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Increased reliance on socially acquired information while foraging in risky situations?

BENNETT G. GALEF, JR & ELAINE E. WHISKIN
Department of Psychology, McMaster University

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We undertook three experiments to investigate the hypothesis that as the potential costs of individual learning increase, reliance on social learning also increases. We found no effect of indirect cues of predation risk on use of previously acquired social information by Norway rats, *Rattus norvegicus*, choosing between unfamiliar foods (experiment 1). We also found decreased (not increased) use of socially acquired information by rats choosing between unfamiliar foods when exposed to direct cues of predation risk (experiment 2). Furthermore, experiences of gastrointestinal upset following ingestion of unfamiliar foods (intended to act as a cue to the presence of toxic potential foods) failed to increase rats' use of social information when choosing between additional unfamiliar foods (experiment 3). The results of our experiments thus failed to confirm predictions of several formal models of the effects of costs of individual assessment of alternatives on use of socially acquired information.

Formal models of the conditions that should lead decision makers to depend on social rather than individual learning consistently predict that reliance on socially acquired information should increase when potential costs of individual assessment rise (Boyd & Richerson 1985, 1988; Feldman et al. 1996; Laland 2004; Kendal et al. 2005). In particular, when risk of predation is high, costs of individual assessment of potential mates (e.g. Lima & Dill 1990; Reynolds & Gross 1990; Sih 1994), or foods, should increase dependence on previously acquired social information.

To assess the nutritional value of unfamiliar foods an animal must repeatedly sample each available alternative (Rozin 1969; Rozin & Schulkin 1990). Repeated sampling of alternative foods requires an increase in time spent searching for and eating foods away from safe harbourage sites. Consequently, when choosing between unfamiliar foods, foragers facing enhanced risk of predation might be expected to reduce potential costs of individual assessment by relying more heavily on previously acquired social information than foragers not exposed to predation risk.

Cues indicative of predation risk can be either direct, as when an individual detects a predator or cues directly associated with the presence of a predator (e.g. Powell & Banks 2004), or indirect, indicating that a predator's attack is likely to be successful if it occurs, for example, when distance to shelter is great and concealment is impossible (e.g. Hughes & Ward 1993; Genaro & Schmidek 2000; Arcis & Desor 2003; Orrock et al. 2004). Numerous empirical studies have examined effects of both indirect and direct cues of predation risk on foraging patterns (e.g. Herman & Valone 2000; Pusenius & Ostfeld 2002; Arcis & Desor 2003). Such studies have generally found that animals under threat of predation forage more frequently under or near cover, sometimes increasing (Lima & Valone 1986; Leaver & Daly 2003) and sometimes decreasing (e.g. Cerri & Fraser 1983; Metcalfe et al. 1987; Ibraham & Huntingford 1989) their choosiness or selectivity with respect to potential food items. However, we know of no experiments investigating the focus of interest here, the effect of predation risk on dependence on socially acquired information when foraging.

Results of studies both in our laboratory and elsewhere have shown repeatedly that after a naïve Norway rat, *Rattus norvegicus* (an observer) interacts with a conspecific that has recently eaten a distinctively flavoured food (a demonstrator), the observer shows an enhanced preference for whatever food its demonstrator ate (for reviews, see Galef 1988, 1996, 2001). In the three experiments reported here, we examined effects of indirect (experiment 1) and direct (experiment 2) cues of predation risk as well as risk of ingesting toxins (experiment 3) on rats' use of previously acquired social information when choosing

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

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between two foods that they had not previously eaten. We expected, as predicted by the formal models referenced above (Boyd & Richerson 1985, 1988; Feldman et al. 1996; Laland 2004; Kendal et al. 2005), as well as by common sense, that increasing the potential cost to observers of individually assessing alternative unfamiliar foods by increasing predation risk would increase observers' reliance on information previously acquired from demonstrators in deciding what to eat.

EXPERIMENT 1: INDIRECT PREDATION RISK

In experiment 1, we looked for effects of both distance from shelter and opportunity for concealment on Norway rats' use of previously acquired social information when choosing between two unfamiliar foods. If indirect predation risk affects dependence on social learning, then rats choosing between two unfamiliar foods when relatively far from a harbourage site and in the open should be more reliant on previously acquired social information concerning one of the two foods available to them than should rats feeding close to a harbourage site and under cover.

Methods

Subjects

Forty-four, 7-week-old male, female Long–Evans rats acquired from Charles River Canada (St Constant, Quebec) when 7 weeks of age served as observers. An additional 44 female Long–Evans rats that had served as observers in previous experiments served here as demonstrators.

To examine effects of indirect cues of predation risk on reliance on socially acquired information, we systematically varied: (1) the distance from the nestbox to the two foods available to each observer and (2) the presence or absence of cover at the feeding site. Consequently, each observer was randomly assigned to one of four conditions: (1) near-open ($N = 10$), (2) near-covered ($N = 10$), (3) far-open ($N = 12$) and (4) far-covered ($N = 12$).

Diets

We composed two roughly equipalatable diets (diet cin and diet coc) by adding either 1.0 g McCormick's Ground Cinnamon (McCormick Canada, London, Ontario), or 2.0 g of Hershey's Pure Cocoa (Hershey Canada Inc., Mississauga, Ontario), respectively, to sufficient Teklad Rodent Diet (W) 8640 (diet 8640: Harlan-Teklad, Madison, Wisconsin, U.S.A.) to equal 100 g. Similar diets (differing only in whether they have been flavoured with cinnamon or cocoa) have been used successfully in numerous previous studies of social influence on food choice in rats both in our laboratory and elsewhere.

Apparatus

Preference induction. During the preference-induction stage of the experiment, demonstrators and observers lived in individual stainless-steel hanging cages measuring 21 × 24 × 27 cm. We presented food to subjects in semicircular stainless-steel food cups (10-cm diameter, 5 cm deep) that we attached to one wall of the cage and, to prevent spillage, filled to less than half their depth.

Testing of observers. We tested each observer in a floor enclosure constructed of angle iron and hardware cloth, measuring 1 × 2 × 0.3 m. The galvanized sheet metal floor of each enclosure was covered to a depth of 2 cm with wood shavings, and each enclosure contained a wooden nestbox, measuring 16 × 16 × 24 cm, and two 10-cm diameter, 5-cm-high Pyrex bowls, one containing diet cin and the other diet coc.

We placed the food bowls of observers assigned to eat under cover inside a three-sided structure, measuring 25 × 20 × 14 cm, that provided a 25 × 20-cm roof supported on two 20 × 14-cm legs. The food bowls rested on the floor under the roof.

For observers assigned to the 'near condition', we placed food bowls and cover (when appropriate) abutting the entrance to the nestbox, so that observers could eat without crossing open ground. For observers assigned to the far condition, we placed both food bowls and cover (when appropriate) 1.3 m from the nestbox entrance (Fig. 1).

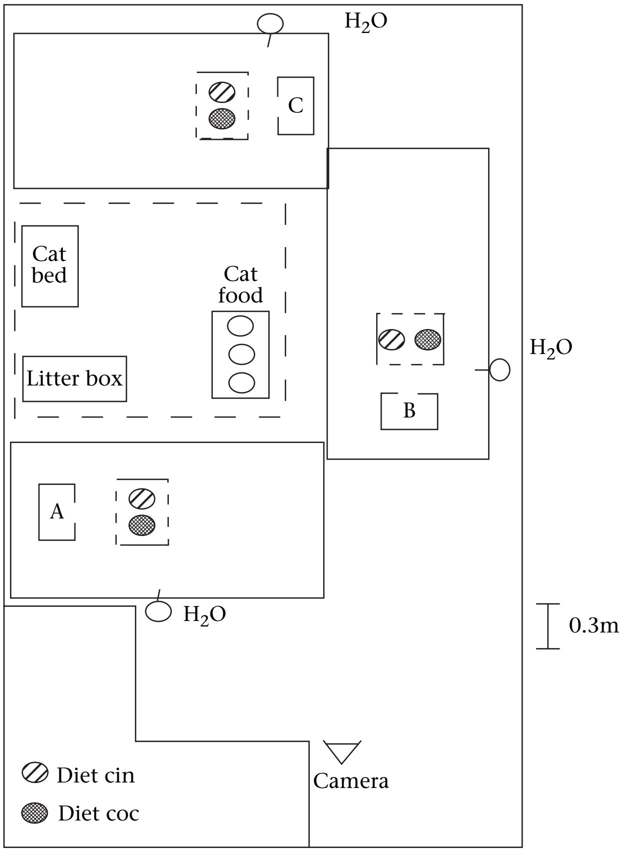

Figure 1. Overhead view of the room where we conducted experiments 1 and 2. Enclosure A is configured for the near-covered condition in experiment 1, enclosure C for the far-covered condition in the same experiment and enclosure B for experiment 2.The dashed line indicates the area where we held cats in the 24-h and 4-h caged conditions of experiment 2.

Procedure

After observer rats arrived in the laboratory, we placed them in groups of three or four in shoebox cages and left them undisturbed for 1 week to recover from the stress of transport. During this week, observers had ad libitum access to water and pellets of diet 8640.

Preference induction. We used procedures for social induction of food preference that have been standard in our laboratory for many years (e.g. Galef & Wigmore 1983; Galef 2001). In brief, to ensure that demonstrators ate when given an opportunity to do so, we placed them on a 23-h schedule of food deprivation and provided them with powdered diet 8640 for 1 h/day for 2 consecutive days. After a third 23-h period of food deprivation, we gave half the demonstrators access, for 1 h, to a weighed sample of diet cin and half access to a weighed sample of diet coc. Immediately after demonstrators were fed either diet cin or diet coc, we confirmed that each demonstrator had eaten more than 5 g, then placed each demonstrator with an observer and allowed the pair to interact for 30 min.

Habituating observers. To accustom observers to feeding in floor enclosures, we also placed them on a 23-h/day schedule of food deprivation. On each of the 2 days that demonstrators ate powdered diet 8640, we moved each observer from its hanging cage to the nestbox of the floor enclosure (Fig. 1) where that observer was to be tested, and left it there for 1 h. During these two 1-h feeding periods, we offered each observer a single food bowl containing powdered diet 8640 in the same location where it would be offered diets cin and coc during testing (see below) and either in the open or under cover depending on how the observer was to be tested.

Testing of observers. At the end of the 30-min period of interaction between demonstrators and observers, we moved each observer to the nestbox in the floor enclosure where it had fed on the previous 2 days. We then placed two weighed food bowls, one containing diet cin and other diet coc, in the appropriate position, and left the observer to feed for 23 h. We weighed each food bowl twice, once 4 h after the start of testing and again 19 h later. After each weighing, we determined the percentage of each observer's total intake of the diet that its demonstrator had eaten (i.e. the percentage of diet cin eaten by observers whose demonstrators had eaten diet cin and the percentage of diet coc eaten by observers whose demonstrators had eaten diet coc).

Ethical note. The procedures used here as well as in experiments 2 and 3 are described in Animal Utilization Proposal 04-06-28 approved by the McMaster University Research Board in June 2004.

Results and Discussion

We lost data from one observer assigned to the far-covered condition because it failed to eat during testing.

As expected (Galef & Wigmore 1983), subjects assigned to all eight groups showed a significant preference for the diet that their respective demonstrators had eaten (Table 1). The implication of this finding is that subjects were choosing foods to eat, not feeding randomly.

Table 1. One-tailed Student's *t* tests on the amount of demonstrators' diets eaten by observers assigned to the eight groups in experiment 1 (Fig. 2)

Group	t	df	P
Near			
4-h covered	3.74	9	<0.005
4-h open	6.10	9	<0.0002
23-h covered	4.56	9	<0.001
23-h open	7.56	9	<0.0001
Far			
4-h covered	6.96	10	<0.0001
4-h open	6.56	11	<0.0001
23-h covered	4.44	10	<0.002
23-h open	5.37	11	<0.0002

However, we found no effect of distance to the nestbox (2 × 2 ANOVA: $F_{1,39} = 0.35$, $P = 0.56$; Fig. 2), presence of cover at the feeding site ($F_{1,39} = 0.06$, $P = 0.82$), or their interaction ($F_{1,39} = 0.32$, $P = 0.86$) on observers' preferences for the diet that their respective demonstrators had eaten. Most importantly, subjects that fed in the open at a distance from the nestbox, and therefore, that were most susceptible to predation, ate no greater percentage of the diet that their respective demonstrators had eaten than did subjects eating under cover and close to the nestbox, and therefore, that were most secure from predation (Student's *t* tests: 4 h: $t_{20} = 0.41$, $P = 0.69$; 23 h: $t_{20} = 0.45$, $P = 0.65$).

Either Norway rats fail to increase their reliance on socially acquired information in response to indirect threat of predation or our manipulations of cover and distance to a harbourage site were not sufficient to elicit antipredator behaviours in our subjects. There is reason to suspect that our experimental conditions failed to elicit strong antipredator responses in observers.

If subjects feared predation when eating in the open and relatively far from the safety of a nestbox, they would be expected to eat less than subjects eating under cover

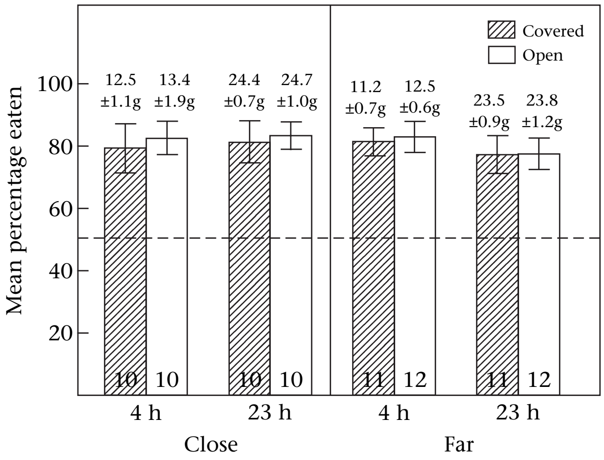

Figure 2. Mean ± SE percentage of demonstrators' diet eaten by observers in experiment 1. Numbers within histograms = *N*/group; numbers above histograms = $\overline{X} \pm$ SE g eaten by observers. Dashed line = expected value on the null hypothesis.

and close to home. However, we found no effect of distance to the nestbox (2 × 2 ANOVA: $F_{1,39} = 0.01$, $P = 0.928$), presence of cover at the feeding site ($F_{1,39} = 0.11$, $P = 0.74$), or their interaction ($F_{1,39} = 0.08$, $P = 0.77$) on the amount of food eaten by subjects. Subjects feeding in the open at a distance from the nestbox ate no less than did subjects eating under cover close to their nestbox (4 h: $t_{20} = 0.00$, $P = 0.99$; 23 h: $t_{20} = 0.11$, $P > 0.95$; Fig. 2), suggesting that the indirect cues that we used to signal predation risk did not elicit strong antipredator responses.

EXPERIMENT 2: DIRECT PREDATION RISK

In experiment 2, we examined effects of direct rather than indirect cues of predation risk on use of social cues in foraging. Although observer rats were always safe in their floor enclosures, a pair of domestic cats, *Felis domesticus*, was present in the room where testing of observer rats took place. The effectiveness of this procedure in eliciting antipredator behaviour in our subjects was clearly demonstrated in a pilot study.

During a 23-h pilot test, we placed food bowls and cover 1.3 m from the nestbox and allowed the pair of cats to wander freely about the room in which observers were confined in the enclosures. Two of six observers ate less than 2 g in 23 h, and the remaining four observers ate no food at all. Only when we moved food bowls and cover to within 15 cm of the nestbox did subjects ($N = 6$) reliably eat during the 23-h test ($\overline{X} \pm SE = 9.9 \pm 0.7$ g in 23 h), but they still ate less than subjects in a control group ($N = 6$) that were allowed to feed without cats in the room (24.4 ± 1.9 g in 23 h).

Although indirect predation risk (distance from nestbox to feeding site) had no effect on observers' food intake in experiment 1, during which no predators were present, in the present pilot study, when predators were present, distance from the nest site to the feeding site profoundly affected the subjects' food intake. Apparently, effects of indirect and direct cues of predation risk on feeding interacted, resulting in prey responding to indirect cues of predation risk only when there were direct cues of predators present.

Methods

Subjects

Seventy-four experimentally naïve, female Long–Evans rats served as observers and an additional 74 rats that had served as subjects in previous experiments served as demonstrators. Two neutered, adult male house cats served as predators.

Apparatus and diets

The apparatus and diets were the same as those used in experiment 1 except that we always placed food bowls both under cover and 15 cm from the entrance to the nestbox.

Procedure

The procedure was identical to that of experiment 1 except that for the 39 subjects assigned to three predator conditions, two house cats either: (1) roamed free in the room containing the floor enclosures where we tested observers ($N = 12$), (2) were confined in a large cage in the middle of the room ($N = 12$ observers), or (3) were confined in the large cage in the middle of the test room for 4 h, and then removed ($N = 15$ observers). We treated observers assigned to three control groups ($N = 35$) just as we treated observers assigned to their respective predator conditions except that we never introduced cats into the experimental room while observers assigned to control conditions were there.

Ethical note. Behaviour of the rats assigned to the predator condition and of the cats was monitored on CCTV and recorded on a time-lapse video recorder. We reviewed tapes the day after they were recorded to ensure that there was no physical contact between cats and rats. Although the cats sometimes stalked rats as they emerged from the nestbox and occasionally attempted to pounce on them, the enclosures containing the rats prevented any contact between predators and potential prey.

Results and Discussion

Because 29 of the 39 observers assigned to the various predator conditions ate less than 0.5 g during the first 4 h of testing, we discuss below only data describing observers' food intake during the entire 23 h of testing. One observer assigned to the control condition failed to eat during the 23-h test period.

Subjects assigned to experimental conditions ate much less during the 23-h test period than subjects assigned to control conditions (ANOVA: $F_{1,67} = 96.9$, $P < 0.0001$; Fig. 3), indicating that subjects in the experimental condition were responding to the potential threat of predation. Furthermore, the significant interaction in total amount eaten by observers between condition (experimental and

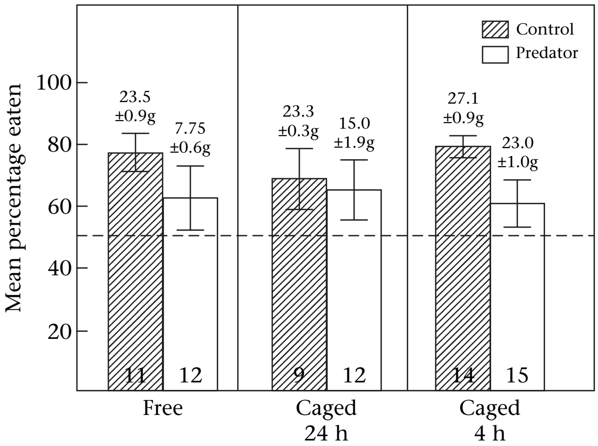

Figure 3. Mean ± SE percentage of demonstrators' diet eaten by observers in experiment 2. Numbers within histograms = N/group; numbers above histograms = $\overline{X} \pm SE$ g eaten by observers. Dashed line = expected value on the null hypothesis.

control) and type of exposure to predators ($F_{2,67} = 13.9$, $P < 0.0001$; Fig. 3) indicates that subjects assigned to experimental conditions perceived the risk of predation as we had intended.

Despite the apparent adequacy of our independent variable, subjects assigned to experimental and control conditions did not differ in their preferences for their respective demonstrators' diets ($F_{1,67} = 2.33$, $P = 0.13$; Fig. 3). Whereas observers assigned to each of the three control groups showed a significant tendency to eat more of their respective demonstrators' diets than would be expected by chance, subjects in none of the three predator groups did so (Table 2, Fig. 3). This tendency for subjects exposed to predators to eat a lesser (not greater) percentage of the diet eaten by demonstrators than subjects not exposed to predators is not consistent with the hypothesis that increasing predation risk leads to increased dependence on social learning. Similar reduced choosiness has been reported for food preferences (e.g. Cerri & Fraser 1983; Metcalfe et al. 1987; Ibraham & Huntingford 1989) and mate preferences of females (Forsgren 1992; Hedrick & Dill 1993) when risk of predation is elevated.

EXPERIMENT 3: RISK OF INGESTING TOXINS

Although formal models have focused on effects of predation risk on use of social information, other environmental factors that increase potential costs of individual assessment of foods (e.g. Dewar 2004) should have effects similar to those of enhanced risk of predation.

Animals are sensitive to individually acquired information regarding the risks of sampling new foods. For example, wild Norway rats that have repeatedly experienced illness after ingesting each of a series of unfamiliar foods will starve themselves for days rather than ingest a new, safe, unfamiliar food placed in their cages (Richter 1953; Rozin & Schulkin 1990). The rats generalize from experience of repeated associations between food novelty and illness and subsequently treat all unfamiliar foods as toxic and dangerous to sample.

In the present experiment, we examined the effect of previous encounters with toxic, unfamiliar foods on domesticated rats' use of socially acquired information when selecting between further unfamiliar foods. On the hypothesis that increased potential risk of individual assessment of alternatives increases reliance on socially acquired information in decision making, we predicted that increased experience with unfamiliar, toxic foods should result in enhanced reliance on socially acquired information when choosing between new foods.

Table 2. One-tailed Student's *t* tests on the amount of demonstrators' diets eaten by observers assigned to the six groups in experiment 2 (Fig. 3)

Group	*t*	df	*P*
Free			
Predator	1.21	11	<0.25
Control	4.43	10	<0.002
Caged 24 h			
Predator	1.55	11	<0.15
Control	8.08	8	<0.05
Caged 4 h			
Predator	1.41	14	<0.18
Control	8.08	13	<0.0001

Methods

Subjects

Sixty-four 7-week-old, female Long–Evans rats served as observers. An additional 64 9-week-old female rats that had served as subjects in other experiments served here as demonstrators.

Apparatus

The experiment was conducted in the stainless-steel hanging cages used during preference induction in experiments 1 and 2.

Diets

By adding respectively 1 g of ground anise (diet ani), 2.0 g of ground marjoram (diet mar), 0.5 g of ground thyme (diet thy), or 0.5 g of ground cumin (diet cum) to sufficient powdered diet 8640 to equal 100 g, we prepared four distinctively flavoured diets in addition to diets cin and coc that we used in experiments 1 and 2. We purchased all four flavourants from The Horn of Plenty (Dundas, Ontario). Diets ani, mar, thy and cum, like diets cin and coc, have each been shown previously to support social learning of food preferences (Galef & Whiskin 1992).

Procedure

Training. To ensure that observers ate the unfamiliar foods offered to them, we placed all observers on 23-h/day deprivation schedule and offered them powdered diet 8640 for 1 h/day for 2 consecutive days. After a third 23-h period of food deprivation, we gave observers assigned to the 1-experience/experimental condition ($N = 10$) a bowl of diet ani and then injected each observer with a 0.13-M lithium-chloride solution (LiCl) equivalent to 1% of its body weight.

Observers assigned to the 2-experience/experimental condition ($N = 10$) remained on the feeding schedule for a total of 5 days. They ate: (1) diet ani on the third day of deprivation, (2) diet 8640 on the fourth day of scheduled feeding and (3) diet mar on the fifth day of scheduled feeding. We injected the observers with LiCl immediately after they ate diets mar and ani. Observers assigned to the 4-experience/experimental condition ($N = 12$) remained on scheduled feeding for a total of 12 days. Each of these observers ate diet ani on day 3, diet 8640 on days 4 and 5, diet mar on day 6, diet 8640 on days 7 and 8, diet thy on day 9, diet 8640 on days 10 and 11, and diet cum on day 12. We injected them with LiCl immediately after they ate each of the four unfamiliar, distinctively flavoured diets ani, mar, thy and cum. At the end of training, each observer had ad libitum access to pellets of diet 8640 for 24 h before the start of testing.

We treated observers assigned to 1-experience ($N = 10$), 2-experience ($N = 10$) and 4-experience ($N = 12$) control conditions exactly as we treated observers assigned to their respective experimental conditions except that we injected them with isotonic saline solution instead of LiCl.

Social learning. Twenty-four hours after each observer had completed training, we placed her together with a demonstrator rat that had just eaten either diet cin or diet coc for 1 h. To ensure that demonstrators ate the diet we offered to them before they interacted with observers, 3 days before a demonstrator was to interact with its observer, we placed the demonstrator in a hanging cage on a 23-h schedule of food deprivation, eating diet 8640 for 1 h/day for 2 days. On the third day of scheduled feeding, 1 h before a demonstrator was scheduled to interact with an observer, we placed a weighed container of either diet cin or diet coc in the demonstrator's cage for 1 h.

Testing. Immediately after an observer interacted with a demonstrator, we returned the observer to its home cage and gave it access to two weighed food cups, one containing diet cin and the other diet coc. Twenty-three hours later, we removed both food cups, weighed them and calculated the percentage of each observer's total intake of the diet that its demonstrator had eaten.

Results and Discussion

We lost data from three of the 24 subjects assigned to the 4-experience treatment condition when one demonstrator failed to learn to eat during training and two observers spilled food during testing.

Observers in both experimental and control groups ate significantly more than 50% of the diet that their respective demonstrators had eaten (Student's t tests: experimental group: $t_{30} = 4.58$, $P < 0.0001$; control group: $t_{29} = 5.56$, $P < 0.0001$; Fig. 4), indicating that they used socially acquired information when selecting foods. However, neither observers assigned to control and experimental conditions (2 × 3 ANOVA: $F_{1,55} = 0.05$, $P = 0.82$; Fig. 4), nor observers assigned to 1-experience, 2-experience and 4-experience conditions ($F_{2,55} = 1.60$, $P = 0.21$) differed in the percentage of their intake of the diet eaten by their respective demonstrators, and the interaction between the effects of independent variables was not significant ($F_{2,55} = 0.371$, $P = 0.692$).

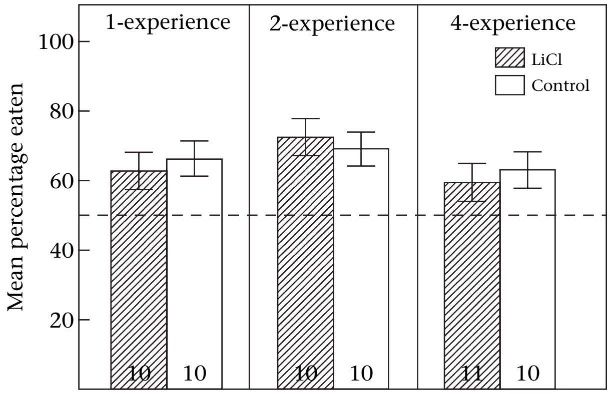

Figure 4. Mean ± SE percentage of demonstrators' diet eaten by observers in experiment 3. Numbers within histograms = *N*/group. Dashed line = expected value on the null hypothesis.

In summary, observers' prior experience of illness after ingesting unfamiliar foods had no effect on their reliance on socially acquired information when choosing between two unfamiliar foods. It might be argued that, if we had examined subjects' food intakes sooner than we did, before they had the opportunity to learn that the two foods offered to them were equally valuable, we might have found an effect of predation risk on use of social information. We did weigh food cups 4 h after we introduced them into subjects' enclosures, but only 12 subjects in the six groups ate during that 4-h period.

GENERAL DISCUSSION

Experiments 1 and 2 are not the first to fail to find that cues of enhanced risk of predation increase reliance on socially acquired information in decision making. For example, Briggs et al. (1996) examined effects of the presence of a restrained predatory fish on mate-choice copying in guppies, *Poecilia reticulata*. They found that, although female guppies showed a significantly enhanced preference for males that they had observed mating, presence of a predator did not increase the females' tendency to mate-choice copy, as would be predicted on the hypothesis that increased predation risk increases both the cost of individual mate assessment and reliance on socially acquired information.

Briggs et al. (1996) suggested three potential explanations for their failure to find the anticipated effect. First, the guppies used in Briggs et al.'s (1996) experiments had been captured in the Quare River, where predators are prevalent. Consequently, guppies from the Quare River may have evolved to act as though predation risk was always high, and may not have assessed predation risk as having increased significantly when a potential predator was in sight. Second, female guppies may have evolved to always rely on social information, because the benefits of doing so remain high regardless of predation risk. Third, when predators are present, female guppies' choosiness may be reduced and their choices may become more random. The finding in experiment 2 of reduced effects of socially acquired information on food preferences of rats when in the presence of a predator are consistent with the last of Briggs et al.'s three explanations for their failure to find increased copying when risk of predation was increased. In experiment 2, all three groups of subjects directly exposed to predators failed to show significantly enhanced preferences for their demonstrators' diets. In more than 20 years of using the same procedures for social induction of food choice that we used in experiment 2, we have never before seen, three times in succession, nonsignificant effects of foods fed to demonstrators on their observers' diet choices.

Some formal models also predict that foragers will be choosy when predation risk is low and will become relatively indiscriminate as risk increases because reducing the time spent in search for and assessment of alternatives should not only reduce exposure to predators but should also reduce selectivity (e.g. Real 1990; Crowley et al. 1991). The results of experiment 2 are consistent with such models. It seems reasonable to assume that when risk of predation is high and spending time outside harbourage sites increases the probability of attack, rats may tend to eat any acceptable foods that they encounter without assuming additional risks searching for potentially more desirable alternatives and evaluating them. We know of no other experiments with mammalian subjects that provide evidence of decreased food selectivity when risk of predation is increased. However, Metcalfe et al. (1987) found that the ability of juvenile salmon to discriminate large (and therefore inedible food pellets) from small, edible ones was impaired when predation risk increased.

Although, as indicated in the Introduction, most models directly concerned with trade-offs between costs of individual assessment and reliance on social cues predict that reliance on social learning will increase with increasing costs of individual exploration and assessment, some formal ecological models suggest that animals' increasing risk of predation should not invariably increase reliance on information acquired from conspecifics. For example, Dewar's (2004) cue reliability model predicts that the cost of making a wrong decision affects the probability of reliance on social information when making foraging decisions. In Dewar's (2004) model, use of socially acquired information is to be expected only when costs of errors resulting from individual assessment exceeds some threshold value.

In experiments 1 and 2, there were no 'wrong' choices; both foods available to subjects were palatable and nutritious. Consequently, the potential cost of choosing one food rather than another was negligible. Possibly, if we increased the potential cost of 'errors', for example, by combining the procedures of experiments 1 and 3 or experiments 2 and 3, so that before we exposed subjects to enhanced predation risk, we had exposed them to experiences that would lead to the expectation that choosing the wrong food would be costly, then subjects would have increased their reliance on social information in the presence of predators. Of course, subjects assigned to each of the three control groups in experiment 2 (those not exposed to predators) used social information in choosing foods, so on Dewar's (2004) model, they must have perceived the situation as one in which there was some cost to making an error in food selection.

We did not expect to fail to find increased reliance on socially acquired information in the foraging decisions of rats when we elevated potential costs of acquiring information independently. Both common sense and most formal theory suggest that when individual learning becomes costly, increased reliance should be placed on previous social learning. Still, despite repeated efforts, we found no evidence of the anticipated effect of increasing the cost of individual assessment on utilization of previously acquired social information when making foraging decisions.

In discussing empirical tests of predictions from ecological theories, Bolker (2005, page 550) proposed: '…almost all of the explanations that were suggested in the heroic age [of theoretical ecology] are true – somewhere, to some extent'. If so, failure to confirm particular theoretical predictions are at least as important as empirical confirmation of such predictions, suggesting both boundary conditions on the particular predictions tested and directions for the future development of models.

Acknowledgments

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