Strategies for Social Learning: Testing Predictions from Formal Theory

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I. Introduction

Although the past two decades have seen a significant increase in both theoretical analyses and experimental studies of social learning in animals, there has been relatively little productive interchange between theoreticians and empirical investigators; formal models have had relatively little impact on the experiments undertaken by empiricists, and experimental data have played little role in the construction of models. As Laland (2004, p. 12) has suggested, ‘‘There is a need for empirical research explicitly evaluating the strategies proposed by theoretical models.’’

Animals can acquire adaptive information either directly, as a result of their own personal experience of the consequences of engaging in alternative behaviors, or indirectly, using various aspects of the behavior of others to guide development of their own behavioral repertoires. Personal sampling results in acquisition of accurate, current information about the environment. However, the errors that are an inescapable part of individual, trial-and-error learning can be costly, and personal exploration of the environment not only requires time and energy but also increases exposure to both predation and other environmental threats.

Social learning has the potential to reduce costs of individual learning. However, in environments that change over time, social learning is likely to be less reliable than individual learning because, in changing environments, social information can be outdated. Similarly, in environments that vary spatially, there is a risk that potential models are engaged in behavior more suited to environmental conditions other than those facing a potential social learner. Relative reliance on social and individual learning can thus be

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viewed as involving a tradeoff between accuracy and cost (e.g., Boyd and Richerson, 1985, 1988; Enquist et al., 2007; Giraldeau et al., 2002; Kendal et al., 2005; Laland, 2004; Rogers, 1988).

Although, intuitively, it might seem that an individual would always increase its fitness by avoiding the potential costs of individual learning, formal, mathematical analyses of the tradeoffs between relatively inexpensive, but potentially inaccurate, social learning and relatively expensive, but accurate, individual learning indicate that both the circumstances under which an individual learns and the characteristics of those that it learns from can affect the relative fitness value of engaging in social as compared with individual learning (Boyd and Richerson, 1985, 1988; Enquist et al., 2007; Giraldeau et al., 2002; Kendal et al., 2005; Laland, 2004; Rogers, 1988).

Table I, modified from Laland (2004), provides a list, based on an extensive theoretical literature (reviewed in Laland, 2004), of predictions from formal theory as to when animals should increase their reliance on social cues (''when strategies'') and the characteristics of individuals whose behavior should provide the most valuable information (''who strategies''). These ''when strategies'' and ''who strategies,'' are, in essence, information-gathering tactics that formal models indicate should have been favored by natural selection.

TABLE I

SUMMARY OF PREDICTIONS FROM FORMAL MODELS OF SOCIAL LEARNING STRATEGIES (ADAPTED FROM LALAND, 2004)

''When'' strategies of social learning
Copy when established behavior is unproductive
Copy when asocial learning is costly
Copy when uncertain
Copy when dissatisfied
Copy when the environment is relatively stable[a]
''Who'' strategies of social learning
Copy the majority
Copy successful individuals
Copy good social learners
Copy kin
Copy familiar individuals
Copy older individuals

[a] Not considered in Laland (2004).

A. Tests of Predictions from Theory

Both Galef (2006) and Kendal et al. (2005) have recently provided general reviews of findings in the literature that largely by happenstance, provide evidence relevant to predictions from formal models, and I shall not repeat that exercise here. Rather, I shall review a series of experiments conducted over the past several years in which my coworkers and I have used social learning of food preferences by Norway rats, *Rattus norvegicus*, as an experimental system in which to investigate predictions from theoretical models as to when animals should increase their reliance on social information relative to individual learning and whom they should select as models. Below, I summarize and discuss the results of both of these studies and of other animal studies explicitly testing predictions from formal models of social learning.

B. The Experimental System: Norway Rats' Social Learning About Foods

Studies of the role of social learning in the development of feeding repertoires of Norway rats show that rats' food choices are open to many kinds of socially induced bias (for review, see Galef, 1996). Possibly the most potent of the many social-learning processes involved in the development of rats' food choices is a robust enhancement of the preference of a naïve rat (''an observer'') for a food following interaction with a ''demonstrator'' rat that has recently eaten that food (Galef and Wigmore, 1983). The breath of a demonstrator rat carries odor cues that enable other rats to identify the foods that it has recently eaten. After such diet-identifying cues are experienced by an observer rat together with contextual cues, metabolic products that are a normal part of rats' breath, an observer rat exhibits a long-lasting, enhancement of its preference for foods that its demonstrator ate (Galef and Stein, 1985; Galef et al., 1985, 1988).

Rats' social transmission of food choice is unlikely to be a laboratory artifact. Free-living, wild Norway rats are central-place foragers that should have ample opportunity to extract information from colony mates returning to their shared burrow between foraging bouts. Indeed, field observations indicate that the food choices of wild rats are strongly influenced by the food choices that others of their social group are making. For example, Steiniger (1950), an applied ecologist who investigated methods to increase the efficiency of poison baits used in rodent control, observed that if the same poison bait were used in an area for an extended period of time, despite initial success, later acceptance of the bait was extremely poor. Naïve young that were born to colony members that had survived their initial ingestion of the poison bait and had learned to avoid eating it, ate only foods that adults of their colony were eating and would not even taste the poison bait for themselves so long as knowledgeable adults were present in their colony. The young rats appeared to be learning from their elders either what foods to eat or what foods to avoid eating (Galef, 1985).

Our laboratory procedure for exploring such social transmission of information concerning foods in Norway rats consists of three stages (Galef, 2002) that provide a laboratory analogue of interactions that might occur in a rat burrow between a returning, successful forager and a burrow mate. We first (stage 1) feed a demonstrator rat one of two roughly equally palatable, distinctively flavored foods, diets A and B. We then (stage 2) place the recently fed demonstrator rat in the home cage of an observer rat and allow the observer and demonstrator to interact freely before (stage 3) removing the demonstrator and offering the observer a choice between diets A and B, one of which is the diet that its demonstrator ate.

We invariably find that during stage 3, observer rats show an enhanced preference for whatever diet their demonstrator ate during step 2 (for review, see Galef, 1996). Mammals ranging from short-tailed fruit bats (*Carollia perspicillata*; Ratcliffe and ter Hofstede, 2005) to spotted hyenas (*Crocuta crocuta*; Yoerg, 1991) have been shown, similarly, to learn from conspecifics what foods to eat, though the behavioral processes supporting such social learning have been investigated more thoroughly in Norway rats than in other species.

II. Testing Formal Models of Social Learning

A. When Strategies

Theory suggests five circumstances in which animals faced with a decision should increase in their reliance on socially acquired information (Table I; see Laland, 2004 for review): (1) when individual learning is unproductive, (2) when individual learning is costly, (3) when uncertain, (4) when the environment is relatively stable, and (5) when dissatisfied. Below, I describe experiments in which Norway rats' social learning about foods was used as an empirical system in which to examine each of these five predictions.

1. Copy When Individual Learning Is Unproductive

Boyd and Richerson (1988, p. 44) suggested some years ago, in discussing unproductive behavior, that "... for a particular species, there will be some aspects of diet about which it will be difficult for individuals to learn what is best, but there will be other aspects about which it will be easy for individuals to learn. The models predict that the former will be acquired disproportionately by social learning and the latter disproportionately by individual learning.''

Like other mammals examined to date, Norway rats find it easy to detect some nutrients in potential foods and difficult to detect others. For example, the first time that a rat experiences a sodium deficiency and is offered a cafeteria of foods only one of which contains a sodium salt, the rat will prefer to ingest the food that is rich in sodium and will do so within minutes of first sampling it (Epstein and Stellar, 1955; Friedman, 2000; for review, see Stricker, 2000). In contrast, protein-deficient rats find it difficult to learn which of several foods presented to them contains protein (for review, see Friedman, 2000; Galef, 2000). Depending on details of the experimental situation, it can take from days to weeks for a rat to learn to focus its intake on a single protein-rich food presented in a cafeteria together with several protein-poor foods (Galef, 1991).

Our procedure for testing Boyd and Richerson's (1988) prediction was straightforward (Galef and Whiskin, 2008b). First, we induced either a sodium deficiency or a protein deficiency in rats by feeding them either sodium-deficient or protein-deficient diet for seven consecutive days. We then used these deficient animals as observers in our three-stage procedure for social induction of food preference. We offered observers that had interacted in stage 2 with a demonstrator rat that had eaten either cinnamon-flavored or cocoa-flavored food in stage 1, a choice in stage 3 between cinnamon- and cocoa- flavored foods rich in both protein and sodium.

If, as Boyd and Richerson's (1988) model predicts, animals that, individually, are unable to make productive decisions as to what to eat rely more heavily on socially acquired information than animals able to make productive food choices, then protein-deficient rats should show greater social influence on their food choices than sodium-deficient rats. In fact, whether severely or moderately deprived, protein-deprived observer rats relied more heavily on socially acquired information than did sodium-deprived observer rats (Fig. 1), confirming Boyd and Richerson's (1988) prediction.

2. *Copy When Dissatisfied*

Laland (2004) categorized copy-if-dissatisfied as a ''who strategy'' reflecting its origins in Schlag's (1998) prediction that animals should tend to copy individuals more successful than themselves. In particular, Schlag (1998) proposed that an individual should adjust its probability of copying to make that probability proportional to the difference in success between itself and an individual that it might copy. Laland (2004) labeled this a ''copy-if-

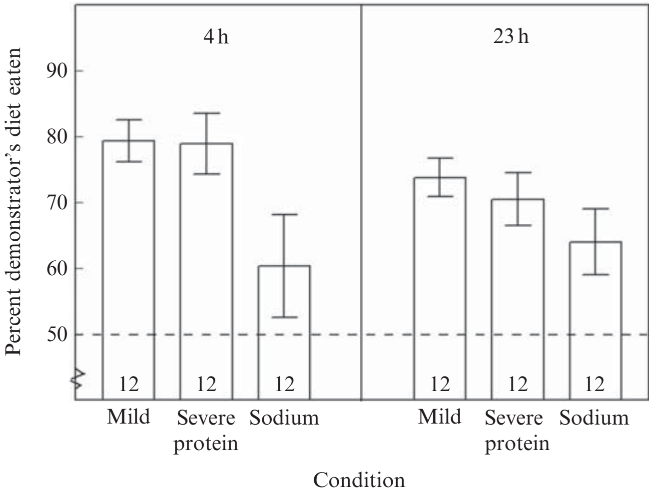

FIG. 1. Mean ± S.E. percentage demonstrators' diet eaten by protein-deficient and sodium-deficient observers during 4 h (left panel) and 23 h (right panel) of testing Number in histograms = *N*/group (from Galef and Whiskin, 2008b reprinted with permission of Elsevier).

better'' strategy and preferred an alternative model that Schlag (1998) had called ''proportional reservation'' and Laland (2004) subsequently labeled ''copy-if-dissatisfied.''

In copy-if-dissatisfied, the reward that an individual receives for its current behavior is positively related to its current level of satisfaction, and the probability that it will copy others is inversely related to its current level of satisfaction. Schlag (1998) had shown that, at evolutionary equilibrium, copy-if-better and copy-if-dissatisfied have equivalent fitness consequences. However, because copy-if-dissatisfied requires evaluation only of one's own success, not of the relative success of oneself and of others, copy-if-dissatisfied seems more likely than copy-if-better to have evolved (Laland, 2004). Consequently, we investigated the possibility that rats would be more likely to ''copy if dissatisfied,'' which is a ''when strategy.''

a. Copy when sick We proceeded on the premise that, relative to a healthy animal, a sick animal, for example, one deprived of a needed nutrient or injected with a toxin, would have a reduced level of satisfaction. Sick animals would, therefore, be predicted on both Laland (2004) and Schlag's (1998) models to be more likely to copy the food choices of others than healthy animals.

Results of previous experiments in our laboratory that were not explicitly designed to examine effects of dissatisfaction on reliance on socially acquired information were consistent with the prediction that dissatisfied animals would be more reliant than healthy animals on socially acquired information. For example, when Galef et al. (1991) compared the effectiveness of demonstrator rats in influencing the food choices of protein-replete and protein-deprived observers, we found protein-deprived observers significantly more susceptible to social influence than protein-replete observers.

In explicit tests of the hypothesis that dissatisfied rats are more susceptible to social influence than satisfied rats, we made observer rats dissatisfied in three different ways and then compared the susceptibility to social influence on food preference of dissatisfied observers and relevant controls.

b. Diluted diets We maintained rats randomly assigned to the dissatisfied condition for 7 days on powdered rat chow diluted 15% by weight with cellulose, a nonnutritive filler (Galef et al., 2008). When given a choice between the calorically dilute diet and undiluted chow, rats will eat eight times as much undiluted as diluted food, indicating that they find the diluted food distasteful. None the less, subjects given access only to calorically dilute chow increase their intake to compensate for dilution and gained weight normally.

Despite being able to maintain their body weights and presumably remain healthy, observer rats fed only diluted diet had to eat a relatively unpalatable food and experienced greater food-handling costs than rats maintained on undiluted diet. Thus, rats maintained on diluted diet should have been healthy, but, we hoped, somewhat dissatisfied. Indeed, as Laland's (2004) and Schlag's (1998) model would predict, rats maintained on calorically diluted rat chow exhibited greater social influence on their food choices than did more-satisfied rats maintained on unadulterated chow (Fig. 2).

c. Unpalatable diets We also maintained observer rats for 7 days on a diet made relatively unpalatable by the addition of cayenne pepper (a substance rats find aversive) and found that these observer rats, when subsequently allowed to interact with a demonstrator rat fed either cinnamon- or cocoa-flavored diet and then offered a choice between those two diets showed significantly greater social influence on their food choices than did rats maintained for 7 days on a relatively palatable base diet (Galef and Whiskin, unpublished data; Fig. 3).

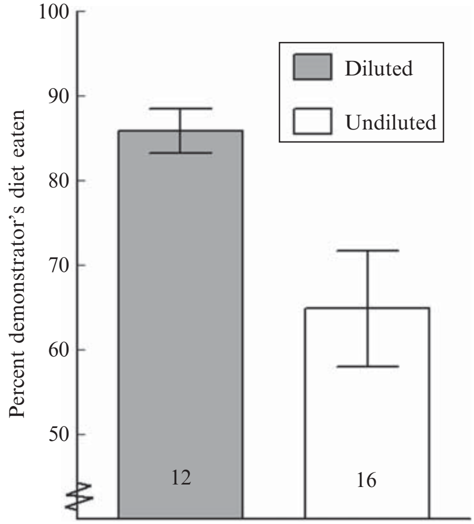

FIG. 2. Mean ± S.E. percentage demonstrator's diet eaten by observers fed either diluted or undiluted rat chow for 1 week before interacting with a demonstrator. Number in histograms = *N*/group (from Galef et al., 2008, reprinted with permission of Elsevier).

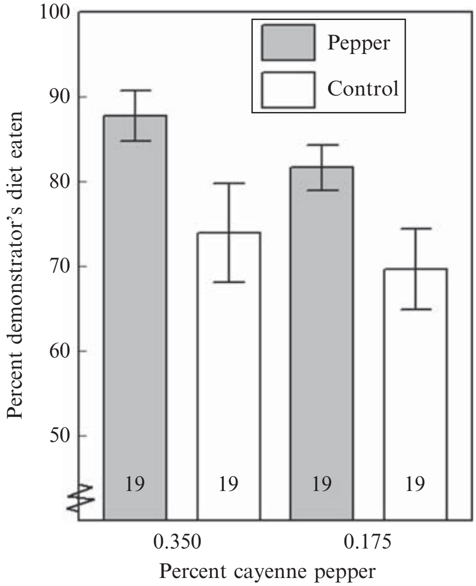

FIG. 3. Mean ± S.E. percentage demonstrator's diet eaten by observers fed either cayenne-pepper flavored rat chow (pepper groups) or unflavored rat chow (control) for 1 week before interacting with a demonstrator. Number in histograms = *N*/group (Galef and Whiskin, unpublished data).

d. Uncomfortable living conditions We also attempted to make rats dissatisfied by maintaining them for 7 days in uncomfortable circumstances (Galef et al., 2008). We housed rats assigned to the uncomfortable condition in a cage with a wire-mesh floor, placed the cage in a constantly illuminated room and heated the room to an uncomfortably warm (for rats) 30 °C. Observer rats made uncomfortable, like those maintained on diluted or unpalatable diets, were significantly more reliant on socially-acquired information than observer rats maintained under standard laboratory conditions (Fig. 4). Thus, the results of three experiments, two previously published in peer-reviewed journals and one not, were consistent in supporting the prediction that dissatisfied animals would be more susceptible than satisfied animals to social influence on their food choices.

3. Copy When Uncertain

Boyd and Richerson's (1985, 1988) population genetics-based models consider the fitness consequences of reliance on individual and social learning as a function of the degree of environmental variability. Starting with the assumption that individuals must determine the current state of the environment before they can engage in behavior appropriate to that

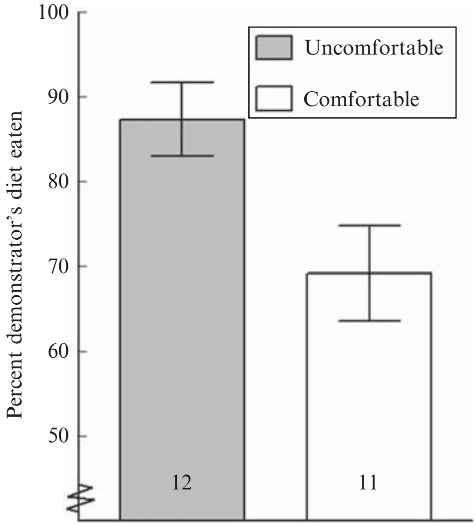

FIG. 4. Mean ± S.E. percentage demonstrator's diet eaten by observers maintained under either comfortable or uncomfortable conditions for 1 week before interacting with a demonstrator. Number in histograms = *N*/group (from Galef et al., 2008, reprinted with permission of Elsevier).

environment, the models predict that individuals uncertain as to which of two environments they are in should be more reliant on socially acquired information than individuals that are sure of the current state of the world. Laland (2004) labeled this bias toward reliance on social learning a ‘‘copy when uncertain’’ strategy, and. we have carried out two experiments, one that has undergone peer review, and one that has not, examining effects of uncertainty on reliance on socially acquired information (Galef and Whiskin, unpublished data; Galef et al., 2008).

a. Uncertainty as to the cause of illness We first undertook manipulations to make Norway rats either certain or uncertain about the causal relationship between ingesting an unfamiliar flavor and experiencing gastrointestinal upset. All subjects were equally ill; they differed only in the certainty with which they could attribute their illness to specific foods that they had ingested. We then examined the susceptibility of these ‘‘certain’’ and ‘‘uncertain’’ rats to socially induced food preferences (Galef et al., 2008).

To produce observer rats certain as to the cause of their illness, we fed them a food with a single unfamiliar flavor (cinnamon) and then injected them with a toxin (lithium chloride). To cause uncertainty in observer rats, we fed them a food containing two unfamiliar flavors (cinnamon and cocoa) and then injected them with lithium chloride. Rats assigned to the former group were certain as to the cause of their illness. Whereas those assigned to the latter condition could not know whether cinnamon, cocoa, or the combination of cinnamon and cocoa was related to their discomfort. After poisoning, we allowed subjects assigned to both conditions to interact with demonstrator rats that had just eaten either anise- or marjoram-flavored food and then gave all observers access to weighed samples of anise- and marjoram-flavored food for 23 h.

If uncertainty increases reliance on socially acquired information, then during the 23-h choice between anise- and marjoram-flavored foods, uncertain subjects should have eaten more of the diet that their respective demonstrators had eaten than subjects certain as to the cause of their illness. Consistent with Boyd and Richerson’s (1985, 1988) models, uncertain rats showed a significantly greater preference for their respective demonstrators’ diets than did certain rats (Fig. 4 in Galef et al., 2008).

b. Uncertainty as to the safety of unfamiliar foods A rat presented with unfamiliar potential foods should be less certain as to whether those foods are safe to eat than a rat presented with foods it has previously eaten without ill effect. If so, a rat choosing between unfamiliar foods should be more uncertain, and therefore more reliant on socially acquired information than a rat choosing between foods that it previously ate and found safe.

We fed one group of observer rats both cinnamon-flavored chow and cocoa-flavored chow for 24 h while we fed another group of observer rats unflavored chow. We then allowed each member of both groups to interact with a demonstrator rat fed either cinnamon- or cocoa-flavored diet before offering each observer a choice between cinnamon- and cocoa-flavored diets.

As predicted from the hypothesis that uncertainty increases reliance on social learning, demonstrators had significantly greater influence on the food choices of rats choosing between unfamiliar than familiar foods (Galef and Whiskin, unpublished data; Fig. 5). Consistent with this unpublished finding, Forkman (1991) and Visalberghi and Fragaszy (1995) have reported, respectively, that Mongolian gerbils (*Meriones unguiculatus*) and capuchin monkeys (*Cebus apella*) increased their consumption of food in the presence of feeding conspecifics when the food was unfamiliar, but not when it was familiar.

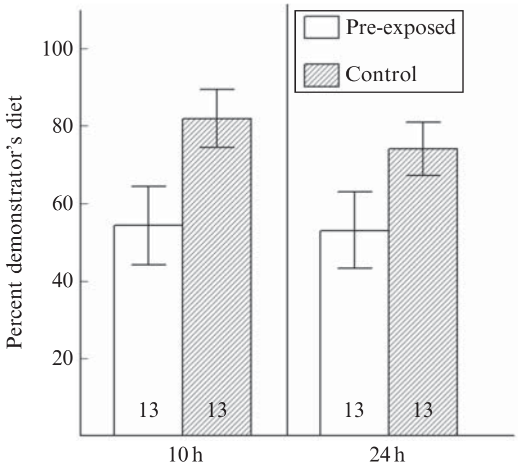

Fig. 5. Mean ± S.E. percentage demonstrator's diet eaten after 10 and 24 h by observer rats offered a choice between cinnamon- and cocoa-flavored diet following maintenance for 7 days with *ad libitum* access to either both cinnamon- and cocoa- flavored rat diet or to unflavored rat chow. Number in histograms = *N*/group (Galef and Whiskin, unpublished data).

4. *Copy When Individual Learning is Costly*

Sampling unfamiliar, potentially toxic substances has greater potential cost than ingesting familiar foods known to be safe. Consequently, the finding that rats choosing between two foods are less reliant on socially acquired information when those foods are familiar than when they are unfamiliar (Galef and Whiskin, unpublished data) is consistent not only with the prediction that uncertain rats should be more reliant on social information than certain rats, but also with the prediction from formal models that animals should increase reliance on socially acquired information as the potential cost of individual learning increases (Boyd and Richerson,1985; Feldman et al., 1996; Kendal et al., 2005). For example, as the risk of predation rises so does the cost of individual assessment of alternatives (e.g., Lima and Dill, 1990; Sih, 1994), and theory therefore predicts that dependence on socially acquired information should increase when cues are present that indicate enhanced risk of predation.

Cues indicating enhanced predation risk can be either direct (if a predator or cues directly associated with the presence of a predator are detected, e.g., Powell and Banks, 2004) or indirect (if environmental cues indicate that an attacking predator would be likely to be successful), for example, when a potential prey animal is far from shelter (e.g., Orrock et al., 2004). We examined effects of both direct and indirect cues of predation risk on rats' social learning of food preferences.

a. ***Direct cues of predation risk*** Assessing the relative nutritive value of alternative potential foods, requires that an individual sample them repeatedly (Beck et al., 1988; Rozin, 1969; Rozin and Schulkin, 1990), and such sampling can necessitate spending time at a distance from cover and therefore at heightened risk of predation. Consequently, cues of enhanced predation risk in an environment should decrease individual assessment of alternative foods and increase reliance on social information.

To examine effects of direct risk of predation on reliance on socially acquired information, we first exposed observer rats to conspecific demonstrators that had eaten either cinnamon- or cocoa-flavored diet. We then placed each observer rat in a large floor enclosure and offered it a choice, for 24 h, between cinnamon- and cocoa-flavored diets. We exposed observers assigned to experimental conditions to one of three types of direct cues of predation risk: (1) a pair of domestic cats, *Felis catus*, roaming free in a room containing a caged (and therefore safe) rat, or (2) a pair of cats caged some distance from the rat's cage either throughout the 24-h test period, or (3) for the first 4 h of the 24-h test period (Galef and Whiskin, 2006).

We treated control subjects assigned to each of these three conditions just as we treated experimental subjects, except that we did not expose control subjects to any cues of predation.

Although observer rats showed clear indications of a response to the physical presence of cats, eating substantially less during 24 h than observers not exposed to cats, we found no indication that observers assigned to experimental conditions relied more heavily than observers assigned to control conditions on information provided by demonstrators (Galef and Whiskin, 2006; Fig. 6). To the contrary, the effect of the presence of cats was, if anything, to reduce attention to social information, possibly by reducing the "choosiness" of observers when exposed to direct cues of enhanced risk of predation (e.g., Briggs et al.,1996; Crowley et al., 1991; Real, 1990). Although none of the differences between groups in Fig. 6 was statistically reliable, contrary to prediction from theory, observer rats assigned to the control group in each of the three conditions ate more, not less, of the diet that their demonstrator had eaten than observer rats feeding in the presence of predators.

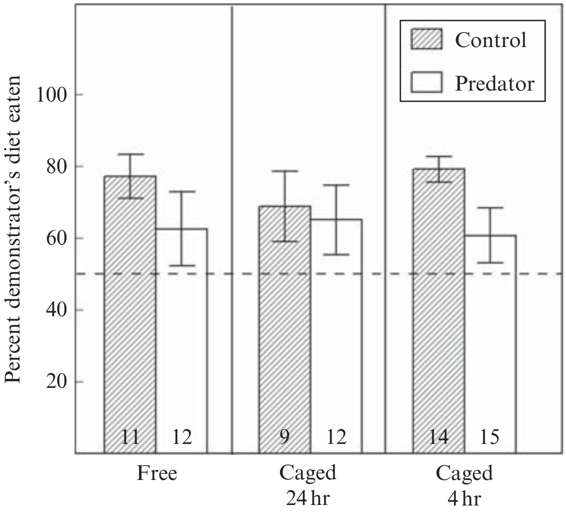

Fig. 6. Mean ± S.E. percentage demonstrator's diet eaten during testing when observers were tested in the presence or absence of a predator. Dashed line = expected percentage demonstrator's diet eaten by observers if observers' food choices were not influenced by prior interaction with demonstrators. Number in histograms = *N*/group (from Galef and Whiskin, 2006, reprinted with permission of Elsevier).

When we subsequently exposed observer rats to cat odor during testing by placing a piece of cloth rubbed on a cat near the food bowls available to observer rats, presumably providing weak direct cues of predation risk relative to the actual presence of cats, observer rats preferred the diet their respective demonstrators had eaten, but still showed no greater reliance on socially acquired information than rats choosing between foods in the absence of cat odor (Galef and Yarkovsky, 2009; Fig. 7).

b. Indirect cues of predation risk The farther an animal ventures from cover when foraging and the more exposed a feeding site, the greater its risk of predation. Consequently, if indirect cues of predation risk increase reliance on socially acquired information, then animals feeding far from a harborage site or in the open should be more reliant on socially acquired information than animals either foraging near a harborage site or eating whilst under cover.

We first gave all observer rats an opportunity to interact with demonstrator rats fed either cinnamon- or cocoa-flavored diet, then in a 2 × 2 design, varied the distance from harborage site to feeding site (near or far) and the presence or absence of cover at the feeding site where cinnamon- and

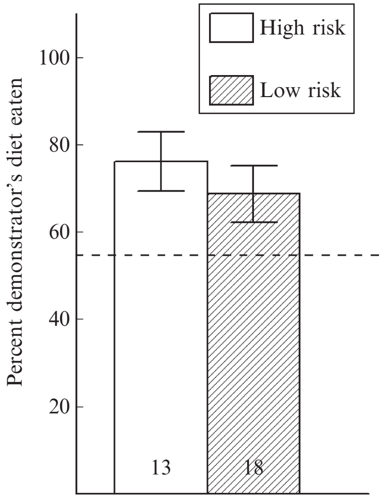

Fig. 7. Mean ± S.E. percentage demonstrator's diet eaten during testing by observers assigned to high-risk and low-risk conditions. Dashed line = expected percentage demonstrator's diet eaten by observers' if observers' food choices were not influenced by prior interaction with demonstrators. Number in histograms = *N*/group (from Galef and Yarkovsky, 2009, reprinted with permission of Elsevier).

cocoa- flavored foods were available. We found no effect of either distance to a harborage site or presence of cover at a feeding site on observer rats' reliance on socially acquired information. Unfortunately, we also found no effect of indirect cues of predation on the amount that observer rats ate during testing, suggesting that their foraging behavior may have been unaffected by the indirect cues of predation that we were using (Galef and Whiskin, 2006).

In a subsequent study, we attempted to magnify the effects of indirect cues of predation on foraging by comparing the behavior of observer rats that could both move from harborage site to feeding site and feed whilst under cover with that of observer rats that had both to travel a meter to food and to eat in the open. In this experiment, although observers moving and feeding under cover ate significantly more (9.4 ± 1.1 g) than observers moving and feeding in the open (6.0 ± 65 g), we still found no effect of indirect cues of predation risk observers' reliance on socially acquired information (Galef and Yarkovsky, 2009; Fig. 8).

Studies of foraging behavior in guppies (*Poecelia reticulate*) and sticklebacks (*Gasterosteus aculeatus* and *Pungitius pungitius*) have been more successful than our studies with Norway rats in providing evidence of

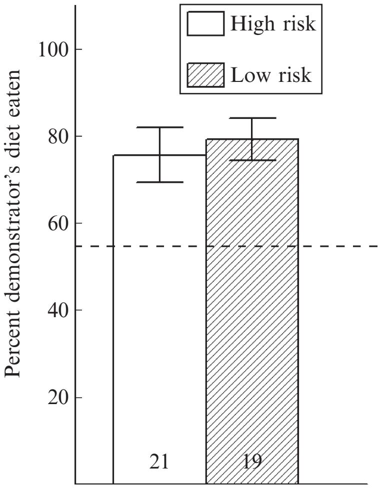

FIG. 8. Mean ± S.E. percentage demonstrator's diet eaten during testing by observers assigned to high-risk and low-risk conditions. Dashed line = expected percentage demonstrator's diet eaten by observers if observers' food choices were not influenced by prior interaction with demonstrators. Number in histograms = *N*/group (from Galef and Yarkovsky, 2009, reprinted with permission of Elsevier).

increased reliance on socially acquired information in the face of indirect cues of predation risk. For example, Kendal et al. (2004) report that guppies rely more heavily on social information in choosing a foraging site when the choice involves leaving the protection of contact with a shoal than when it does not, and Coolen et al. (2003) found that three-spined sticklebacks, that are at greater risk of predation than nine-spined sticklebacks, are also more susceptible to social influence when selecting a feeding site. However, studies of effects of direct cues of predation risk on social influences on mate choice in guppies, like studies of direct cues of predation risk on food choice in rats, have failed to provide evidence of enhanced reliance on social information in the presence of predators (Briggs et al., 1996)

c. Increased risk of ingesting toxins Although tests of predictions from formal models concerning effects of increased cost of individual learning on reliance on social learning have generally looked at effects of threats of predation on reliance on social learning, factors other than predation risk that also increase the cost of individual assessment should similarly increase reliance on social learning (e.g., Dewar, 2004). In particular, observer rats with experiences suggesting that sampling unfamiliar foods can lead to illness might be expected to increase their reliance on socially acquired information when subsequently choosing between additional unfamiliar foods.

We fed observer rats assigned to experimental conditions either one, two, or four different unfamiliar foods and injected them with a mild toxin after they ate each, whereas we injected rats assigned to corresponding control conditions with saline solution after they ate each of one, two or four unfamiliar foods. We then allowed all observer rats to interact with demonstrator rats that had been fed one of two additional diets that were unfamiliar to the observers before allowing observers to choose between those two diets. Experience with toxic foods had no effect on observers' use of socially acquired information (Galef and Whiskin, 2006; Galef and Yarkovsky, 2009).

5. *Copy When the Environment Is Relatively Stable*

A number of models (e.g., Aoki and Feldman, 1987; Boyd and Richerson, 1988; Laland et al., 1996; Rogers, 1988) predict that social learning is more likely to be adaptive when environments are relatively stable than when environments are highly unpredictable because in rapidly changing environments, the behavior of a potential model is likely to reflect past rather than current conditions. Consequently, copying the behavior of others in rapidly changing environments may prove maladaptive.

We maintained observer rats that we had assigned to an experimental group for 12 days under rapidly changing conditions (each day, we fed each observer a different food at a different time of day for a different length of time, and moved each observer from one cage to another). We left observer rats assigned to a control group in the same cage for 12 days (but removed each observer from and returned it to its cage daily) and fed each of the observers on one of the 27 feeding regimes to which we exposed each observer assigned to the experimental condition (Galef and Whiskin, 2004).

After 12 days of exposure to either relatively stable or highly variable environments, each observer rat interacted with a demonstrator rat fed a diet unfamiliar to its observer and the observer then chose between that diet and a second unfamiliar diet. As predicted, although both groups of observer rats showed significantly enhanced preferences for their respective demonstrators' diets, interaction with demonstrator rats had a significantly greater effect on the food choices of observer rats assigned to the to the stable than to the highly variable condition (Fig. 9).

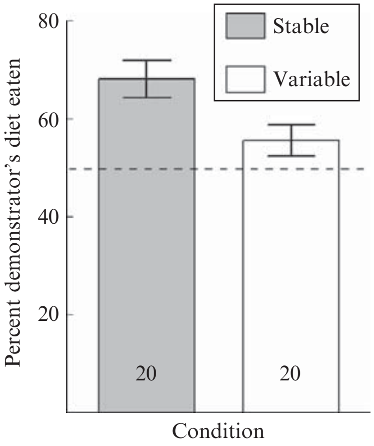

FIG. 9. Mean ± S.E. percentage demonstrator's diet eaten during testing by observers assigned to stable and variable conditions. Dashed line = expected percent demonstrator's diet eaten by observers if observers' food choices were not influenced by prior interaction with demonstrators. Number in histograms = *N*/group (from Galef and Whiskin, 2004, reprinted with permission of Elsevier).

B. WHO STRATEGIES

Formal models make predictions concerning not only the conditions that should lead to enhanced reliance on social information, but also as to the characteristics of individuals whose behavior would be most advantageous to copy. Like the ''when strategies'' discussed in the preceding section, these ''who strategies'' are open to empirical investigation.

1. Copy Older Individuals

Survival to adulthood depends on adequate response to myriad environmental challenges. Consequently, behaviors engaged in by adults are likely to be well adapted to the demands of the locales in which those adults live. Juveniles are more likely than adults to be in the error phase of trial-and-error learning, and a naïve, young individual might, therefore, be expected to have a greater probability of acquiring adaptive behavior if it copied the behavior of an adult rather than that of a fellow juvenile.

In our first exploration of possible effects of demonstrator age on observers' social learning (Galef et al., 1984), we used a 2 × 2 design to examine the consequences of interaction of both old and young observer rats with both old and young demonstrators. The results indicated that both young and old observers learned from both old and young demonstrators, and that there was little difference in the magnitude of social learning as a consequence of the relative ages of demonstrators and observers (Galef et al., 1984).

More recently (Galef and Whiskin, 2004), we both repeated a portion of Galef et al.'s (1984) experiments and directly compared the relative influence of old and young demonstrators, one fed cinnamon-flavored diet and the other cocoa-flavored diet when those demonstrators were presented sequentially to the same observer. The results were in complete accord with those of Galef et al. (1984). Adult and juvenile demonstrators had equivalent effects on their observers and direct comparison of the effectiveness of older and younger demonstrators revealed no reliable difference. If anything, juvenile demonstrators had greater effect than adult demonstrators on their observers' diet choices.

Failure to find greater effectiveness of older demonstrators is not unique to social learning about food in rats. For example, Lachlan et al. (1998) report that small guppies prefer to shoal with others their own size rather than with larger guppies, and shoaling is known to play a major role in selection of a feeding site (Laland and Williams, 1997). On the other hand, Gerrish and Alberts (1995) found that weanling Norway rats prefer a feeding site where an adult is eating to one where a juvenile is feeding, and Dugatkin and Godin (1993) report that mate choices of small female guppies are affected by observing the choices of larger (and presumably older) females, whereas the mate choices of large female guppies are not affected by observing those of smaller individuals. Clearly, much remains to be learned about when and how demonstrator age affects demonstrator effectiveness.

2. *Copy Kin or Familiar Individuals*

Theoretically, copying familiar individuals or kin should have greater fitness benefits than copying unfamiliar or unrelated potential models because: (1) social learning is useful only when models and copiers are exposed to similar environments and experience similar outcomes as a result of engaging in similar behaviors and (2) an individual is more likely to share environments and behavioral outcomes with kin or familiar individuals than with nonkin or strangers (Boyd and Richerson, 1985, 1988).

In many species, young spend more time interacting with parents, siblings, or other kin than with unrelated conspecifics, and should therefore have greater opportunity to acquire information from relatives than from nonkin (Coussi-Korbel and Fragaszy, 1995) Consequently, any observed differences in the frequencies with which juveniles living in natural circumstances behave like relatives than like nonrelatives cannot be used to infer that young treat information acquired from related individuals differently than they treat information acquired from others. A ‘‘strategy’’ of copying kin or familiar individuals requires such differential treatment of information acquired from familiar/kin and unfamiliar/nonkin, and is probably demonstrable only under controlled conditions.

In our first exploration of effects of familiarity and kinship on social learning about foods in Norway rats (Galef et al., 1984), we found that familiar and unfamiliar nonkin were equally effective in influencing the food choices of their observers. Consequently, we were surprised when Valsecchi et al. (1996) found, in studies of social influence on the food choices of Mongolian gerbils (*M. unguiculatus*), that only demonstrators that were both genetically related to and familiar with observers exerted any influence on their observers’ food choices.

Subsequent work by Choleris et al. (1998) revealed that treatment of gerbils with benzodiazepine chloride, an anxiolitic agent, resulted in familiar kin and unfamiliar nonkin being equally effective in altering their observers’ food preferences. This result suggests that at least part of the difference between Mongolian gerbils and Norway rats in the role of kinship and familiarity in affecting social influence on food choice might be due to differences in the probability of anxiety-induced behaviors when rats or gerbils first meet conspecifics.

The unfamiliar/unrelated, young female rats that have acted as demonstrators and observers in essentially all studies of social learning about food in *R. norvegicus* rarely fight when they meet for the first time, whereas unrelated/unfamiliar adult *M. unguiculatus*, frequently interact aggressively during a first encounter. If, as seems likely, aggressive interaction interferes with extraction of information from conspecifics concerning foods that they have recently eaten and anxiolitic agents reduce the probability of such aggression when unfamiliar gerbils first encounter one another, then the observed difference in the effects of familiarity and relatedness on social learning about foods in gerbils and rats might be expected.

In a pair of recent studies employing 2 × 2 designs, we examined the impact on an observer rats' preferences between two foods, one fed to each of two demonstrators, one familiar and the other unfamiliar to the observer, when we presented the two demonstrators simultaneously to an observer. We found, somewhat surprisingly, that observers in each of two experiments tended to eat more of a diet after interacting with an unfamiliar than with a familiar demonstrator fed that diet (Galef and Whiskin, 2008a; Fig. 10).

To test the hypothesis that the greater effectiveness of unfamiliar demonstrators might reflect a tendency on the part of rats to spend more time interacting with unfamiliar than with familiar conspecifics, we looked at the

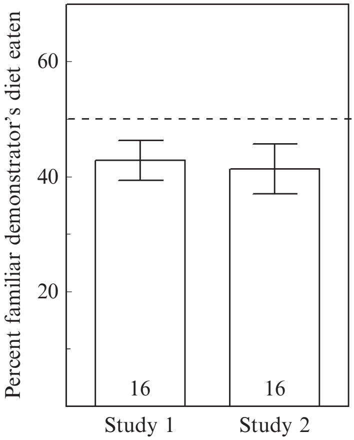

Fig. 10. Mean ± S.E. percentage demonstrator's diet eaten during testing by observers interacting with familiar and unfamiliar demonstrators. Dashed line = expected percent demonstrator's diet eaten by observers if observers' food choices were not influenced by prior interaction with demonstrators. Numbers in histograms = *N*/group (from Galef and Whiskin, 2008a,b, reprinted with permission of Elsevier).

behavior of naïve observer rats placed in a large cage with demonstrator rats fed different foods restrained behind screen barriers (Galef and Whiskin, 2008a). Consistent with the hypothesis that observers spend longer interacting with unfamiliar than familiar demonstrators, observers spent more time at the end of the cage closer to unfamiliar than to familiar individuals (Fig. 11).

Saggerson and Honey (2006) have reported possibly similar results in two experiments in which rats observed members of a familiar or unfamiliar strain pull on a chain to receive a food reward. The subjects behaved similarly to a demonstrator rat of an unfamiliar strain but not to a demonstrator rat of their own familiar strain. Saggerson and Honey (2006) attributed this difference in social learning following observation of relatively familiar and unfamiliar demonstrators to latent inhibition (i.e., reduced attention to familiar stimuli).

The finding that rats spend more time in the vicinity of unfamiliar than of familiar conspecifics (Galef and Whiskin, 2008a) suggests that the greater effect of unfamiliar than familiar demonstrators on observers' food choices is the result of greater amounts of information passing from unfamiliar than familiar demonstrators to observers. However, we have no direct evidence that the duration of interactions between an observer rat and its rat demonstrator affects the magnitude of the effect of demonstrators on their

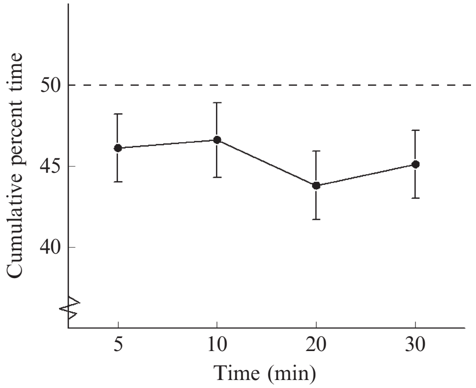

Fig. 11. Mean ± S.E. percentage of 30-min test that observers spent within 10 cm of the familiar demonstrator when choosing between familiar and unfamiliar demonstrators. Dashed line = expected percentage of time observer spent within 10 cm of a familiar demonstrator if familiarity with a demonstrator had no effect on observers' behavior (from Galef and Whiskin, 2008a, reprinted with permission of Elsevier).

observers' food choices. Unfortunately, it is not possible to either control or measure the amount of relevant information passing from interacting rat demonstrators to their rat observers.

As discussed in greater detail in Section I.B., analysis of the processes underlying influence of demonstrator rats on their observers' food preferences has shown that the critical stimulus passing from a demonstrator rat to its observer is a combination of a food odor and chemical cues that are a part of normal rat breath (Galef et al., 1988). We discovered some years ago (Galef, unpublished data; Lupfer-Johnson, personal communication, 2008) that if a human demonstrator eats cinnamon- or cocoa-flavored rat diet and then breathes on a rat, the rat subsequently shows an enhanced preference for the diet that its human demonstrator ate. Of course, a human demonstrator can be instructed to breathe on an observer rat a fixed number of times and can therefore vary systematically the amount of social information provided to an observer rat. Consequently, we could use human demonstrators to examine experimentally any effects of amount of information passing from a demonstrator to an observer on observers' subsequent food choices.

We have compared the magnitude of the effect on observer rats' choices between cinnamon- and cocoa-flavored rat chow of exposure to 1, 2, 10, 20, or 40 breaths from a human demonstrator that had just eaten 10 g of either cinnamon- or cocoa-flavored rat chow. We found a significant ($P < 0.02$) positive linear relationship between the number of human breathes an observer rat experienced and its reliance on such "social" information when subsequently choosing between cinnamon- and cocoa-flavored diet. (Galef and Tong, unpublished data; Fig. 12).

An interesting instance of variation in tendency to associate with familiar individuals social behavior has been provided by Frommen et al. (2007) who recently reported that three-spined stickleback prefer to shoal with familiar fish when sated but with unfamiliar fish when hungry, a finding that Frommen et al. (2007) attributed to avoidance of competition with kin. Shoaling in stickleback is known to affect choice of foraging site (Laland and Williams, 1997), so it might be predicted that stickleback would learn socially from familiar individuals when sated but from unfamiliar fish when hungry.

Taken together, results of explorations of the effects of familiarity/relatedness on the effectiveness of demonstrators suggest a rather complex picture. Apparently, there are circumstances in which familiar/related demonstrators have greater influence than unfamiliar/unrelated demonstrators, and other conditions where the reverse is true.

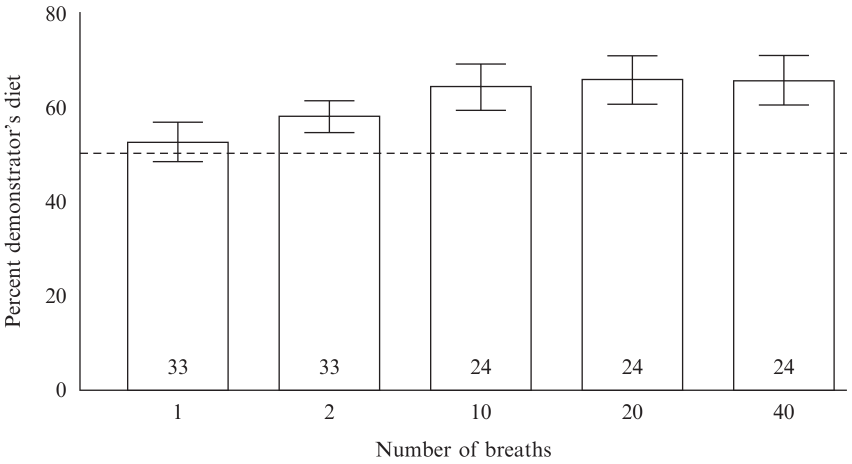

FIG. 12. Mean ± S.E. percentage demonstrator's diet eaten during testing by observer rats offered a choice between cinnamon- and cocoa-flavored diet after interacting with a human demonstrator that had eaten either cinnamon- or cocoa-flavored rat chow and breathed on each observer rat either 1, 2, 10, 20, or 40 times. Horizontal line = expected percent demonstrator's diet eaten by observers if observers' food choices were not influenced by prior interaction with a human demonstrator. Numbers in histograms = *N*/group (Galef and Tong, unpublished data).

3. *Copy Successful Individuals*

Successful foragers that are eating a nutritionally balanced diet and avoiding ingesting deleterious quantities of naturally occurring toxins will be healthier than those failing to secure a balanced diet or ingesting naturally occurring toxins. In particular, successful foragers should be less likely than unsuccessful foragers to be suffering observable gastrointestinal distress.

Numerous investigations both in our laboratory and elsewhere have explored the possibility that healthy demonstrators are more effective than ill demonstrators in altering their observers' food choices. Some laboratories (Galef et al., 1983, 1990; Grover et al., 1988) have been unable to provide evidence of a superiority of successful to unsuccessful demonstrators; others, for example, Hishamura (1998, 2000) and Kuan and Colwill (1997) may have had better luck. However, Hishamura (2000, p. 185) injected his ill demonstrators with an extremely hypertonic LiCl solution (0.7 M) that severely disrupted their behavior. "The injected demonstrator rats struggled wildly immediately after injection. After a few seconds they became quiet, and crouched for a few hours." Perhaps such debilitated demonstrators were unwilling to engage in social interaction with potential observers and consequently failed to affect their observers' food choices. An attempt in our laboratory to replicate Kuan and Colwill (1997) provided marginal evidence of a superiority of poisoned to unpoisoned demonstrators in altering their observers' food choices, a result opposite that reported by Kuan and Colwill (Galef and Whiskin, 2000).

Hill and Ryan (2006) report that female sailfin mollies (*Poecilia latipinna*), a species in which males mate with both conspecific and heterospecific females but prefer conspecific to heterospecific females as partners (1) increase their affiliation with nonpreferred conspecific males seen consorting with conspecific females, but (2) decrease their tendency to affiliate with nonpreferred males seen consorting with heterospecific females. Hill and Ryan (2006) interpreted this finding as providing evidence that females copy the mate choices of high, but not of low quality females, although alternative interpretations of the observed result are surely possible. For example, if male sailfin mollies compete for access to conspecific females, observation of a male molly with a conspecific female would provide an observing female molly with information as to the male's quality, and she might be expected to increase her preference only for males that appeared to have been successful in competition for access to preferred females. Consequently, whether focal female mollies should be thought of as copying the mate choices of successful but not of unsuccessful female models is not clear.

4. *Copy the Majority*

Chou and Richerson (1992) used social transmission of food choice to look for evidence that the relative number of demonstrators eating each of two diets would influence the subsequent preference of a naïve observer rat choosing between those diets. In each of four experiments, Chou and Richerson (1992) found that the greater the proportion of five demonstrator rats with which a single observer rat interacted that had eaten a diet, the greater that observer's preference for that diet in a subsequent choice test. Galef and Whiskin (1995) have repeated that result.

In related experiments, Beck and Galef (1989) showed that three demonstrator rats were significantly more effective than one in causing young rats to ingest a relatively unpalatable diet containing protein when that diet was presented together with three more-palatable, protein-poor diets, and Galef (1986) found that interaction with two demonstrators that had eaten a diet to which observers had previously learned a poison-induced aversion were more effective in reversing that aversion than was interaction with a single demonstrator that had eaten the averted diet. Studies by Lachlan et al. (1998) and Laland and Williams (1998) in guppies and by Lefebvre and Giraldeau (2002) in pigeons (*Columba livia*) provide additional evidence that the probability that a naïve animal will adopt a pattern of behavior increases as the proportion or number of demonstrators exhibiting that behavior increases. However, it has been argued that a linear association between the proportion of demonstrators exhibiting a behavior and the probability that an observer will adopt that behavior does not provide convincing evidence of a strategy of copying majorities (Laland, 2004).

All else being equal, a naïve individual should be exposed more frequently to information provided by a majority than by a minority of demonstrators, and as indicated in earlier discussion of copying familiar and unfamiliar demonstrators, (Section II. B. 2) may simply respond to the relative amount of information received regarding available alternatives. Indeed, the relatively linear response of observers to the ratio of demonstrators that have eaten each of two foods reported by Chou and Richerson (1992) and Galef and Whiskin (1995) is consistent with the view that the greater the amount of information an observer rat receives from conspecifics regarding a food, the greater the social enhancement of its preference for that food. Only if observers were to show a disproportionate tendency to copy a majority of demonstrators would there be evidence of a strategy of copying majorities (Laland, 2004).

5. *Copy Good Social Learners*

Whether copying good imitators is an effective strategy is a matter of debate. Some theoreticians follow Blackmore (1999) in suggesting that an enhanced ability to acquire cultural memes should prove adaptive (e.g., Higgs, 2000), while others maintain the opposite, (e.g., Kendal, 2003). Empirical work on the issue is limited, although results of a few studies suggest that at least some birds can identify good social learners and are therefore consistent with the hypothesis that good social learners might be preferred models. For example, Nowicki et al. (2002) report that female song sparrows (*Melospiza melodia*) prefer the songs of males that copy accurately, and suggest that ability to copy songs is a reliable index of a male's quality, while Hile et al. (2005) have proposed that, early in courtship, female budgerigars (*Melopsittacus undulatus*) prefer males that learn rapidly to mimic their vocalizations.

Although it remains unclear just how rats, unlike birds, might identify individuals that were better social learners than others, we have recently completed a study in which, in each of three replicates, we allowed 18 naïve observer rats to interact with demonstrator rats fed a cinnamon-flavored diet, and then selected the six that, when subsequently offered a choice between cinnamon and cocoa-flavored diets for 24 h, showed greatest and least preference for cinnamon-flavored diet. The social learning exhibited by the six "best" and six "worst" social learners differed dramatically, with the best social learners eating an average of 94.0 ± 2.7% and the worst social learners eating only 36.3 ± 2.0% cinnamon-flavored diet. We then used these 12 observer rats as demonstrators for 12 new observer rats (Galef and Whiskin, unpublished data) that first interacted with a demonstrator fed cinnamon-flavored diet and then chose for 23 h between cinnamon- and cocoa-flavored diets.

Although there was a tendency for observers to eat more cinnamon-flavored diet after interacting with a best than with a worst social learner as demonstrator, the effect was not significant (Fig. 13). Further, when we repeated the experiment with an additional group of 12 observers each of which interacted simultaneously with two demonstrators, one chosen from among six "best" social learners and the other from among six "worst" social learners and one fed cinnamon-flavored diet and the other cocoa-flavored diet (counterbalanced across the quality of demonstrators' prior social learning), we found no effect of demonstrators' previous performance as social learners on their observers' preferences (Fig. 13).

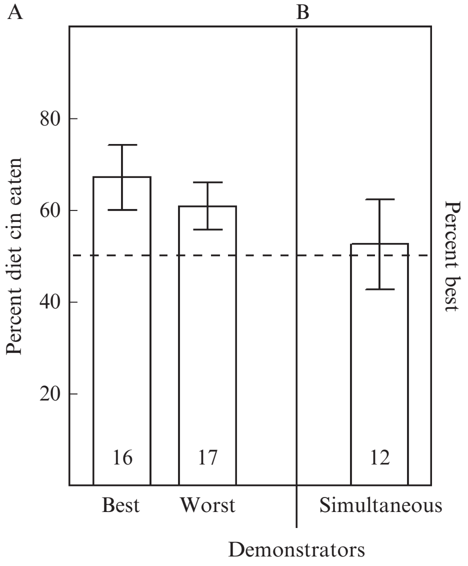

Fig. 13. Mean ± S.E. percentage demonstrator's diet eaten during testing by observers that interacted (A) with either "best" or "worst" demonstrators and (B) simultaneously with both a "best" and "worst" social learner. Dashed line = expected percent demonstrator's diet eaten by observers if observers' food choices were not influenced by prior interaction with demonstrators. Numbers in histograms = *N*/group (Galef and Whiskin, unpublished data).

III. CONCLUSIONS

A. OVERVIEW OF RESULTS

The series of experiments discussed above was undertaken to examine predictions derived from formal models of social learning as to when animals should increase their reliance on socially learning and from whom they should learn. I hoped that examining multiple predictions from theory in a single empirical system would provide both a picture of the adequacy of current models and data of potential use in increasing their accuracy.

My students and I found that formal models had considerably greater success in predicting when rats will rely on social learning than in predicting who rats would copy (Table II). Our data were consistent with four of five "when strategies," (copy when dissatisfied, when unproductive, when uncertain, and when the environment is relatively stable), whereas only one of six "who strategies" ("copy the majority") received any empirical support, resulting in a nearly statistically reliable difference in the success of formal models in predicting who and when rats would copy (Fisher's exact probability test, $P = 0.08$; Table II). Further, as indicated in the preceding discussion of "copy the majority," (Section II.B.4) although the results of several studies indicate that both rats and other animals show a positive relationship between the proportion of demonstrators exhibiting

TABLE II

SUMMARY OF RESULTS OF EXPERIMENTS REVIEWED IN THE PRESENT MANUSCRIPT EXAMINING STRATEGIES OF NORWAY RATS LEARNING SOCIALLY ABOUT FOODS

"When" strategies of social learning	
Copy when established behavior is unproductive	Yes
Copy when asocial learning is costly	No
Copy when uncertain	Yes
Copy when dissatisfied	Yes
Copy when the environment is stable[a]	Yes
"Who" strategies of social learning	
Copy older individuals	No
Copy kin	No!
Copy familiar individuals	No!
Copy successful individuals	No
Copy if better	No
Copy the majority	Maybe
Copy good social learners	No

Not!, the opposite of the predicted outcome.

[a] Not considered in Laland (2004).

a behavior and the probability that their observers will adopt that behavior, the support such findings offer for a ‘‘copy the majority strategy’’ is weak at best. Such proportional copying may reflect not a strategy of observers, but a difference in the amount of information demonstrators in the majority and minority provide to their observers.

If the data in Table II, describing the results of experiments using Norway rats’ social learning about foods are analyzed, ignoring the ambiguous evidence consistent with a strategy of ‘‘copy the majority,’’ then the difference in success of predictions of ‘‘when’’ and ‘‘who’’ strategies reaches statistical significance (Fisher’s exact test, $P < 0.05$). Further evidence of the lack of success of formal models in predicting who rats will copy, if further evidence is needed, is provided by the tendency of observer rats, in contradiction to theory, to copy unfamiliar demonstrators in preference to familiar demonstrators. In general, Norway rats choosing between foods do not seem to use the ‘‘who strategies’’ formal theory predicts.

B. Why the Greater Success of Predictions from ‘‘When’’ Than from ‘‘Who’’ Strategies?

Why formal models should be more successful in predicting when social learning will occur than who will serve as a model for such learning is not clear. Perhaps correlations between states of the environment and the value of reliance on socially acquired information are stronger than correlations between characteristics of potential models and the value of information that they provide. If so, natural selection for attention to the state of the environment would have been stronger than natural selection for attention to characteristics of potential informants, and the greater success of predictions of ‘‘when’’ than ‘‘who’’ strategies would be explained. However, attention to at least some characteristics of potential models would seem almost certain to have a powerful effect on the value of social leaning. For example, selection might be expected to act strongly to favor copying the behavior of healthy, successful rather than of obviously ill, unsuccessful foragers. Indeed, the failure, despite many years of attempts both in my laboratory and elsewhere, to find any evidence that rats are more likely to adopt the behaviors of healthy, conscious potential models than of unhealthy or unconscious ones remains something of a mystery.

Noble et al. (2001) have provided a model demonstrating that in environments containing exclusively lethal toxins, rats should copy the food choices of both healthy and sick individuals, though it is of course unlikely rats evolved in such an environment. Galef (1985, 1991) has proposed that, because rats may most often become ill for reasons that have nothing to do with the foods they have eaten, lost opportunity costs resulting from not eating foods ingested by unhealthy demonstrators might be greater than any benefits resulting from avoiding such foods.

Although creating both formal models (Noble et al., 2001) and informal arguments (Galef, 1985, 1991) as to why rats should not learn to avoid foods eaten by ill or unconscious conspecifics is relatively simple, such *post hoc* explanations are inherently suspect. Explanations in the literature of other failures to find evidence consistent with predictions from social-learning theory (e.g., Briggs et al., 1996; Frommen et al., 2007) are similarly *post hoc*.

1. Adaptive Specialization

Hoppitt and Laland (2008, p. 133) have recently proposed that the social enhancement of food preferences found in Norway rats is the expression of a specialized learning mechanism that evolved to implement the general adaptive strategy "eat what others eat." If so, social learning about foods might resemble taste-aversion learning, the other proposed adaptive specialization seen in rats' food selection, in restricting the range of stimuli to which rats attend when learning about foods.

As the name taste-aversion learning implies, rats learn far more easily to associate tastes than exteroceptive stimuli (e.g., sights or sounds) with subsequent aversive gastrointestinal events, a phenomenon referred to in the psychological literature as cue-to-consequence specificity (Garcia and Ervin, 1968) or preparedness (Seligman, 1970). Such preferred association of taste cues with gastrointestinal upset seems sensible in that food is tasted in the mouth and ingestion has gastrointestinal consequences.

Three of the four "when strategies" (copy when individual learning is unproductive, when dissatisfied, and when uncertain) that accurately predicted rats' increased reliance on social learning each involve an animal monitoring either the consequences of its own behavior (whether that behavior was productive) or its own internal state (its level of comfort or certainty about the state of the environment). The "when strategy" (copy when predators are present) and the seven "who strategies" that were not confirmed (copy familiar individuals, older individuals, etc.) each involved monitoring features of the external environment.

As in taste-aversion learning, rats may have difficulty using information about the external environment to modulate their responses to socially acquired information about foods. If so, as Hoppitt and Laland's (2008) analogy between rats' social learning of food preferences and their taste-aversion learning suggests, then the greater success of predictions from "when" than from "who" strategies might be expected. However, why failure to attend to exteroceptive cures in social learning about foods might be adaptive is not nearly so obvious as why rats should fail to attend to such cues in individual taste-aversion learning. Consequently, positing evolution of a strategy to ‘‘eat what others have eaten,’’ as have Hoppitt and Laland (2008) begs the question of why a strategies of ‘‘eat what healthy others have eaten’’ or ‘‘eat what kin have eaten’’ did not evolve instead.

2. Problems with Failures to Find Evidence

It might be argued that failure to find evidence consistent with predictions from ‘‘who strategies’’ is not particularly informative because, as is always the case with failures to find evidence consistent with predictions from theory, the design of failed experiments might have been inadequate to test the prediction. However, problems inherent in failures to reject null hypotheses does not explain the difference in outcomes of tests of ‘‘who strategies’’ and ‘‘when strategies,’’ especially given the greater ease of designing experiments with high face validity to test the former than the latter. Convincing tests of the hypotheses that rats attend to kin, to older individuals, to the majority, etc., are far easier to design than are convincing tests of whether rats are more likely to rely on social learning when, for example, dissatisfied or engaged in unproductive behavior.

3. Alternative Priorities

As discussed in the sections on ‘‘copy kin or familiar individuals’’ (Section II.B.2) and ‘‘copy older individuals,’’ (Section II.B.1) when individuals participate in a social interaction, the social interaction itself may be more important to participants than whatever social information might be available during the interaction. For example, Choleris et al.’s (1998) finding, in Mongolian gerbils, of an anxiety-induced failure to learn socially from unfamiliar demonstrators and Lachlan et al.’s (1998) report of young guppies preferring to feed with age mates to reduce predation risk suggest, as does our finding that rats spend more time interacting with unfamiliar than with familiar demonstrators, that considerations having nothing to do with social learning itself may be important in determining whether social learning occurs in many potential social-learning situations. More generally, characteristics of interacting individuals along dimensions orthogonal to their suitability as models for social learning, might determine the likelihood that social learning would occur during an interaction (for review, see Coussi-Korbel and Fragaszy, 1995). For example, demonstrators of high social status might be less effective than demonstrators of low social status despite the potential superiority of individuals with high social status as models, because the presence of high status individuals inhibits behavior in low-status individuals (Drea and Wallen, 1999; Nicol and Pope, 1994).

4. Where is the Problem?

The fact that results of our tests of predictions from ‘‘who strategies’’ of social learning were not consistent with theory suggests that there is something wrong either (1) with the theories from which the predictions derive, (2) with our methods of testing those predictions, or (3) with our choice of Norway rat’s social learning about foods that makes it inappropriate for testing predictions formal theory. As discussed above, tests of copy familiar individuals, copy older individuals, etc., are fairly straightforward, so it is unlikely that methodological errors are the source of the problem. As is also discussed above, there may be some reason to question the validity of Norway rats’ social learning about foods as an empirical system for examining predictions from general theory. Indeed, instances in which empirical tests of some ‘‘who strategies’’ have provided confirming evidence, for example, the tendency of guppies to copy the mate choices of larger and presumably older individuals, more experienced individuals (Dugatkin and Godin, 1993) is consistent with the view that Norway rats may be idiosyncratic in some way.

Last, it is of course possible that the models from which ‘‘who strategies’’ are derived are incomplete. In particular, as noted in Section II.B.1, results of analyses of success (Choleris et al., 1998) and of failure (Galef and Whiskin, 2008a) of predictions concerning the effects of familiarity and kinship on social learning about foods by Mongolian gerbils and Norway rats suggest that social interactions between individuals with differing characteristics that are not considered in formal models of social learning may be critical in determining whether predictions from such models are confirmed or refuted. For example, the tendency of Mongolian gerbils to attack unfamiliar, unrelated conspecifics the first time that they encounter them and of Norway rats to spend more time in olfactory investigation of unfamiliar than familiar conspecifics may interact with the processes that support social learning about foods (i.e., exposure to diet related cues carried on the breath of mammals that have recently eaten) to produce either consistent or inconsistent with predictions from social-learning theory. Thus, whether ‘‘who strategies’’ are confirmed or disconfirmed may depend on how the specific mechanisms resulting in social learning in any particular case are affected by the types of social interaction engaged in by potential social learners and models with various characteristics. If the social interactions elicited by the characteristics of potential models and social learners determine the likelihood of social learning occurring, then accurate prediction of the characteristics of individuals that increase the probability that they will be exploited as sources of information may require incorporation into models of social learning of variables other than those shaping the evolution of social learning itself,. Our theories may be focused on the factors affecting the evolution of reliance on socially acquired information, but our animal subjects may have priorities other than acquiring social information when they encounter potential models.

Acknowledgments

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References

Aoki, K., Feldman, M.W., 1987. Toward a theory for the evolution of cultural communication: coevolution of signal transmission and reception. Proc. Natl. Acad. Sci. USA 84, 7164–7168.

Beck, M., Galef Jr., B.G., 1989. Social influences on the selection of a protein-sufficient diet by Norway rats. J. Comp. Psychol. 103, 132–139.

Beck, M., Hitchcock, C., Galef Jr., B.G., 1988. Diet sampling by wild Norway rats (*Rattus norvegicus*) offered several unfamiliar foods. Anim. Learn. Behav. 16, 224–230.

Blackmore, S., 1999. The Meme Machine. Oxford University Press, Oxford.

Boyd, R., Richerson, P.J., 1985. Culture and the Evolutionary Process. Chicago University Press, Chicago.

Boyd, R., Richerson, P.J., 1988. An evolutionary model of social learning: the effects of spatial and temporal variation. In: Zentall, T.R., Galef Jr., B.G. (Eds.), Social Learning: Psychological and Biological Perspectives. Lawrence Erlbaum, Hillsdale, NJ, pp. 29–48.

Briggs, S.E., Godin, J.G., Dugatkin, L.A., 1996. Mate-choice copying under the risk of predation in the Trinidadian guppy (*Poecilia reticulata*). Behav. Ecol. 7, 151–152.

Choleris, E., Valsecchi, P., Wang, Y., Ferrari, P., Kavaliers, M., Mainardi, M., 1998. Social learning of food preferences in male and female Mongolian gerbils is facilitated by the anxiolytic chlordiazepoxide. Pharmacol. Biochem. Behav. 60, 575–584.

Chou, L.S., Richerson, P.J., 1992. Multiple models in social transmission of food selection by Norway rats. Anim. Behav. 44, 337–343.

Coolen, L., van Bergen, Y., Day, R.L., Laland, K.N., 2003. Species differences in the adaptive use of social information in sticklebacks. Proc. R. Soc. Lond. B 270, 2413–2419.

Coussi-Korbel, S., Fragaszy, D.M., 1995. On the relation between social dynamics and sSocial learning. Anim. Behav. 50, 1441–1453.

Crowley, P., Travers, S., Linton, M., Cohn, S., Sih, A., Sargent, C., 1991. Mate density, predation risk and the seasonal sequence of mate choice: a dynamic game. Am. Nat. 137, 567–596.

Dewar, G., 2004. Social and asocial cues about new food: cue reliability influences intake in rats. Learn. Behav. 32, 82–89.

Drea, C.M., Wallen, K., 1999. Low status monkeys "play dumb" when learning in mixed social groups. Proc. Natl. Acad. Sci. USA 96, 12965–12969.

Dugatkin, L.A., Godin, J.G.J., 1993. Female mate copying in the guppy (*Poecilia reticulata*): age-dependent effects. Behav. Ecol. 4, 289–292.

Enquist, M., Eriksson, K., Ghirlanda, S., 2007. Critical social learning: a solution to Roger's paradox of nonadaptive culture. Am. Anthropol. 109, 727–734.

Epstein, A.N., Stellar, E., 1955. The control of salt preference in the adrenalectomized rat. J. Comp. Physiol. Psychol. 48, 167–172.

Feldman, M.W., Aoki, K., Kumm, J., 1996. Individual versus social learning, evolutionary analysis in fluctuating environments. Anthropol. Sci. 104, 209–232.

Forkman, B., 1991. Social facilitation is shown by gerbils when presented with novel but not with familiar food. Anim. Behav. 42, 860–861.

Friedman, M.I., 2000. Too many choices? A critical essay on macronutrient selection. In: Berthoud, H.R., Seeley, R.J. (Eds.), Neural and Metabolic Control of Macronutrient Intake. CRC Press, Baton Rouge, pp. 11–18.

Frommen, J.G., Luz, C., Bakker, T.C.M., 2007. Nutritional state influences shoaling preference for familiars. Zoology 110, 369–376.

Galef Jr., B.G., 1985. Direct and indirect behavioral processes for the social transmission of f food avoidance. In: Bronstein, P., Braveman, N.S. (Eds.), Experimental Assessments and Clinical Applications of Conditioned Food aversions. New York Academy of Sciences, New York, pp. 203–215.

Galef Jr., B.G., 1986. Social interaction modifies learned aversions, sodium appetit*e*, and both palatability and handling-time induced dietary preference in rats (*R. norvegicus*). J. Comp. Psychol. 100, 432–439.

Galef Jr., B.G., 1991. A contrarian view of the wisdom of the body as it relates to dietary self selection. Psychol. Rev. 98, 218–223.

Galef Jr., B.G., 1996. Social influences on the food preferences and feeding behaviors of vertebrates. In: Capaldi, E.D. (Ed.), Why We Eat What We Eat, second ed American Psychological Association. Washington, DC, pp. 207–230.

Galef Jr., B.G., 2002. Social learning of food preferences in rodents: A rapidly learned appetitive behavior. Curr. Protoc. Neurosci. 8.5 D1–8.5 D8, 76, 1381–1388.

Galef Jr., B.G., 2006. Theoretical and empirical approaches to understanding when animals use socially acquired information and from whom they acquire it. In: Lucas, J.R., Simmons, J. R., L, J.R. (Eds.) Essays in Animal Behaviour: Celebrating 50 Years of Animal Behaviour. Academic Press, San Diego, pp. 161–182.

Galef Jr., B.G., Stein, M., 1985. Demonstrator influence on observer diet preference: Analyses of critical social interactions and olfactory signals. Anim. Learn. Behav. 13, 31–38.

Galef Jr., B.G., Whiskin, E.E., 1995. Learning socially to eat more of one food than of another. J. Comp. Psychol. 109, 99–101.

Galef Jr., B.G., Whiskin, E.E., 2000. Demonstration of a socially transmitted flavor aversion in rats? Kuan and Colwill (1997) revisited. Psychon. Bull. Rev. 7, 631–635.

Galef Jr., B.G., Whiskin, E.E., 2004. Effects of environmental stability and demonstrator age on social learning of food preferences by young Norway rats. Anim. Behav. 68, 897–902.

Galef Jr., B.G., Whiskin, E.E., 2006. Increased reliance on socially acquired information while foraging in risky situations? Anim. Behav. 72, 1169–1176.

Galef Jr., B.G., Whiskin, E.E., 2008a. Effectiveness of familiar kin and unfamiliar non-kin demonstrator rats in altering food choices of their observers. Anim. Behav. 77, 1329–1335.

Galef Jr., B.G., Whiskin, E.E., 2008b. Use of social information by sodium- and protein-deficient rats: a test of a prediction (Boyd and Richerson 1988). Anim. Behav. 75, 627–630.

Galef Jr., B.G., Wigmore, S.W., 1983. Transfer of information concerning distant foods: a laboratory investigation of the "information-centre" hypothesis. Anim. Behav. 31, 748–758.

Galef, B.G., Yarkovsky, N., 2009. Further studies of reliance on socially acquired information when foraging in potentially risky situations. *Anim. Behav.* 77, 1329–1335.

Galef Jr., B.G., Wigmore, S.W., Kennett, D.J., 1983. A failure to find socially mediated taste-aversion learning in Norway rats (*R. norvegicus*). J. Comp. Psychol. 97, 358–363.

Galef Jr., B.G., Kennett, D.J., Wigmore, S.W., 1984. Transfer of information concerning distant foods in rats: A robust phenomenon. Anim. Learn. Behav. 12, 292–296.

Galef Jr., B.G., Kennett, D.J., Stein, M., 1985. Demonstrator influence on observer diet preference: Effects of simple exposure and the presence of a demonstrator. Anim. Learn. Behav. 13, 25–30.

Galef Jr., B.G., Mason, J.R., Preti, G., Bean, N.J., 1988. Carbon disulfide: a semiochemical mediating socially-induced diet choice in rats. Physiol. Behav. 42, 119–124.

Galef Jr., B.G., McQuoid, L.M., Whiskin, E.E., 1990. Further evidence that Norway rats do not socially transmit learned aversions to toxic baits. Anim. Learn. Behav. 18, 199–205.

Galef Jr., B.G., Beck, M., Whiskin, E.E., 1991. Protein deficiency magnifies socialinfluences on the food choices of Norway rats (*Rattus norvegicus*). J. Comp. Psychol. 105, 55–59.

Galef Jr., B.G., Dudley, K.E., Whiskin, E.E., 2008. Social learning of food preferences in'dissatisfied' and 'uncertain' rats. Anim. Behav. 75, 631–637.

Garcia, J., Ervin, F.R., 1968. Gustatory-visceral and telerectptor-cutaneous conditioning—adaptation to internal and external milieus. Commun. Behav. Biol. Part A. 1, 389–415.

Gerrish, C.J., Alberts, J.R., 1995. Differential influence of adult and juvenile conspecifics on feeding by Norway rats (*Rattus norvegicus*). J. Comp. Psychol. 109, 61–67.

Giraldeau, L.A., Valone, T.J., Templeton, J.J., 2002. Potential disadvantages of using socially acquired information. Philos. Trans. R. Soc. Lond. B 357, 1559–1566.

Grover, C.A., Kixmiller, J.S., Erickson, C.A., Becker, A.H., Davis, S.F., Nallan, G.B., 1988. The social transmission of information concerning aversively conditioned liquids. Psychol. Rec. 38, 557–566.

Higgs, P.G., 2000. The mimetic transition: a simulation study of the evolution of learning by imitation. Proc. R. Soc. Lond. B 270, 1355–1361.

Hill, S.E., Ryan, M.J., 2006. The role of model female quality in the mate choice copying behaviour of sailfin mollies. Biol. Lett. 2, 203–205.

Hile, A.G., Burley, N.T., Coopersmith, C.B., Foster, S., Stiedter, G.F., 2005. Effects of male vocal learning on female behavior in the budgerigar, *Melopsittacus undulatus*. Ethology 111, 901–923.

Hishimura, Y., 1998. Food choice in rats (*Rattus norvegicus*): the effect of exposure to a poisoned conspecific. Jpn. Psychol. J. 42, 183–187.

Hishimura, Y., 2000. Enhancement of food aversion by exposure to a poisoned conspecific in Norway rats (*Rattus norvegicus*). Jpn. Psychol. J. 40, 172–177.

Hoppitt, W., Laland, K.N., 2008. Social processes influencing learning in animals: a review of the evidence. Adv. Study Behav. 38, 105–165.

Kendal, R.L., Coolen, I., Laland, K.N., 2004. The role of conformity in foraging when personal and social information conflict. Behav. Ecol. 15, 269–277.

Kendal, J.R., 2003. An investigation into social learning: mechanisms, diffusion dynamics and evolutionary consequences. *Unpublished doctoral thesis*. University of Cambridge.

Kendal, R.L., Coolen, I., van Bergen, Y., Laland, K.N., 2005. Trade-offs in the adaptive use of social and asocial learning. Adv. Study Behav. 38, 333–379.

Kuan, L.A., Colwill, R.M., 1997. Demonstration of a socially transmitted aversion in the rat. Psychon. Bull. Rev. 4, 374–377.

Lachlan, R.F., Crooks, L., Laland, K.N., 1998. Who follows whom? Shoaling preferences and social learning of foraging information in guppies. Anim. Behav. 56, 181–190.

Laland, K.N., 2004. Social learning strategies. Learn. Behav. 32, 4–14.

Laland, K.N., Williams, K., 1997. Shoaling generates social learning of foraging information in guppies. Anim. Behav. 53, 1161–1169.

Laland, K.N., Williams, K., 1998. Social transmission of maladaptive information in guppies. Behav. Ecol. 9, 493–499.

Laland, K.N., Richerson, P.J., Boyd, R., 1996. Developing a theory of animal social learning. In: Heyes, C.M., Galef Jr., B.G. (Eds.), Social Learning in Animals: The Roots of Culture. Academic Press, San Diego, pp. 129–154.

Lefebvre, L., Giraldeau, L.A., 1994. Cultural transmission in pigeons is affected by the number of tutors and bystanders present during demonstration. Anim. Behav. 47, 331–337.

Lima, S.L., Dill, L.M., 1990. The behavioral decisions made under risk of predation- a review and prospectus. Can. J. Zool. 68, 619–640.

Nicol, C.J., Pope, S.J., 1994. Social learning in small flocks of laying hens. Anim. Behav. 52, 767–774.

Noble, J., Todd, P.M., Tuci, E., 2001. Explaining social learning of food preferences without aversions: an evolutionary simulation model of Norway rats. Proc. R. Soc. Lond. B 268, 141–149.

Nowicki, S., Searcy, W.A., Peters, S., 2002. Quality of song learning affects female response to male bird song. Proc. R. Soc. Lond. B 269, 1949–1954.

Orrock, J.L., Danielson, B.J., Brinckerhoff, R.J., 2004. Rodent foraging is affected by indirect but not direct cues of predation risk. Behav. Ecol. 15, 433–437.

Powell, F., Banks, P.B., 2004. Do house mice modify their foraging behavior in response to predator odours and habitat? Anim. Behav. 67, 753–759.

Ratcliffe, J.M., ter Hofstede, H.M., 2005. Roosts as information centres: social learning of food preference in bats. Biol. Lett. 1, 72–74.

Rogers, A., 1988. Does biology constrain culture? Am. Anthropol. 90, 819–831.

Rozin, P., 1969. Adaptive food sampling patterns in vitamin deficient rats. J. Comp. Physiol. Psychol. 69, 126–132.

Rozin, P.N., Schulkin, J., 1990. Food selection. In: Stricker, E.M. (Ed.), Handbook of Behavioral Neurobiology, vol. 10. Neurobiology of Food and Fluid Intake. Plenum Press, New York, pp. 297–321.

Real, L.A., 1990. Search theory and mate choice. Am. Nat. 136, 376–405.

Saggerson, A.L., Honey, R.C., 2006. Observational learning of instrumental discriminations in the rat: the role of demonstrator type. Q. J. Exp. Psychol. 59, 1909–1920.

Schlag, K.H., 1998. Why imitate, and if so, how? A bounded rational approach to multi-armed bandits. J. Econ. Theory 78, 130–156.

Seligman, M.E.P., 1970. On the generality of the laws of learning. Psychol. Rev. 77, 406–418.

Sih, A., 1994. Predation risk and the evolutionary ecology of reproductive behavior. J. Fish Biol. 45, 111–130.

Steiniger, von.F., 1950. Beitrage zur Soziologie und sonstigen Biologie der Wanderratte. Zeitschrift fur Tierpsycholgie 7, 356–370.

Stricker, E.M., 2000. Specific appetites and homeostatic systems. In: Berthoud, H.R., Seeley, R. J. (Eds.), Neural and Metabolic Control of Macronutrient Intake. CRC Press, Baton Rouge, pp. 3–11.

Valsecchi, P., Choleris, E., Moles, A., Guop, C., Mainardi, M., 1996. Kinship and familiarity as factors affecting transfer of food preferences in Mongolian gerbils (*Meriones unguiculatus*). J. Comp. Psychol. 110, 243–251.

Visalberghi, E., Fragaszy, D.M., 1995. The behavior of capuchin monkeys, *Cebus apella*, with novel food: the role of social context. Anim. Behav. 49, 1089–1095.

Yoerg, S.I., 1991. Social feeding reverses learned flavor aversions in spotted hyena (*Crocuta crocuta*). J. Comp. Psychol. 105, 185–189.