

## Further studies of reliance on socially acquired information when foraging in potentially risky situations

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Results of three previous experiments conducted in our laboratory (Galef & Whiskin 2006, *Animal Behaviour*, **72**, 1169–1176) failed to provide support for the prediction from formal theory that increasing the potential cost of engaging in individual learning increases reliance on socially acquired information. However, weaknesses in the data of each of the three experiments reported in Galef & Whiskin (2006) complicated interpretation of results. Here, we repeated the three experiments using procedures that we modified to improve the quality of the data. Despite success in removing the problems with Galef & Whiskin's (2006) methods, we again found no evidence that exposure to either direct or indirect cues of predation risk increased Norway rats', *Rattus norvegicus*, reliance on socially acquired information. We discuss implications of our repeated failures to confirm a logically consistent prediction from formal theory.

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Formal models exploring environmental conditions that might lead to increased reliance on socially acquired information examine evolutionary trade-offs between potentially expensive, highly reliable, personal information and less expensive, less reliable information acquired from the behaviour of others. Such models predict that as the price of determining for oneself the potential costs and benefits of engaging in alternative courses of action increases, individuals will become more likely to rely on social information (e.g. Boyd & Richerson 1985; Feldman et al. 1996; Laland 2004; Kendal et al. 2005). For example, predation risk increases the cost of personal assessment of alternatives. Consequently, cues indicating increased risk of predation should enhance dependence on information acquired socially whilst decreasing time spent on individual assessment of alternatives (e.g. Lima & Dill 1990; Reynolds & Gross 1990; Sih 1994).

Both individual assessment of the value of alternative foods and information acquired during social interaction with conspecifics influence the food choices of Norway rats, *Rattus norvegicus* (Galef & Whiskin 2001). To personally assess the relative value of alternative, unfamiliar foods, an animal must repeatedly sample each food (Rozin 1969; Rozin & Schulkin 1990), and such sampling

requires individuals to increase the time that they spend finding and sampling alternatives and at enhanced risk of predation. Thus, rats exposed to cues of enhanced risk of predation should decrease the time that they spend evaluating potential foods for themselves, and increase their reliance on any relevant, social information previously acquired from conspecifics.

When attending solely to their own evaluation of alternative foods, rats show no impact of interaction with conspecifics on their food choices, whereas reliance on social information when selecting among foods causes rats to ingest more of the foods that their respective demonstrators ate (Galef & Wigmore 1983), making it easy to determine rats' relative reliance on socially and personally acquired information when selecting foods. Food choices of Norway rats thus provide a useful empirical system in which to explore effects of enhanced predation risk on relative reliance on individually and socially acquired information (Galef & Whiskin 2006).

Although the results of experiments reported in Galef & Whiskin (2006) were not consistent with the hypothesis that increasing predation risk, and thus, potential costs of individual assessment, increased use of socially acquired information, there were problems with the data in each experiment that reduced the likelihood of finding an effect of predation risk on reliance on social learning. As discussed in greater detail in the introductions to experiments 1 and 2, we had difficulty establishing whether our manipulations of predation risk affected subjects' foraging behaviour (experiment 1)

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and whether rats remained sensitive to social information when at high-risk of predation (experiment 2). Here, we modified the procedures of Galef & Whiskin (2006) to eliminate the causes of the problems with the data in previous experiments in our laboratory.

### EXPERIMENT 1: INDIRECT CUES OF PREDATION RISK

Animals foraging either in the open or at a distance from a place of safety are presumably more susceptible to predation than are animals foraging under cover or close to a harbourage site. Consequently, animals exposed to such indirect cues of predation risk might be expected to experience greater potential costs of individual assessment of alternative foods than those foraging under cover or close to shelter. If so, animals foraging in the open would be expected to increase their reliance on socially acquired information when selecting a food to ingest.

In experiment 1 of Galef & Whiskin (2006), observer rats first interacted with demonstrator rats that had eaten one of two distinctively flavoured diets. Individual observers were then placed for 24 h in large floor cages where they could choose between the two diets when diets were: (1) either in the open or under cover and (2) either close to or far from a place of refuge. Galef & Whiskin (2006) found that although observers in all conditions preferred their respective demonstrators' diets, observers feeding in the open and far from shelter showed no greater reliance on the socially acquired information than observers feeding under cover and close to shelter.

On the hypothesis that the manipulations of the presence of cover and distance to a harbourage site while eating altered indirect cues of predation, we predicted that observers eating under conditions that increased their apparent risk of predation would show not only a greater preference for their respective demonstrators' diets than observers foraging in safer conditions, but would also eat less, in total, than observers eating under conditions that minimized their potential exposure to predation. Unfortunately, our manipulations of indirect risk of predation failed to alter not only observers' reliance on socially acquired information, but also the total amount of food that they ate during the 24 h test period. This failure to alter food intake cast some doubt on the adequacy of our manipulations of distance to the nest site and availability of cover at the feeding site as cues of indirect predation risk.

A series of pilot studies that preceded the present experiment allowed us to identify a situation in which indirect cues of predation risk substantially reduced rats' food intake during 10 h of testing. Here, we examined the effect of exposure of observers to these indirect cues of predation risk on their reliance on socially acquired information when choosing a food to eat.

### Methods

#### Subjects

Subjects were 84 female Long-Evans rats that were obtained from Charles River Canada (St Constant, Quebec, Canada) when they were 7 weeks old. At the initiation of these experiments, observers were 10–11 weeks old ( $N = 42$ ) and demonstrators were 11–13 weeks old ( $N = 42$ ). All subjects had participated in other social learning experiments in our laboratory, but had no previous experience of either of the flavoured diets used here.

#### Diets

We prepared two diets, anise diet and marjoram diet, by mixing, respectively, 1 g of bulk ground anise (Horn of Plenty, Dundas, ON, Canada) with 99 g of Teklad Rodent Chow (W) 8640 (Harlan-Teklad, Madison, WI, U.S.A.: diet 8640) and 2 g of bulk ground marjoram (Horn of Plenty) with 98 g of diet 8640.

#### Apparatus

*Preference induction.* Both demonstrators and observers resided in individual stainless-steel hanging cages, measuring  $35 \times 20 \times 20$  cm, and fed from semicircular food cups, measuring 10 cm in diameter  $\times$  5 cm deep, that we filled to less than half their depth, thus preventing spillage.

*Testing observers.* We tested observers individually in floor cages, measuring  $93 \times 63 \times 53$  cm, constructed of galvanized sheet metal,  $\frac{1}{2}$ -inch (1.27 cm) screen and angle iron. The floor of each cage was covered to a depth of approximately 2 cm with wood shavings, and each cage contained a nestbox, measuring  $22 \times 18 \times 15$  cm, with a single entrance, a water bottle and two semicircular food cups identical to those used during preference induction. One food cup contained anise diet and the other marjoram diet (Fig. 1a, b).

Cages of observers assigned to the high-risk condition had uncovered roofs and three open, screen sides, each of which was 45 cm or more from the nearest wall (Fig. 1a). Cages of subjects assigned to the low-risk condition had all four walls and two-thirds of their roofs covered with black Bristol board (Fig. 1b). We illuminated the rooms containing floor cages continuously throughout the 10 h test period.

#### Procedure

*Preference induction.* To begin the experiment, we placed each demonstrator and observer in an individual hanging cage, offered observers ad libitum access to diet 8640 and placed demonstrators on a feeding schedule, eating diet 8640 for 1 h/day for 2 consecutive days. On the third day of demonstrators' scheduled feeding, we provided half the demonstrators with a weighed sample of anise diet and the remainder with a weighed sample of marjoram diet. After 1 h, we weighed each demonstrator's food cup to ensure that it had eaten at least 5 g of diet. We then placed each demonstrator in the hanging cage of an observer, and left the pair undisturbed to interact for 30 min.

*Testing observers.* At the end of the 30 min period of interaction between demonstrator and observer, we placed each observer in a floor cage, randomly assigning observers to high-risk ( $N = 21$ ) and low-risk ( $N = 21$ ) conditions. Ten hours later, we determined each observer's intake of both anise and marjoram diets and then calculated the percentage of its total intake that was the diet that its demonstrator had eaten (i.e. the percentage of anise diet eaten by each observer whose demonstrator had eaten anise diet and the percentage of marjoram diet eaten by each observer whose demonstrator had eaten that diet).

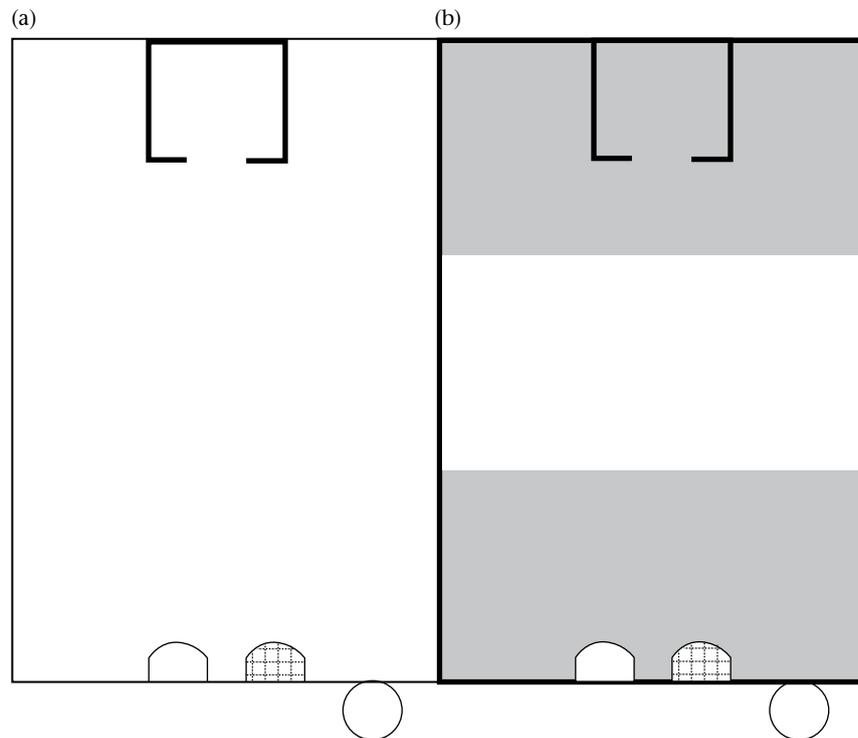
#### Ethical note

The Methods used in the three experiments reported here were approved by the McMaster University Research Ethics Board in June of 2007 (Animal Utilization Proposal no. 07-06-35).

#### Results and Discussion

Two observers assigned to the low-risk group failed to eat more than 1.0 g during testing, and we did not use their data when calculating the mean percentage of demonstrators' diet that observers ate.

As the results of our pilot experiments had led us to expect, observers assigned to the high-risk condition ate significantly less during the 10 h of testing than did observers assigned to the low-risk condition (Student's  $t$  test:  $t_{40} = 2.68$ ,  $P < 0.01$ ; Fig. 2a).



**Figure 1.** Overhead schematic of (a) high-risk and (b) low-risk floor cages in which observers' food preferences were determined in experiments 1, 2 and 3. Heavy lines represent opaque walls and light lines represent screen barriers. Shaded areas were covered with black Bristol board.

Furthermore, observers assigned to both high-risk and low-risk conditions ate significantly more of their respective demonstrators' diets than would be expected by chance (high-risk:  $t_{20} = 4.06$ ,  $P < 0.0003$ ; low-risk:  $t_{18} = 6.03$ ,  $P < 0.0001$ ; Fig. 2b).

However, despite the evident effectiveness of our independent variable in reducing the food intake of observers assigned to the high-risk condition and the access of observers to relevant social information, we found no effect of exposure to indirect cues of predation risk on the percentage of demonstrators' diets eaten by observers ( $t_{38} = 0.44$ ,  $P = 0.66$ ; Fig. 2b). Indeed, subjects assigned to the low-risk condition showed a slightly greater influence of their demonstrators' diets on their food choices than did observers assigned to the high-risk condition.

## EXPERIMENT 2: DIRECT CUES OF PREDATION RISK

Experiment 2 of Galef & Whiskin (2006) examined effects of the physical presence of potential predators (domesticated cats, *Felis domesticus*) on Norway rats' use of socially acquired information when selecting a food. Although such direct cues of predation risk reduced observer rats' food intakes during testing, in each of three studies that differed in the extent of the exposure of observers to predators, observers failed to show a preference for their respective demonstrators' diets. This was the first time in more than 25 years of studying effects of demonstrator rats on their observer rats' food preferences (for review, see Galef 1988, 1996, 2001) that we had seen even two successive failures of demonstrator rats to influence their observers' subsequent food choices. Possibly, when the risk of predation is sufficiently high, rats will accept any potential food that they encounter, thus reducing the time that they spend searching for and evaluating alternatives and, consequently, exposed to predators (Briggs et al. 1996). Others have reported similar reductions in choosiness or selectivity when the direct threat of predation was elevated (e.g. Cerri & Fraser 1983; Metcalfe

et al. 1987; Ibraham & Huntingford 1989; Forsgren 1992; Hedrick & Dill 1993).

Here, we exposed observer rats to the odour of a potential predator rather than to the presence of the predator itself (Galef & Whiskin 2006, experiment 2), and examined the effect of such exposure on reliance on socially acquired information when selecting foods. We anticipated that the odour of a cat would produce a lower level of alarm than the actual presence of a cat, and might, therefore, provide a situation where observer rats would show both reduced levels of intake, thus indicating that they were aware of the elevated risk of predation, and increased reliance on social cues when selecting a food to eat.

## Methods

### Subjects

We used 72 female Long-Evans rats with histories identical to those of subjects in experiment 1: 36 served as demonstrators and 36 served as observers in this experiment.

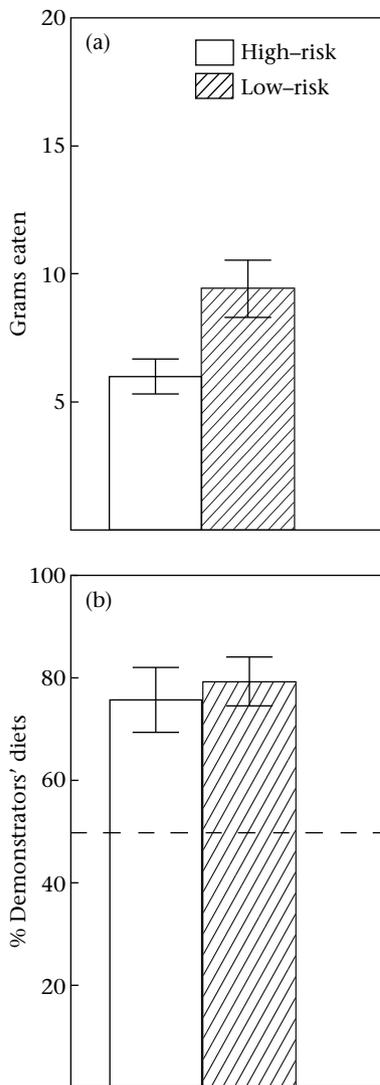
### Diets and apparatus

We used the same diets and apparatus that we had used in experiment 1.

### Procedure

The procedure of experiment 2 was similar to that of experiment 1 with one exception: following each observer's interaction with a demonstrator and just before we moved an observer rat into a low-risk floor cage (Fig. 1b), we fastened a piece of cloth, measuring  $18 \times 22$  cm, between the Bristol board and the screen behind and between the two food cups in each cage.

Immediately before attaching a cloth to the cage of each subject that we had randomly assigned to the high-risk condition, we rubbed the cloth on a domestic cat for 5 min (Zangrossi & File 1992).



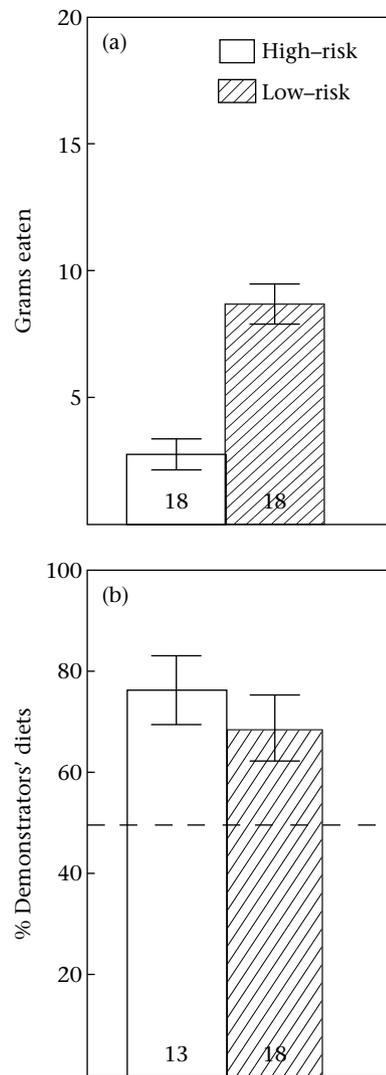
**Figure 2.** Results of experiment 1. (a) Mean grams eaten during a 10 h test by observers assigned to high-risk and low-risk conditions. (b) Mean percentage of demonstrators' diets eaten during testing by observers assigned to high-risk and low-risk conditions. Dashed line = expected percentage of demonstrators' diet eaten by observers' if observers' food choices were not influenced by prior interaction with demonstrators. Numbers inside histograms =  $N/\text{group}$ . Flags =  $\pm 1$  SE.

To roughly equate the dampness of cloths attached to the cages of observers assigned to high- and low-risk conditions, we slightly dampened the cloth that we attached to the cage of each observer assigned to the low-risk condition. To ensure that observers assigned to the low-risk condition were not exposed to cat odour, we placed cages of observers assigned to high- and low-risk conditions in separate rooms without air exchange.

### Results and Discussion

Five of the 18 observers assigned to the high-risk condition failed to eat during testing, and we could not use their data in calculating the percentage of demonstrators' diets eaten.

Presence of cat odour severely depressed the intake of observers assigned to the high-risk condition relative to observers assigned to the low-risk condition (Student's  $t$  test:  $t_{34} = 5.79$ ,  $P < 0.0001$ ; Fig. 3a). Even when we removed from consideration the five observers that failed to eat during testing, the marked effect of the presence of cat odour on intake was still evident ( $t_{29} = 4.39$ ,  $P < 0.0001$ ).



**Figure 3.** Results of experiment 2. (a) Mean grams eaten during a 10 h test by observers assigned to high-risk and low-risk conditions. (b) Mean percentage of demonstrators' diets eaten during testing by observers assigned to high-risk and low-risk conditions. Dashed line = expected percentage of demonstrators' diet eaten by observers' if observers' food choices were not influenced by prior interaction with demonstrators. Numbers inside histograms =  $N/\text{group}$ . Flags =  $\pm 1$  SE.

Observers assigned to both high- and low-risk conditions showed a significant tendency to prefer their respective demonstrators' diets (high-risk:  $t_{12} = 3.99$ ,  $P < 0.002$ ; low-risk:  $t_{17} = 2.57$ ,  $P < 0.02$ ; Fig. 3b). However, despite the effectiveness of cat odour in reducing both the food intake of observers and the attention of observers to information previously acquired from their respective demonstrators, we failed to find a significant effect of the presence of cat odour on observers' reliance on socially acquired information ( $t_{29} = 1.00$ ,  $P = 0.33$ ; Fig. 3b).

### EXPERIMENT 3: RISK OF INGESTING TOXINS

Failures to find predicted effects are, of course, difficult to interpret. It is always possible that some minor modification in experimental procedures would have produced the predicted outcome. For example, Webster & Laland (2008) suggested that Galef & Whiskin's (2006) failure to find predicted effects of cues of predation risk on reliance on socially acquired information was the result of presenting demonstrated and nondemonstrated foods in

the same location, thus minimizing costs associated with evaluating alternatives. Webster & Laland (2008) suggested that if the food bowls containing demonstrated and nondemonstrated foods had been some distance apart, the predicted effect would have been observed. Unfortunately, when food bowls are spatially separated and cues of predation are present, most rats eat from only a single food bowl, presumably the one that they first encounter (B. G. Galef & E. E. Whiskin, unpublished observation), so the use of spatial separation of food bowls to increase the cost of individual assessment of alternatives was not possible.

More generally, Webster & Laland's (2008) argument suggests that increasing the cost of individual assessment of alternatives would increase the effects of predation on reliance on socially acquired information. Indeed, although many formal models predict that reliance on social learning should generally increase with increasing cost of individual assessment, there is also reason to believe that the cost of making a wrong decision should also influence the probability of reliance on socially acquired information. For example, Dewar's (2004) cue-reliability model predicts that use of socially acquired information is to be expected only when the cost of errors from individual assessment exceeds some threshold value. Consequently, it might be argued that observers choosing between diets in experiments 1 and 2 of the present series and of Galef & Whiskin (2006) failed to show increased reliance on socially acquired information when the cost of individual assessment increased because the cost of making an error as a result of individual assessment was insufficient. If so, increasing the perceived risk to observers of assessing diets for themselves should increase the probability that observers will attend to socially acquired information when the cost of engaging in individual assessment is increased. In experiment 3, we increased the baseline level of risk of assessment of alternative diets to examine the possibility that our failure to find effects of predation risk on reliance on socially acquired information in experiments 1 and 2 reflected the generally low cost of assessing alternatives in those two experiments. Experiment 3 was essentially a replication of experiment 2, but in experiment 3, we used as observers animals that had previous experience eating unfamiliar foods and becoming ill. Such observers should have perceived personal assessment of alternative diets as potentially costly, and might therefore be more responsive to cues of predation than observer rats without prior experience ingesting unfamiliar foods and becoming ill when deciding whether to rely on socially acquired information in choosing a food.

## Methods

### Subjects

Fifty-two female, Long-Evans Norway rats, similar to those that participated in experiments 1 and 2, but 3 weeks older, served as subjects: 26 as observers and 26 as demonstrators. None had previous experience of any of the four flavoured diets used in the present experiment.

### Diets

We prepared cumin and nutmeg diets by combining, respectively, 0.5 g of bulk ground cumin (Horn of Plenty) or 0.5 g of bulk ground nutmeg (Horn of Plenty) with 99.5 g of diet 8640. We also used the anise- and marjoram-flavoured diets that we used in experiments 1 and 2.

### Procedure

*Learning aversions to novel diets.* We placed observer rats in individual hanging cages and fed them diet 8640 for 1 h/day for 2 consecutive days. Following a third 23 h period of food deprivation,

we fed 13 observers the cumin diet and 13 observers the marjoram diet for 1 h and, after ensuring that each observer had eaten at least 5 g, we injected each observer with 0.13 M lithium-chloride solution equal to 1% of its body weight. We then gave each observer ad libitum access to diet 8640 for 24 h to recover from the effects of injection.

At the end of the 24 h recovery period, we again food deprived each observer for 23 h before offering them a different diet: observers that had eaten the cumin diet received the nutmeg diet for 1 h and those that had eaten the nutmeg diet received the cumin diet for 1 h. We again determined that each observer had eaten at least 5 g before injecting each with 0.13 M lithium-chloride solution equal to 1% of its body weight. We then gave each observer ad libitum access to diet 8640 for 24 h before starting preference induction.

*Preference induction.* As in experiments 1 and 2, each observer interacted for 30 min with a demonstrator rat that had eaten either the anise or the marjoram diet.

*Testing.* As in experiment 2, each observer was placed in a covered floor cage (Fig. 2b) and given a choice between anise and marjoram diets either in the presence (high-risk condition) or absence (low-risk condition) of cat odour.

## Results and Discussion

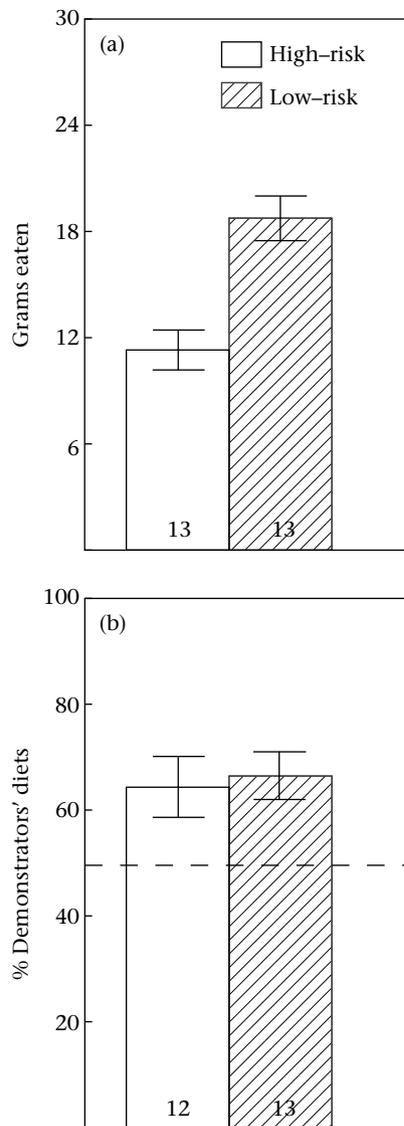
One observer assigned to the high-risk condition failed to eat during testing, so we could not use its data in calculating the mean percentage of demonstrator's diet eaten.

As in experiment 2, observers assigned to the high-risk condition ate significantly less than observers assigned to the low-risk condition ( $t_{24} = 2.74$ ,  $P < 0.001$ ) and this difference in intake was still present when data from the subject that failed to eat during testing was excluded ( $t_{23} = 2.62$ ,  $P < 0.001$ ; Fig. 4). Again, as in experiment 2, observers assigned to both high-risk and low-risk conditions showed significant preferences for their respective demonstrators' diets (high-risk:  $t_{11} = 2.50$ ,  $P < 0.03$ ; low-risk  $t_{12} = 3.65$ ,  $P < 0.01$ ; Fig. 4), and once again we found no difference in the reliance of subjects assigned to high- and low-risk conditions on socially acquired information ( $t_{23} = 0.41$ ,  $P = 0.79$ ; Fig. 4). In summary, a manipulation intended to increase observers' perception of the costs of assessing unfamiliar foods had no effect on the extent of their reliance on socially acquired information when direct cues of predation were present.

## GENERAL DISCUSSION

Common sense suggests, and formal models predict, that as the cost to an individual of personally assessing alternatives increases, reliance on relevant socially acquired information should also increase. Indeed, Webster & Laland (2008) reported that minnows, *Phoxinus phoxinus*, increase their reliance on social cues when selecting a prey patch in the presence of a predator. Our repeated failure to find a similar effect in Norway rats either here or in Galef & Whiskin (2006) is problematic and requires discussion.

First, it might be argued that using domesticated animals as subjects in laboratory tests of hypotheses derived from evolutionary theory is inappropriate. Indeed, it might be argued that failure to find evidence of an adaptive response to cues indicating enhanced risk of predation in animals that have been maintained for hundreds of generations in environments where predation pressures are absent would be expected. However, laboratory experiments with domesticated rats testing other predictions from formal models have repeatedly found evidence consistent with



**Figure 4.** Results of experiment 3. (a) Mean grams eaten during a 10 h test by observers assigned to high-risk and low-risk conditions. (b) Mean percentage of demonstrators' diets eaten during testing by observers assigned to high-risk and low-risk conditions. Dashed line = expected percentage of demonstrators' diet eaten by observers' if observers' food choices were not influenced by prior interaction with demonstrators. Numbers inside histograms =  $N/\text{group}$ . Flags =  $\pm 1$  SE.

theory. For example, formal theory predicts that dissatisfied animals should be more reliant on socially acquired information than satisfied animals (Schlag 1998; Laland 2004), and, in accord with this prediction, domesticated rats show increased reliance on socially acquired information when dissatisfied (Galef et al. 1990; Galef & Whiskin 2006) even though laboratory-maintained rats are protected from the dissatisfactions that trigger enhanced reliance on social information. Thus, neither the artificiality of laboratory situations nor the domestication of subjects seems adequate to explain inconsistencies between theoretical predictions and empirical findings regarding rats' responses to cues of predation risk.

Second, it is of course always possible that under conditions other than those examined here or in Galef & Whiskin (2006), we would have found robust effects of both direct and indirect cues of predation risk on observers' reliance on socially acquired information. Still, the results of the present experiments together with

those reported in Galef & Whiskin (2006) suggest that, at the least, the effect of increasing potential costs of individual assessment of alternatives on reliance on socially acquired information is less general than theory suggests.

This is not the first time that we have been unable to find evidence of behaviours that would seem to have the potential to considerably enhance the ability of Norway rats to survive in natural circumstances. For example, despite the robust tendency of both wild and domesticated Norway rats to show enhanced preferences for foods that healthy conspecific demonstrators have eaten (for reviews see Galef 1988, 1996, 2001), many years of effort both in our laboratory and elsewhere have failed to provide any evidence that rats avoid ingesting foods that sick or unconscious demonstrators have eaten. Indeed, rats' preferences for foods eaten by ill or unconscious demonstrators are at least as strong as their preferences for foods eaten by healthy demonstrators (e.g. Galef et al. 1983; Galef et al. 1990). Although creating both formal models (Noble et al. 2001) and informal arguments (Galef 1985) as to why rats should behave as they do and not learn to avoid foods eaten by ill or unconscious conspecifics is relatively simple, such post hoc explanations (including the one provided below for the failure of rats to increase reliance on socially acquired information when individual learning is costly) are inherently suspect.

When not living as human commensals, Norway rats are exploited by a broad range of mammalian, avian and reptilian predators. Possibly, rats' failure to increase reliance on socially acquired information under enhanced risk of predation reflects a history of selection in environments where predation risk while foraging is always high and reliance on socially acquired information is always advantageous, even when cues of enhanced predation risk are not present. If so, evidence of effects of increased predation risk on reliance on socially acquired information might be more likely to be found in species that, outside the laboratory, are less heavily preyed upon than are the Norway rats that were subjects in the present experiments.

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