



Effects of environmental stability and demonstrator age on social learning of food preferences by young Norway rats

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We used socially learned food preferences of Norway rats, *Rattus norvegicus*, to examine two common predictions of formal models of social learning in animals: (1) that animals living in relatively stable environments should be more attentive to socially acquired information than animals living in highly variable environments, and (2) that older demonstrators should have greater influence than younger demonstrators on the behaviour of young observers. Old and young demonstrators were equally effective in modifying the food preferences of juveniles that interacted with them. However, food choices of rats that were moved daily from one cage to another and fed at unpredictable times for unpredictable periods were less affected by demonstrators than were rats maintained in stable environments. Our results thus provided experimental support for the first, but not the second, prediction from theory.

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For many years, studies of social influence on behavioural development lacked a general theoretical framework. However, this lacuna was largely filled in the 1980s by mathematically minded, evolutionary biologists who constructed models similar to those used in population genetics to analyse both human culture (e.g. Cavalli-Sforza & Feldman 1981; Lumsden & Wilson 1981; Boyd & Richerson 1985) and animal traditions (Boyd & Richerson 1988).

One conclusion common to Boyd & Richerson's (1988) and similar models (e.g. Aoki & Feldman 1987; Rogers 1988; Laland et al. 1996) is that social learning is more likely to be adaptive when environments are relatively stable within and across generations. When environments are changing rapidly, the probability increases that the behaviours of others will reflect past, rather than current, conditions, and the probability that copying the behaviour of others will be maladaptive increases (Laland 1996; Laland & Kendal 2003).

Boyd & Richerson (1985, 1988) also suggested that when more than one potential demonstrator is available for an individual to copy, differences in the characteristics of potential demonstrators (e.g. their ages or relative social

ranks) might bias the probability that an observer would adopt their behaviour. Although such 'indirect bias' (Boyd & Richerson 1985; Coussi-Korbel & Fragaszy 1995; Laland et al. 1996) is believed to be particularly important in the development of human traditions (Rogers 1995), recent papers indicate that, even in animals, demonstrators with certain characteristics have greater influence than do others (Nicol & Pope 1999; Benskin et al. 2002). Depending on prevailing conditions, it can be predicted that older, more experienced, more successful, more common, or even rarer models might be attended disproportionately (for discussion, see Laland 2004).

In the experiments described below, we examined effects of both environmental stability and indirect bias on social learning of food preferences by Norway rats, *Rattus norvegicus*, a species that has served for several decades as a useful model system in laboratory studies of social learning (for reviews, see Galef 1977, 1988, 1996). Free-living Norway rats are social animals that live in colonies inhabiting burrows from which foragers depart to feed and to which they return between foraging bouts. Consequently, there is opportunity for exchange of foraging information between colony members concerning available foods (e.g. Ward & Zahavi 1973; Galef 1991). As numerous laboratory studies have shown, rats can use information acquired from conspecifics to decide when, where or what to eat (for review, see Galef & Giraldeau 2001).

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EXPERIMENT 1

After a naïve Norway rat (an observer) interacts with a conspecific that has recently eaten (a demonstrator), the observer shows substantial enhancement of its preference for whatever food its demonstrator ate (Galef & Wigmore 1983). For example, when observer rats are offered a choice between cinnamon- and cocoa-flavoured foods, observers that have previously interacted with a demonstrator rat fed cinnamon-flavoured food eat significantly more of it than observers that have previously interacted with a demonstrator rat fed cocoa-flavoured food (Galef & Wigmore 1983).

In all previous experiments concerning social influence on food choice conducted in our laboratory, we maintained observer rats under stable laboratory conditions; we fed them the same food at the same time, in the same place throughout their participation in experiments. Here, we maintained observer rats under both stable and unstable conditions to examine effects, if any, of environmental variability on social learning of food preferences. It would be consistent with formal models if decreased environmental stability resulted in decreased social influence on food choice.

Methods

Subjects

Twenty-six 42-day-old, experimentally naïve, female Long-Evans rats acquired from Charles River Canada (St Constant, Quebec) served as observers, and an additional 26 49- to 56-day-old animals from the same source that had previously served as observers in other experiments served here as demonstrators. We used female rats in this and most of our other experiments because male rats that are unfamiliar with one another are more likely than females to interact aggressively when first placed together. Reducing aggression both increases the probability of social learning and decreases the stress to which subjects are subjected.

We maintained each observer and each demonstrator rat in an individual, stainless-steel hanging cage, measuring 21 × 24 × 27 cm, and housed all cages in a temperature- and humidity-controlled colony room illuminated on a 12:12 h light:dark schedule with light onset at 0700 hours.

Procedure

Diets. We used three nutritionally adequate, powdered diets purchased from Harlan-Teklad (Madison, Wisconsin, U.S.A.): (1) Normal Protein Test Diet (diet NPT; catalogue number 170590), composed principally of casein and cornstarch, (2) Fat Sufficient Diet (diet FS; catalogue number TD 69446), composed principally of casein and sucrose, and (3) Teklad Rodent Diet (W) 8640 (diet 8640), a grain-based food. We used diet 8640 both in unadulterated form and as a base diet for preparing cinnamon-flavoured diet (diet Cin) and cocoa-flavored diet (diet Coc). Diet Cin consisted of 10 g of McCormick's Ground Cinnamon (McCormick Canada Inc., London, Ontario)

added to 990 g of diet 8640. Diet Coc consisted of 20 g of Hershey's Cocoa (Hershey Canada Inc., Mississauga, Ontario) added to 980 g of diet 8640. We presented all diets to observers in semicircular, stainless-steel cups (10-cm diameter, 5 cm deep) that we filled to only half their depth to minimize spillage.

Observers. For the first 12 days of the experiment, the 10 observers that we assigned to the variable-environment group experienced a constantly changing environment. Each day, on a random schedule, we introduced unflavoured diet 8640, diet NPT or diet FS into each observer's cage at 1100, 1200 or 1300 hours for 1, 2 or 3 h. Each day, immediately after each observer rat ate, we moved her to a cage adjacent to the one she had occupied during the previous day.

For the first 12 days of the experiment, each of the 16 observers we assigned to the stable-environment condition received only one of the 27 possible combinations of food, duration of feeding, and time of initiation of feeding that we had used with subjects assigned to the variable-environment group. For example, each day for 12 days, we gave one observer assigned to the stable-environment condition diet NPT at 1000 hours for 2 h, and another observer assigned to the stable-environment condition diet 8640 at 1200 hours for 3 h. We treated subjects assigned to the stable-environment condition so that the diets they ate and the mean times at which we gave them food and the duration we left them with food were as closely matched as possible to the same means for subjects assigned to the variable-environment condition. Also, to control for handling of subjects assigned to the variable-environment condition, at the end of each feeding session, we lifted each observer assigned to the stable-environment condition from her cage and then returned her to it.

On day 13 of the experiment, at 1300 hours, we placed a demonstrator rat fed either diet Cin or diet Coc into each observer's cage for 30 min. We then removed the demonstrator and placed two weighed food cups, one containing diet Cin and the other containing diet Coc into each observer's cage. Twenty-two hours later, we removed both food cups, weighed them, determined the amount of each diet eaten, and calculated the percentage of each observer's total food intake during the preceding 22 h that was the food that its demonstrator had eaten. Thus, for observers whose demonstrators had eaten diet Cin, we calculated the percentage of each observer's total intake that was diet Cin, and for observers whose demonstrators had eaten diet Coc, we calculated the percentage of each observer's intake that was diet Coc.

Demonstrators. Throughout the 14 days of the experiment, we housed each demonstrator in an individual hanging cage identical to that in which we housed each observer. Demonstrators ate unflavoured diet 8640 ad libitum until the 10th day of the experiment, when we placed them on a 23-h schedule of food deprivation. For the first 2 days of scheduled feeding, demonstrators ate unflavoured diet 8640 for 1 h starting at 1200 hours, and on the third day of scheduled feeding, we fed one-half of

the demonstrators diet Cin and the remainder diet Coc at 1200 hours for 1 h. Immediately after we fed demonstrators, we placed one demonstrator in the cage of each observer. After demonstrators and their observers had interacted for 30 min, we removed demonstrators from their observers' cages and the participation of demonstrators in the experiment ended.

Results and Discussion

The food choices of observer rats that we maintained under both constant (Student's one-sample t test on untransformed data: $t_{15} = 2.14$, $P < 0.05$; Fig. 1) and variable conditions ($t_9 = 4.97$, $P < 0.001$; Fig. 1) were influenced by the diets that we had fed to their respective demonstrators. However, consistent with predictions of formal models, social effects on food choice were more pronounced in animals living in constant than in variable conditions (Student's two-sample t test: $t_{24} = 2.60$, $P < 0.02$).

EXPERIMENT 2

As mentioned in the introduction, several authors have suggested that phenotypic characteristics of a potential demonstrator may affect the probability that its behaviour will influence that of its observers (Boyd & Richerson 1985, 1988; Coussi-Korbel & Fragazy 1995; Laland et al. 1996), and in many formal models, the relative age of demonstrator and observer is an important determinant of whether an individual will serve as a behavioural

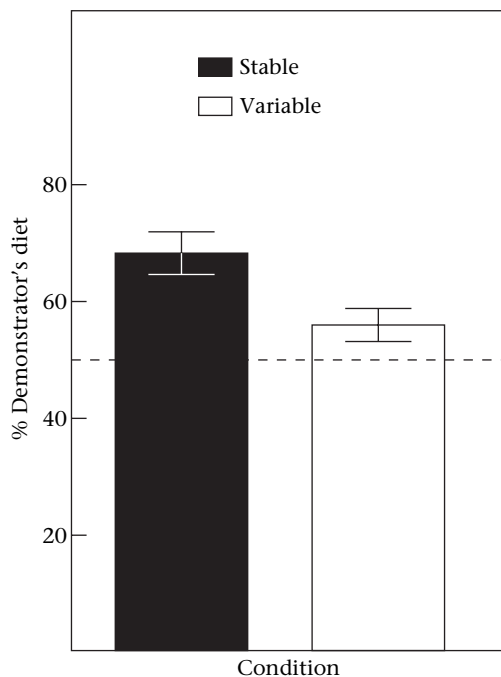


Figure 1. Mean (\pm SE) percentage of each observer's total daily intake that was the same food as that eaten by its demonstrator. Dashed line indicates no effect of demonstrators diet on observer food choice.

model. To have survived to adulthood, an individual must have learned to respond appropriately to each of the many challenges posed by the environment it shares with any juvenile with which it interacts. Juveniles may still be in the error stage of trial-and-error learning. Consequently, juveniles might be expected to have a higher probability of acquiring adaptive behaviours if they copy adults than if they copy fellow juveniles.

There is some empirical support for the view that juveniles are more likely to learn socially from older individuals than from peers. For example, Dugatkin & Godin (1993) found that smaller (possibly younger) female guppies, *Poecilia reticulata*, copy the mate choices of larger (possibly older) females of their species, but that mate choices of smaller females do not influence the mate choices of larger females. Galef et al. (2001) reported, similarly, that young rats are more likely to steal samples of unfamiliar food from older rats than older rats are to steal from their juniors, and preferences of thieves for stolen food items are significantly enhanced.

Transmission from older individuals to juveniles can be either from parents to offspring (vertical) or from non-parental adults to young (oblique). Juvenile mammals in general, and rats in particular, are likely to spend more time interacting with their mothers than with any other adult. However, juvenile rats share burrows with numerous adult conspecifics, and are likely to interact with many adults that are not their mothers. Consequently, social learning in rats should be oblique as well as vertical. Here, we will be concerned only with oblique transmission, although similar studies of vertical transmission would be interesting and ecologically relevant.

Below, we examine, in two ways, the possibility that the relative age of unrelated demonstrator and observer Norway rats affects the amount of influence that demonstrators have on the subsequent food choices of their observers. In study 1, we compared effects on food choices of juvenile rats that interacted with either adult or juvenile demonstrators. In study 2, we examined the food choices of juveniles after they interacted in succession with both an adult and a juvenile demonstrator each fed a different food.

Methods

Study 1

Subjects. Forty-two 6-week-old, experimentally naïve, female Long-Evans rats served as observers, and 18 7-week-old and 24 18-week-old rats that had served as observers in previous experiments served here as demonstrators. For 7 days before the start of the experiment, we fed all subjects on unflavoured diet 8640, and during the experiment, maintained all subjects under standard, relatively constant laboratory conditions.

Procedure. The procedure was one that we have used in our laboratory for 20 years to study social transmission of food preferences in Norway rats (described in detail in Galef & Wigmore 1983; Galef 2002). In brief, we allowed naïve observer rats to interact with conspecific

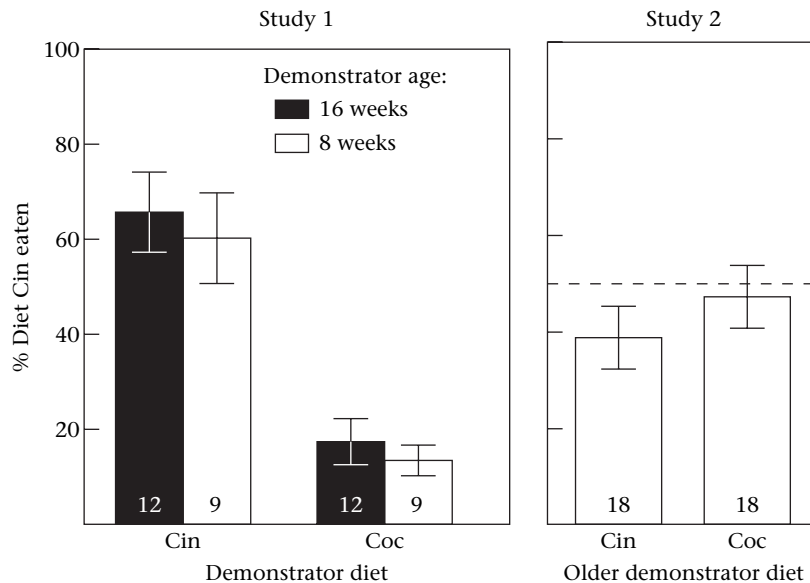


Figure 2. Study 1: amount of diet Cin eaten by observers that had interacted with either young or old demonstrators fed either diet Cin or diet Coc, as a mean (\pm SE) percentage of the observers' total intake during testing. Study 2: amount of diet Cin eaten by observers that had interacted with both an old and a young demonstrator as a mean (\pm SE) percentage of the observers' total intake during testing. Dashed line indicates equal influence of juvenile and adult demonstrators.

demonstrators immediately after the demonstrators had eaten either diet Cin or diet Coc for 1 h. We then offered each observer a choice, in its home cage, between weighed samples of diet Cin and diet Coc. The only novel features of the present study were: (1) we compared effects on young-observer food preferences of interacting with either young or old demonstrators, and (2) we allowed demonstrators and observers to interact for 15 min rather than 30 min. We shortened the period of interaction between each demonstrator and its observer to equate the total duration of demonstrator-observer interactions in the two studies that comprised the present experiment.

Study 2

Study 1 might be considered a relatively weak test of effects of demonstrator age on social influence on young-observer food choices. Even if young observers are biased to attend to older demonstrators, if only one demonstrator is present, young observers may use the information they acquire from that demonstrator irrespective of its age. In study 2, we compared directly the effects of young and old demonstrators on the food choices of observers that acquired conflicting information from demonstrators of different ages.

Subjects. Thirty-six 42-day-old, experimentally naïve, female Long-Evans rats served as observers, and an additional 36 42-day old and 36 84- to 98-day-old females that had served as observers in previous experiments served as demonstrators.

Procedure. Each 42-day-old observer interacted in succession for 15 min with two demonstrators, one 42-days-old and the other 84 or more days of age, and one fed diet

Cin and the other fed diet Coc. We counterbalanced across observers both the order in which observers encountered young and older demonstrators and the diet fed to demonstrators of each age.

Results

Study 1

Although, as expected, the diet fed to demonstrators had a profound effect on the food preferences of observers (two-way ANOVA: $F_{1,38} = 49.32$, $P < 0.0001$; Fig. 2), there was no difference in the effectiveness of old and young demonstrators on the food preferences of their respective observers ($F_{1,38} = 0.68$, NS; Fig. 2), and most important, there was no interaction between main effects ($F_{1,38} = 0.06$, NS).

Study 2

There was no significant difference in the effectiveness of old and young demonstrators in altering the food preferences of young observers (Student's t test: $t_{34} = 0.94$, NS; Fig. 2). The failure to find a preference for the diet eaten by the elder of two demonstrators in the present study is clearly not the result of insufficient power. If anything, younger demonstrators were more effective than older ones in altering young-observer diet preferences.

Discussion

The present finding, that juvenile rats are not more likely to attend to older demonstrators than to young ones, is not unique. For example, guppies learn paths to food by joining shoals travelling to food (Laland & Williams 1997), and small guppies prefer to shoal with

others of similar size (Lachlan et al. 1998) rather than with older, larger guppies. Social learning in guppies is thus predominantly within, rather than between, age classes. However, because remaining near individuals of similar size may increase protection from predators, and benefits of increased predator avoidance may be greater than the benefits of following more experienced adults, social learning by shoaling guppies may be a special case (e.g. Bates & Chappell 2002).

GENERAL DISCUSSION

As Laland & Kendal (2003, page 33) have recently pointed out, although there is formal theory relating to social learning in animals, 'there has been virtually no experimental testing of the models' predictions'. The present pair of experiments was undertaken to provide empirical data relevant to some issues for which models have provided predictions of outcomes.

The results of experiment 1 were consistent with predictions from several formal models that social learning might be expected to be more likely in relatively stable than in rapidly changing environments. This is, so far as we know, the first experimental evidence relevant to the strongest prediction from formal models of animal social learning, although Wilkinson & Boughman (1999) have provided comparative evidence of an effect of environmental stability on probability of following behaviour in socially foraging bats.

The results of experiment 2 failed to confirm the prediction from similar models that young animals should be biased towards attending to adult versus juvenile models. Experiment 2 is but one of a number of studies that have looked for effects of characteristics of demonstrators on the probability of social learning by observers, and some have found the anticipated effect. For example, Nicol & Pope (1999) showed in domestic hens, *Gallus gallus domesticus*, that the social status of a knowledgeable individual affects the probability of social learning by its observers. More recently, Benskin et al. (2002) have shown in the zebra finch, *Taeniopygia guttata*, that the probability of copying the behaviour of a model is affected by sex of both demonstrator and observer, degree of familiarity of male demonstrators and their respective observers, and coloration of male demonstrators.

Why juvenile rats should be unbiased by the age of a potential demonstrator in responding to social cues concerning food is not clear. Of course, it is always possible that under conditions other than those of the present studies, young Norway rats would be more likely to acquire food preferences as the result of interaction with adults than with peers. For example, we have previously reported that weanling rats given a simultaneous choice between two feeding sites, both containing the same food, prefer to feed at the site where an adult is present (Galef 1981). Gerrish & Alberts (1995) subsequently found that weanling Norway rats given a similar choice between feeding sites, when an adult conspecific is eating at one site and a juvenile conspecific is eating at the other, prefer the site where the adult is feeding. Taken

together, the results of Gerrish & Alberts (1995) and of experiment 2 in the present series suggest that young observer rats are more attracted to adults than to peers, but when selecting a food to eat, are equally likely to use food-related information acquired from young and old conspecific demonstrators.

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