

Social learning of food preferences in ‘dissatisfied’ and ‘uncertain’ Norway rats

BENNETT G. GALEF, JR, KRISTINA E. DUDLEY & ELAINE E. WHISKIN

Department of Psychology, Neuroscience and Behaviour, McMaster University

(Received 7 April 2007; initial acceptance 25 May 2007;
final acceptance 21 June 2007; published online 26 December 2007; MS. number: A10738)

Formal models of trade-offs between individual and social learning predict situations in which animals should increase their reliance on socially acquired information. In three experiments, we found, that as theory predicts, ‘dissatisfied’ and ‘uncertain’ Norway rats, *Rattus norvegicus*, increased their reliance on social learning. When choosing between two unfamiliar foods, rats that had been maintained for 1 week on either (experiment 1) an unpalatable, energetically dilute diet or (experiment 2) an unyielding surface in a hot, constantly illuminated room, as well as (experiment 3) rats uncertain as to which of two unfamiliar flavours that they had ingested was associated with illness showed greater reliance on socially acquired information than did their respective ‘satisfied’ and ‘certain’ controls.

© 2007 The Association for the Study of Animal Behaviour. Published by Elsevier Ltd. All rights reserved.

Keywords: food preference; model; Norway rat; *Rattus norvegicus*; social learning

Because learning socially can mitigate any costs of individual, trial-and-error learning, copying the behaviour of others might seem to be always adaptive. However, as numerous theoreticians have pointed out, copying is not always advantageous (e.g. Boyd & Richerson 1985, 1995; Rogers 1988; Giraldeau et al. 2002; Laland 2004; Kendal et al. 2005). For example, if all members of a population copy one another's behaviour, no individual would be monitoring the environment, the behaviour of population members could not track environmental changes, and, in a varying environment, the behaviour of members of a population consisting entirely of copiers would, in time, become suboptimal. Only when copying a potential model's behaviour has a higher probability of enhancing fitness than does learning individually about the consequences of behavioural alternatives is copying the behaviour of others a superior strategy.

Laland (2004) reviewed a number of formal models and provided a list of conditions that various theories suggest should affect the fitness consequences of reliance on social rather than on individual learning (see also Kendal et al. 2005). Here, we examined empirically effects on use of socially acquired information of two conditions:

dissatisfaction with payoffs resulting from current behaviour (Schlag 1998; Laland 2004) and uncertainty as to the current state of the environment (Boyd & Richerson 1985, 1988).

To explore effects of dissatisfaction and uncertainty on dependence on socially acquired information we used, as a model system, the behaviour of female Norway rats, *Rattus norvegicus*, faced with a choice between two foods. Results of many earlier studies show that after a naïve rat (an observer rat) interacts briefly with a conspecific that has recently eaten a distinctively flavoured food (a demonstrator rat), the preference of the observer rat for the food that its demonstrator ate is significantly increased (Galef & Wigmore 1983; for reviews see, Galef 2005, 2007). For example, an observer rat that has interacted with a demonstrator rat fed cinnamon-flavoured food and then chooses between cinnamon- and cocoa-flavoured foods will eat significantly more cinnamon-flavoured food than an observer rat offered the same choice after interacting with a demonstrator rat fed cocoa-flavoured food (Galef & Wigmore 1983).

Social influence on rats' food preferences has been used previously in our laboratory to explore effects of several variables that formal theory suggests should affect whether animals rely on socially acquired information when making decisions (e.g. environmental predictability, Galef & Whiskin 2004; relative age of demonstrator and observer, Galef et al. 1984; Galef & Whiskin 2004; success of the demonstrator, Galef et al. 1983, 1991; costs of individual learning,

Correspondence: B. G. Galef, Jr, McMaster University, Department of Psychology, McMaster University, Hamilton, Ontario, Canada L8S 4K1 (email: galef@mcmaster.ca).

Galef & Whiskin 2006; and success of the observer, Galef et al. 1991). Results of such investigations have sometimes provided evidence consistent with theoretical predictions, and sometimes not (for review, see Galef 2006).

Consistent with the copy-if-dissatisfied strategy that we examine here, we have previously found that observer rats maintained on a protein-deficient diet are more likely than rats maintained on a protein-replete diet to copy the food choices of demonstrator rats (Beck & Galef 1989; Galef et al. 1991). Although the enhanced use of socially acquired information shown by protein-deficient rats is consistent with the hypothesis that dissatisfaction enhances reliance on social learning, such increased reliance on social learning might not be a result of dissatisfaction per se. Protein-deprived rats in the Galef et al. (1991) study, although probably 'dissatisfied' with the situation in which they found themselves, were also obviously ill. Consequently, illness, rather than dissatisfaction might have been the cause of the observed heightened reliance on socially available information in protein-deprived subjects.

In the three experiments described below, observers choosing between two diets had opportunity to learn individually about both the relative palatability and post-ingestive consequences of those diets as well as access to information concerning them acquired socially from a demonstrator. Observers choosing diets on the basis of individual learning would not prefer the diet that their demonstrators had eaten, while observers relying on socially acquired information would prefer that diet.

We examined effects on observers' reliance on socially acquired information of two potential causes of dissatisfaction: (experiment 1) maintenance on an energetically dilute diet, and (experiment 2) maintenance in uncomfortable circumstances and (experiment 3) one possible cause of 'uncertainty', ambiguity as to the cause of illness.

EXPERIMENT 1: DISSATISFACTION, DILUTE DIET

Schlag's (1998) game-theoretical analysis of situations when copying the behaviour of others would be beneficial indicates, first, that an individual should copy others when they are more successful than the potential copier, and second, that the probability of copying should be proportional to the difference in success between potential model and potential copier. In discussing Schlag's work, Laland (2004) labelled this strategy a 'copy-if-better' strategy and suggested an alternative that he labelled 'copy-if-dissatisfied'. In copy-if-dissatisfied, the amount of reward an individual is receiving for current behaviour is linearly related to its satisfaction, and the probability that an individual will copy others is inversely related to its current level of satisfaction. At evolutionary equilibrium, copy-if-better and copy-if-dissatisfied have equivalent fitness consequences (Laland 2004). However, because copy-if-dissatisfied requires evaluation only of one's own success, not of the relative success of oneself and others, copy-if-dissatisfied seems more likely to have evolved than copy-if-better (Laland 2004).

Here, we made subjects 'dissatisfied' by maintaining them on an unpalatable, energetically dilute diet. We chose

a level of energetic dilution such that subjects could compensate by increasing their food intake to maintain both body weight and health. However, subjects maintained on the energetically dilute diet had to eat a relatively unpalatable diet and experienced increased food-handling time as a consequence of having to eat increased amounts. Consequently, they should have been both relatively dissatisfied and healthy.

METHODS

Subjects

We assigned 28, 9-week-old, female Long-Evans rats (observers) obtained from Charles River Canada (St Constant, Quebec, Canada) to dissatisfied ($N = 12$), and satisfied ($N = 16$) conditions. These animals had served as observers in previous studies of social learning, but had no previous experience with one another or with either the anise- or marjoram-flavoured diets or the dilute diet to which they were exposed in the present experiment. An additional 28, 10- to 11-week-old, female rats that had served as observers in previous experiments, served as demonstrators. We used only young female rats as both demonstrators and observers to reduce the probability of aggression when two individuals, unfamiliar with one another, were first placed together.

Apparatus and Diets

Apparatus

Throughout the experiment, we individually housed demonstrators and observers in stainless steel, wire-mesh hanging cages, measuring $20 \times 20 \times 34$ cm. We presented food to all subjects in semicircular, stainless steel food cups (10 cm in diameter and 5 cm deep). To prevent spillage (monitored by inspection beneath cages) we filled food cups to only half their depth.

Diets

We composed two diets by mixing either 1 g of ground anise or 2 g of ground marjoram with sufficient powdered Teklad Rodent Diet 8640 (diet 8640; Teklad Mills, Madison, WI) to bring the mixture to 100 g. We purchased anise and marjoram in bulk from The Horn of Plenty (Dundas, Ontario, Canada).

To construct an energetically dilute diet (diet cell), we mixed 150 g of a non-nutritive substance (cellulose non-nutritive filler; catalogue number 160390, Teklad Mills, Madison, WI) with 850 g diet 8640. In a 24-h choice test between undiluted diet 8640 and diet cell, 20 individual female rats similar in age and previous experience to subjects in the present experiment (see Subjects) ate a mean \pm SE of $13.2 \pm 3.5\%$ of diet cell, indicating that they found diet cell considerably less palatable than diet 8640.

Procedure

Observers

We weighed observers and, for 1 week, fed them ad libitum either diet 8640 ($N = 16$) or diet cell ($N = 12$). At the

end of the week, we reweighed each observer and determined its change in body weight during the preceding week.

Demonstrators

While observers were being fed either diet 8640 or diet cell, to ensure that demonstrators ate when we gave them opportunity to do so, we placed them on a feeding schedule, eating diet 8640 for 1 h/day for 3 consecutive days. On the day that demonstrators were scheduled to interact with observers, we gave the demonstrators access to either diet mar ($N = 14$) or diet ani ($N = 14$) during the 1-h feeding period that occurred just before we moved each demonstrator into the home cage of an observer.

Social learning

Six of the 12 observers maintained on diet cell and eight of the 16 observers maintained on diet 8640 interacted for 30 min with a demonstrator that had been fed diet ani, and the remaining observers interacted with a demonstrator that had been fed diet mar.

Testing

Following the 30-min period of interaction between demonstrators and observers, we removed demonstrators from observers' cages (and from the experiment), then offered each observer, for 24 h, two weighed food cups, one containing diet mar and the other diet ani. At the end of the 24-h testing period, we again weighed the food cups in each observer's cage and calculated the percentage of each observer's total 24-h intake that was the diet that its demonstrator had eaten (i.e. for observers whose demonstrators had eaten diet ani, $100 \times \text{g diet ani} / \text{g diet ani} + \text{g diet mar}$ and, for observers whose demonstrators had eaten diet mar, $100 \times \text{g diet mar} / \text{g diet mar} + \text{g diet ani}$).

Ethical note

The McMaster University Animal Research Ethics Board approved the procedures used in all three experiments reported here (AUP Number 04-06-28).

Results and Discussion

As would be expected based on the hypothesis that dissatisfied rats would make greater use of socially available information than satisfied rats, the food preferences of observers maintained on diet cell for 7 days showed a significantly greater influence of demonstrators than the food preferences of observers maintained on diet 8640 (Student's t test, $t_{26} = 2.56$, $P < 0.02$; Fig. 1a). The data are fully consistent with the hypothesis that dissatisfied animals are more likely to copy the behaviour of others than are satisfied animals.

During the 7 days of feeding, all subjects gained weight (as would be expected of young female rats maintained with ad libitum access to food), and observers fed diet 8640 and diet cell gained equal amounts of weight (Student's t test, $t_{26} = 0.33$, $P = 0.75$; Fig. 1b). Furthermore, there was no relationship between the amount of weight gain of observers

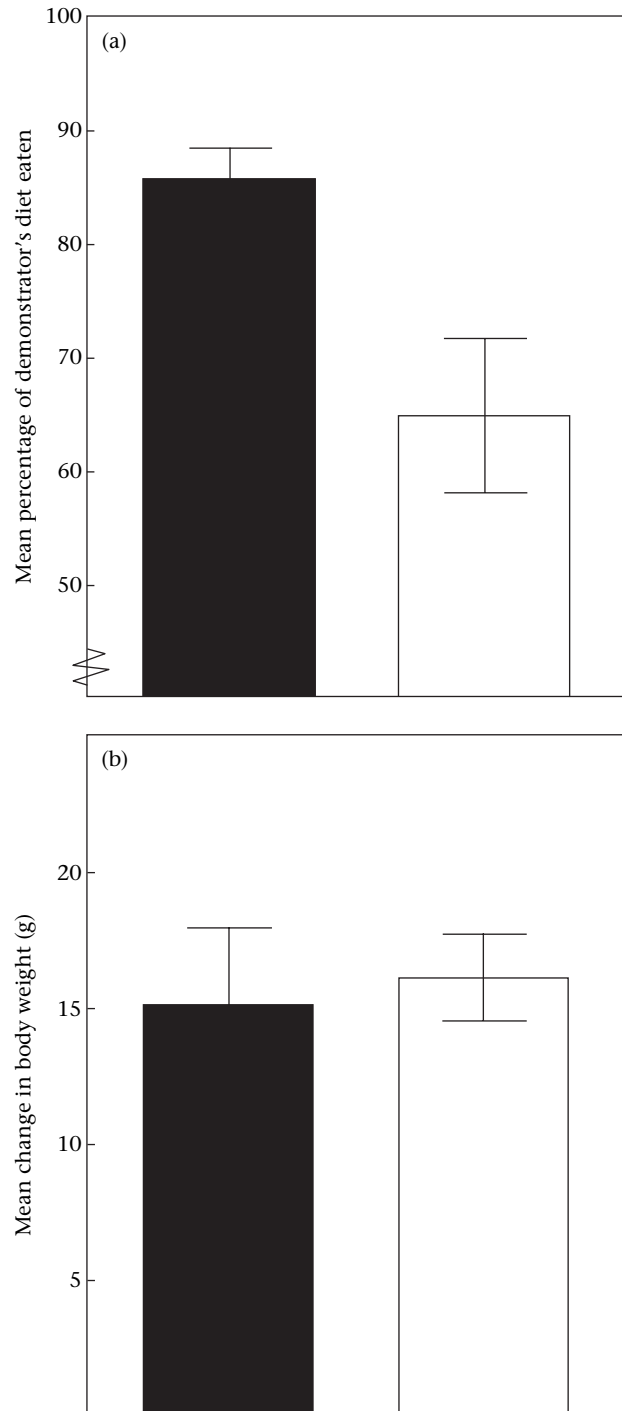


Figure 1. (a) Mean percentage of demonstrator's diet eaten by observers fed diet cell (■) or diet 8640 (□) for 1 week before interacting with demonstrators, and (b) mean change in weight during 1 week maintenance on diet cell or diet 8640. Flags = ± 1 SEM.

during the week preceding testing and their reliance on socially acquired information when choosing between diets during testing (observers fed diet cell, Spearman's rank-order correlation, $r_s = 0.02$, $N = 16$, $P = 0.95$; observers fed diet 8640, $r_s = 0.08$, $N = 12$, $P = 0.80$). The similarity in weight gain of observers maintained for 1 week on diet 8640 and on diet cell and the lack of correlation between

change in body weight and reliance on socially acquired information both suggest that any effect of maintenance diet on subsequent social learning was not a result of illness of subjects maintained on diet cell.

EXPERIMENT 2: DISSATISFACTION, UNCOMFORTABLE ENVIRONMENT

Dissatisfaction is an ambiguous term, and it is therefore easy to suggest any number of environmental circumstances that might make animals dissatisfied. Wild Norway rats are crepuscular animals usually found in temperate climates. They spend much of their lives concealed in underground burrows where they construct nests in which they sleep and rear their young. Here we maintained rats in constant light on a relatively hard substrate without access to nesting material and at an elevated ambient temperature to determine whether such generalized discomfort would increase reliance on social information when choosing a diet.

Methods

Subjects

Forty-eight female rats, identical to observers and demonstrators in experiment 1, served here as observers ($N = 24$) and demonstrators ($N = 24$). We randomly assigned 12 observers to comfortable and uncomfortable conditions and 12 demonstrators to be fed diet ani and 12 to be fed diet mar.

Apparatus

For 1 week, we housed comfortable subjects in pairs in standard transparent polycarbonate shoebox cages measuring $45.7 \times 25.4 \times 21.6$ cm. Wood-chip bedding covered the floor of each cage to a depth of 3 or 4 cm and strips of newspaper were available as nest-building material. The cages resided in a colony room on a 12:12 h day/night cycle and a temperature of $22 \pm 0.5^\circ\text{C}$. We presented food to subjects ad libitum in an overhead bin that provided some cover.

Uncomfortable subjects lived in pairs in shoebox cages similar to those housing comfortable subjects, however, uncomfortable subjects lived on hardware cloth (0.5×1.0 in) floors that covered the wood-chip bedding and had no access to nesting material. The room where cages of uncomfortable subjects lived was constantly illuminated and was heated to $29.5 \pm 0.5^\circ\text{C}$ (The Canadian Council on Animal Care recommends that rats be maintained at $20\text{--}25^\circ\text{C}$). To reduce uncomfortable subjects' access to cover, we presented food to them on the hardware-cloth floors of their cages rather than in the overhead bin that provided some cover for control subjects.

Procedure

The procedure was similar to that of experiment 1. Once observers had spent 1 week in either comfortable or uncomfortable circumstances, we exposed half to demonstrators fed diet mar and the remainder to demonstrators fed diet ani and then determined the intake of each diet by observers during a 24-h choice test.

Results and Discussion

We lost data from one observer when it overturned one of its food cups during testing.

Consistent with the hypothesis that dissatisfied animals are more reliant on socially acquired information than satisfied animals, observers assigned to the uncomfortable condition ate significantly more of their respective demonstrator's diet than did observers assigned to the comfortable condition ($t_{21} = 2.53$, $P < 0.02$; Fig. 2a). There was no significant difference in the change in body weight of observers during their 7 days of maintenance in comfortable and uncomfortable conditions ($t_{21} = 1.12$, $P = 0.27$; Fig. 2b), and no correlation between the weight gain of subjects over 7 days and their reliance on socially acquired information during testing (uncomfortable group: $r_s = 0.14$, $N = 12$, $P = 0.68$; comfortable group: $r_s = -0.26$, $N = 12$, $P = 0.42$).

EXPERIMENT 3: UNCERTAINTY

Boyd & Richerson's (1985, 1988) models consider the relative fitness consequences of individual and social learning in moderately variable environments. The models start with the assumption that individuals must determine the environment that they are in and then choose the behaviour appropriate to that environment. These models lead to the prediction that, when fairly certain as to the environment that they occupy, animals should rely on their own experience, but should depend on socially acquired information when the state of the environment is less certain. Laland (2004) labelled such bias towards depending on social learning in moderately unpredictable environments as a 'copy-when-uncertain' strategy.

In the present experiment, we undertook manipulations to make Norway rats either certain or uncertain about the causal relationship between ingesting an unfamiliar flavour and experience of gastrointestinal upset. We then determined the susceptibility of 'certain' and 'uncertain' rats to socially induced food preferences.

We used a lithium chloride induced toxicosis (Nachman 1970) to teach observers that sampling unfamiliar food was potentially dangerous (Galef & Whiskin 2006, experiment 3) and rendered some of these subjects certain, and others uncertain as to which unfamiliar food they had sampled was the cause of their illness. To produce observers certain as to the cause of their illness, we fed them a food containing a single unfamiliar flavour (cinnamon) and then injected them with toxin. To cause uncertainty, we fed observers a food containing two unfamiliar flavours (cinnamon and cocoa) and, immediately after they had eaten, injected them with lithium chloride. Twenty-four hours following induction of illness, we first allowed subjects assigned to both certain and uncertain conditions to interact with demonstrator rats that had just eaten either anise- or marjoram-flavoured diet and then gave all subjects access to weighed samples of anise- and marjoram-flavoured food for 24 h.

If uncertainty increases reliance on socially acquired information, then during the test, subjects assigned to the uncertain condition, unsure as to whether cinnamon, cocoa or the combination of cinnamon and cocoa caused

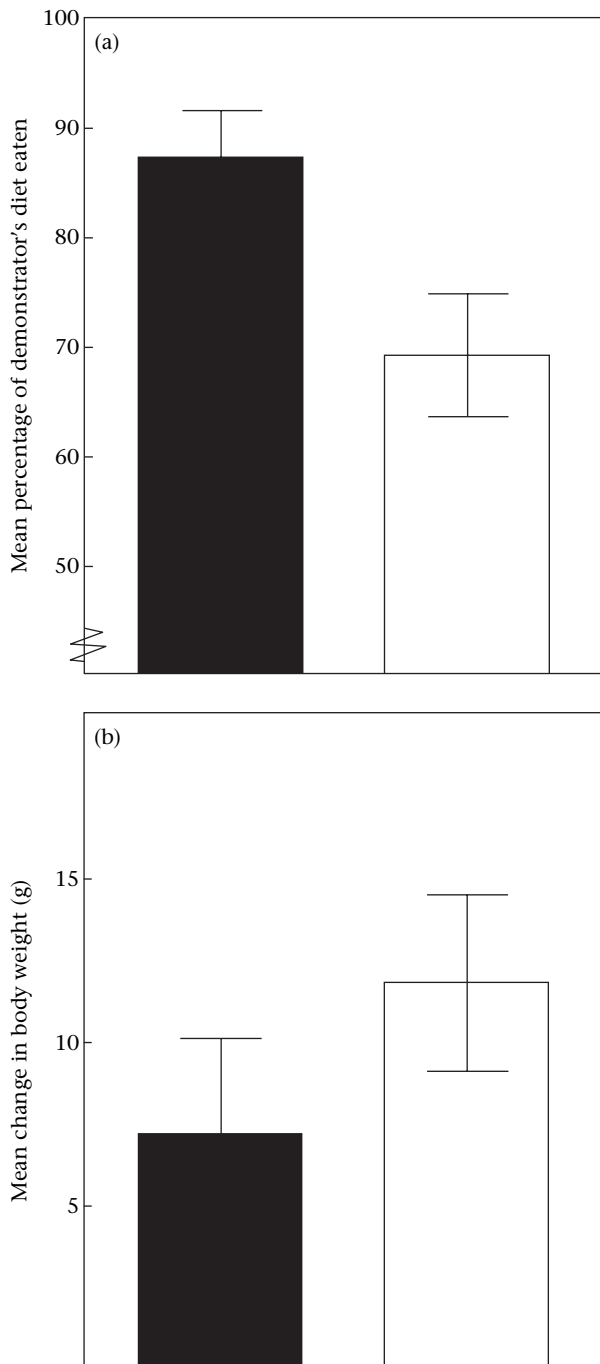


Figure 2. (a) Mean percentage of demonstrator's diet eaten and by uncomfortable (■) and comfortable observers (□), and (b) their mean change in weight during 1 week of maintenance in uncomfortable and comfortable conditions. Flags = ± 1 SEM.

illness, might be expected to eat more of the diet that their respective demonstrators had eaten than subjects assigned to the certain condition.

Methods

Subjects

We randomly assigned 32, 7-week-old, experimentally naïve, female Long-Evans rats (observers) obtained from

Charles River Canada (St Constant, Quebec, Canada) to uncertain ($N = 16$) and certain ($N = 16$) conditions. An additional 32, 8- to 9-week-old female rats that had served as observers in previous experiments served as demonstrators.

Apparatus

The apparatus was that used in experiment 1.

Diets

We composed three diets by mixing (1) 1 g of powdered cinnamon (McCormick Canada, London, Ontario, Canada: diet cin), (2) 2 g of cocoa (Hershey's Canada, Inc., Mississauga, Ontario, Canada: diet coc) or (3) 1 g of powdered cinnamon and 2 g of Hershey's cocoa (diet cin-coc) with sufficient powdered Teklad Rodent Diet 8640 (diet 8640) to bring each diet to 100 g.

Procedure

We placed both demonstrators and observers on a feeding schedule, and gave them access to diet 8640 for 1 h/day for 3 consecutive days. On the third day of scheduled feeding, we gave observers assigned to the certain condition weighed samples of either diet cin ($N = 8$) or diet coc ($N = 8$) for 1 h and immediately thereafter injected them intraperitoneally with 0.5% of their body weight isotonic (0.13 M) lithium chloride solution.

We treated the 16 observers assigned to the uncertain condition exactly as we treated observers assigned to the certain condition except that we fed them diet cin-coc when we fed observers assigned to the certain condition either diet cin or diet coc.

Following induction of illness, we offered all observers pellets of diet 8640 for 24 h, to allow them to recover fully from the effects of injection with lithium chloride. We then introduced a demonstrator rat into each observer rat's home cage for 30 min. Half the observers assigned to the certain and half assigned to the uncertain condition interacted with a demonstrator that had just eaten diet ani for 1 h and the rest of the observers interacted with demonstrators that had just eaten diet mar for 1 h.

Results and Discussion

Consistent with the hypothesis that uncertainty increases reliance on socially acquired information, subjects assigned to the uncertain condition showed a significantly greater reliance on information provided by their respective demonstrators than did observers assigned to the certain condition ($t_{36} = 2.17$, $P < 0.04$; Fig. 3)

GENERAL DISCUSSION

Results of the present experiments offer striking confirmation of predictions from formal models that increases in both dissatisfaction and uncertainty should increase the use that naïve individuals make of information acquired from conspecifics. The possibility that increase in reliance on social information is mediated by a single underlying variable, experience of weight loss, can be rejected on the

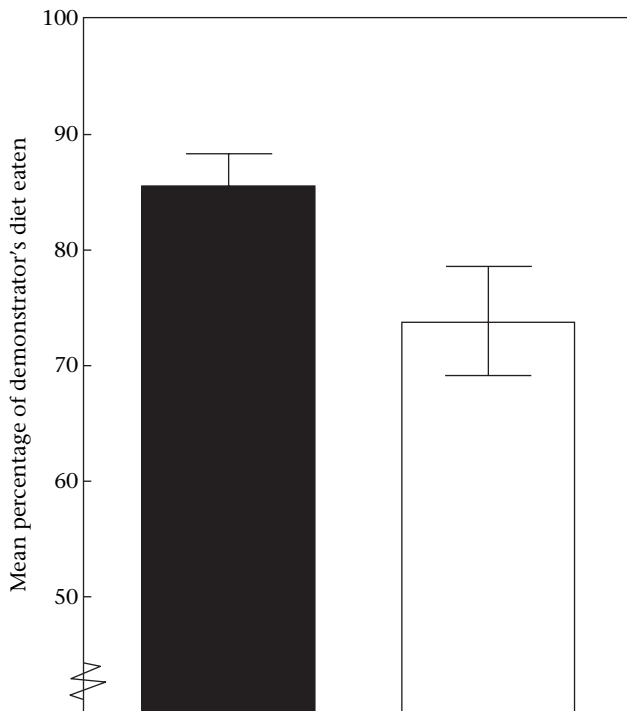


Figure 3. Mean percentage of demonstrator's diet eaten by observers assigned to uncertain (■) and certain (□) conditions. Flags = ± 1 SEM.

basis of the findings that manipulations that failed to affect body weight still affected use of socially acquired information.

When *Boyd & Richerson (1985)* first proposed that social learning was more likely to occur when prior personal experience leaves individuals uncertain as to how to behave, they presented no data in support of that hypothesis. *Kendal et al. (2005)* recently reviewed empirical evidence consistent with it, although most of the experiments that *Kendal et al. (2005)* discuss were not designed specifically to determine whether animals are more likely to attend to socially acquired information when uncertain. The present experiments thus contribute to a small but growing body of literature both directly testing the hypothesis that uncertainty leads to reliance on social learning and producing results consistent with it (e.g. *Coolen et al. 2003; Dewar 2004; Kendal et al. 2004*).

Of course, 'uncertainty' can be defined in many ways. *Kendal et al. (2005)*, for example, identified three reasons why an animal might be uncertain; it might lack relevant prior information or its information might be either unreliable or outdated. Experiment 3 described above involves ambiguous prior information, which could be considered a possible fourth reason for uncertainty.

Like uncertainty, dissatisfaction can have many causes and, in the present paper, we have explored effects on reliance on socially acquired information of only two of them. We know of no previous empirical investigations designed specifically to test the hypothesis that dissatisfied animals are more likely to depend on socially acquired information than satisfied animals and of no circumstantial evidence relevant to that issue. We do not know why dissatisfaction has received less attention than uncertainty

as a cause of increased reliance on social learning. However, manipulations likely to alter the certainty of a potential social learner concerning its environment are fairly commonly used as independent variables in studies of learning generally, whereas manipulations altering individuals' level of satisfaction are rare.

It is important to note that in the experiments reported here, we have explored effects of putative dissatisfaction and uncertainty in only one model system, in only a single sex and in only one species. Because, in nature, Norway rats are a central-place foraging species, the conditions under which they increase reliance on socially acquired information may be unusual. Quite possibly, in other systems or species, other results would be obtained, and although weight loss and illness do not seem to be a necessary substrate of increased attention to social cues, there must surely be neurological or endocrine correlates of increased reliance on social learning awaiting discovery. As recent reviews of the literature on trade-offs between social and asocial learning suggest (*Kendal et al. 2004; Galef 2006*), we are only starting to understand the conditions that affect the extent to which animals rely on socially acquired information when choosing between behavioural alternatives.

Acknowledgment

This research was supported by a Natural Sciences and Engineering Research Council Discovery Grant to B.G.G., Jr.

References

- Beck, M. & Galef, B. G., Jr.* 1989. Social influences on the selection of a protein-sufficient diet by Norway rats. *Journal of Comparative Psychology*, **103**, 132–139.
- Boyd, R. & Richerson, P. J.* 1985. *Culture and the Evolutionary Process*. Chicago: University of Chicago Press.
- Boyd, R. & Richerson, P. J.* 1988. An evolutionary model of social learning: the effects of spatial and temporal variation. In: *Social Learning: Psychological and Biological Perspectives* (Ed. by T. Zentall & B. G. Galef, Jr), pp. 29–48. Hillsdale, New Jersey: Erlbaum.
- Boyd, R. & Richerson, P. J.* 1995. Why does culture increase human adaptability? *Ethology and Sociobiology*, **16**, 125–143.
- Coolen, I., van Bergen, Y., Day, R. L. & Laland, K. N.* 2003. Species difference in adaptive use of public information in sticklebacks. *Proceedings of the Royal Society of London, Series B*, **270**, 2413–2419.
- Dewar, G.* 2004. Social and asocial cues about new food: cue reliability influences intake in rats. *Learning and Behavior*, **32**, 82–89.
- Galef, B. G., Jr.* 2005. Social learning. In: *The Behavior of the Laboratory Rat: a Handbook with Tests* (Ed. by I. Q. Whishaw & B. Kolb), pp. 363–370. Oxford: Oxford University Press.
- Galef, B. G., Jr.* 2006. Theoretical and empirical approaches to understanding when animals use socially acquired information and from whom they acquire it. In: *Essays in Animal Behaviour: Celebrating 50 Years of Animal Behaviour* (Ed. by J. R. Lucas & L. W. Simmons), pp. 161–182. San Diego: Academic Press.
- Galef, B. G., Jr.* 2007. Social learning in rodents. In: *Rodents Societies* (Ed. by P. W. Sherman & J. Wolff), pp. 207–215. Chicago: University of Chicago Press.

- Galef, B. G., Jr & Whiskin, E. E. 2004. Effects of environmental stability and demonstrator age on social learning of food preferences by young Norway rats. *Animal Behaviour*, **68**, 897–902.
- Galef, B. G., Jr & Whiskin, E. E. 2006. Increased reliance on socially acquired information while foraging in risky situations? *Animal Behaviour*, **72**, 1169–1176.
- Galef, B. G., Jr & Wigmore, S. W. 1983. Transfer of information concerning distant foods: a laboratory investigation of the 'information-centre' hypothesis. *Animal Behaviour*, **31**, 748–758.
- Galef, B. G., Jr, Wigmore, S. W. & Kennett, D. J. 1983. A failure to find socially mediated taste-aversion learning in Norway rats (*R. norvegicus*). *Journal of Comparative Psychology*, **97**, 358–363.
- Galef, B. G., Jr, Kennett, D. J. & Wigmore, S. W. 1984. Transfer of information concerning distant foods in rats: a robust phenomenon. *Animal Learning and Behavior*, **12**, 292–296.
- Galef, B. G., Jr, Beck, M. & Whiskin, E. E. 1991. Protein deficiency magnifies social influences on the food choices of Norway rats (*Rattus norvegicus*). *Journal of Comparative Psychology*, **105**, 55–59.
- Giraldeau, L.-A., Valone, T. J. & Templeton, J. J. 2002. Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London*, **357**, 1559–1566.
- Kendal, R. L., Coolen, I. & Laland, K. N. 2004. The role of conformity in foraging when personal and social information conflict. *Behavioral Ecology*, **5**, 269–277.
- Kendal, R. L., Coolen, I., van Bergen, Y. & Laland, K. N. 2005. Trade-offs in the adaptive use of social and asocial learning. *Advances in the Study of Behavior*, **35**, 333–379.
- Laland, K. N. 2004. Social learning strategies. *Learning and Behavior*, **32**, 4–14.
- Nachman, M. 1970. Learned taste and temperature aversions due to lithium chloride sickness after temporal delays. *Journal of Comparative and Physiological Psychology*, **73**, 22–30.
- Rogers, A. R. 1988. Does biology constrain culture? *American Anthropologist*, **90**, 819–831.
- Schlag, K. H. 1998. Why imitate and if so, how? *Journal of Economic Theory*, **78**, 130–156.