, one containing diet Cp and the other containing diet Jh, for 3 h, in each floor enclosure with the replacement subject that we had left there.

At the end of the 3-h feeding period, we (1) removed the two food bowls from each floor enclosure, (2) weighed them, (3) returned the two remaining members of each originating colony to the enclosure from which we had taken them 3 h earlier, (4) added a second replacement subject to each colony and (5) left them undisturbed for 21 h.

We repeated the above procedure on the second day, (1) removing the two remaining members of original colonies from each floor enclosure, (2) discarding one and feeding the other either diet Cp or diet Jh, (3) determining the food intake of the two replacement subjects that we had left in enclosures after we removed food bowls from each floor enclosure at the end of the 3-h feeding period, (4) then returning the one remaining original colony member to each floor enclosure and (5) finally adding one naive replacement subject to each floor enclosure.

The third day, we removed the final founding colony member from each floor enclosure and, after the colony feeding period, added the third and final replacement subject to each enclosure.

On the fourth and last day, we offered each colony a choice between weighed samples of diets Jh and Cp for 3 h and, immediately after completion of the 3-h feeding period, moved each replacement subject to an individual hanging cage, where 21 h later, it was again offered a choice between diets Cp and Jh for 3 h.

Results and Discussion

Replacement subjects developed a reliable preference for the diet eaten by the members of their

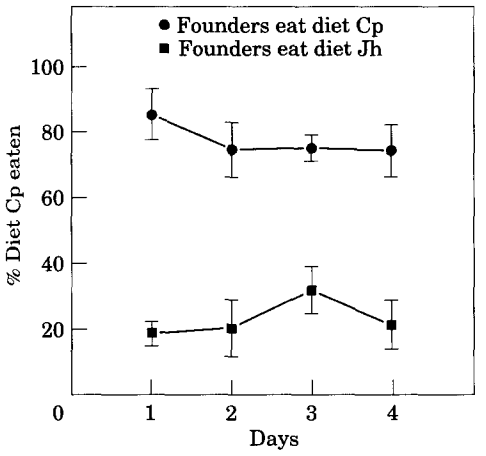

Figure 8. Mean (± SE) amount of diet Cp eaten by replacement subjects in experiment 5 interacting with founding colonies that ate diet Cp or diet Jh.

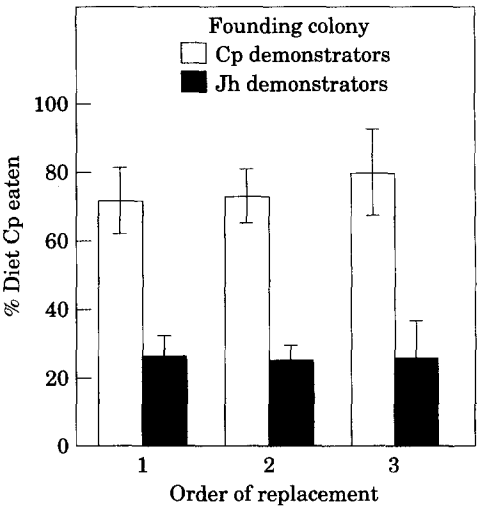

Figure 9. Mean (± SE) of diet Cp eaten during individual testing by first, second and third replacement subjects taken from enclosures where they interacted with members of founding colonies eating either diet Cp or diet Jh.

respective founding colonies (Fig. 8; repeated-measures ANOVA: $F_{1,6}=37{\cdot}60$, $P<0{\cdot}001$) even though members of founding colonies and their replacements never interacted in the presence of food, and members of founding colonies could not deposit excretory deposits in or near feeding sites used by their replacements. Clearly, neither the physical presence of founding colony members at a feeding site nor residual excretory deposits deposited by members of founding colonies were necessary for induction of a food preference in replacement subjects. During the 21 h/day that founding colony members and replacement subjects spent together in enclosures without food, replacement subjects were able to identify the food that the members of their respective founding colonies had been eating and used that information when given the opportunity to choose among unfamiliar foods. For an analysis of the complex of olfactory cues passing from recently fed rats to naive conspecifics which cause the naives to prefer foods that conspecifics have eaten (see Galef & Stein 1985; Galef et al. 1985, 1988).

Comparison of these results (in which replacement subjects and founding colony members could not interact in the feeding situation: see Fig. 8) with those of experiment 2 (in which founding colony members could serve to locally enhance the food bowls from which they were feeding: see Fig. 3) revealed that the size of a socially induced food preference was substantially greater in experiment 2 (repeated-measures ANOVAs; when founding colonies ate diet Cp: $F_{1,7}=5{\cdot}41$, $P<0{\cdot}05$; when founding colonies ate diet Jh: $F_{1,7}=13{\cdot}38$, $P<0{\cdot}01$). This result suggests that although local enhancement and residual excretory deposits are not necessary for transmission of the traditions of food preference under investigation here, one or the other may augment the olfactory transmission of food preferences observed in the present experiment.

Replacement subjects did not differ in the magnitude of their preferences for foods eaten by members of their respective founding colonies as a function of the order in which they had been introduced into floor enclosures (Fig. 9). The tradition of food preference maintained by information exchange outside the feeding situation was stable.

GENERAL DISCUSSION

The results of the present series of experiments (1) establish the reliability of a new model system for laboratory study of the diffusion and maintenance of behavioural traditions in animal populations, (2) allow some insight into the processes of information transmission that support the observed traditional behaviour patterns and (3) provide important clues as to the directions in which

future investigations of the role of social and ecological context on the longevity of socially transmitted behaviour might proceed. The results of experiment 3, in which differences in food preference traditions were maintained across four generations of subjects, provided particularly compelling evidence of the robustness of effects within the present paradigm. The results of experiments 4 and 5 establish that the central social-transmission processes supporting the traditional patterns of food preference demonstrated in experiments 1, 2 and 3 are already well understood (see Galef 1988, 1994 for reviews). Comparison of the results of experiments 1 and 2 indicate (to whatever extent that between-experiment comparisons are valid) that the duration of opportunities to make contact with alternative foods may influence the probability of transmission and longevity of a socially induced pattern of food preference in Norway rats.

Progress in understanding behavioural traditions in animals as they occur in nature has been impeded by the lack of laboratory paradigms in which to undertake systematic investigations of the effects of individual experience, population composition and rate of recruitment into tradition bearing populations on the probability of transmission and longevity of traditional types of behaviour. The present studies establish the reliability of a procedure that will allow study of the effects of such social and ecological variables on the diffusion of traditional behaviour through animal populations.

Further laboratory studies, already underway, of the longevity of traditions in dynamic populations of animals, rather than of social transmission in pairs of animals, promise to provide insight into the ways in which individual and social experience interact with transmission processes to influence the longevity and dispersal of behavioural traditions in free-living animal populations.

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