13 Adaptive Trade-offs in the Use of Social and Personal Information

RACHEL L. KENDAL, ISABELLE COOLEN
& KEVIN N. LALAND

13.1. Introduction

Social learning—the acquisition of knowledge from others—provides naive animals with information relevant to many life skills, including when, where, what, and how to eat (Galef and Giraldeau 2001), with whom to mate (D. White 2004) or fight (Peake and McGregor 2004), and which predators to avoid and how (A. Griffin 2004). Over the last century, a common assumption of behavioral ecologists, ethologists, and anthropologists has been that such copying is inherently adaptive. Animals are deemed to gain fitness benefits by learning from others, since they acquire adaptive information while avoiding some of the costs (predation risk, search costs, etc.) of learning for themselves—the costs of "personal information" acquisition. However, the use of social information does not, in fact, guarantee success (Boyd and Richerson 1985, 1995; Rogers 1988; Giraldeau et al. 2002). Individual animals face evolutionary trade-offs between the acquisition of costly but accurate information and the use of cheap but potentially less reliable information[1] (Boyd and Richerson 1985), here manifest in a trade-off between reliance on personal and social information.

Theoretical models investigating the adaptive advantages of social learning predict that it should not be employed in an indiscriminate manner, but rather, individual animals should have evolved flexible strategies that dictate precise circumstances under which they copy others (Laland 2004). Such analyses

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1. Some readers may object to our use of the phrase "unreliable information," on the grounds that the cues that form the bases of social learning are not so much reliable or unreliable as more or less informative. While we are sympathetic to this objection, we persist with the terminology for three reasons. First, whether appropriate or not, use of such terms is common in the literature that we review. Second, there are no obvious alternative expressions that we find entirely satisfactory. For instance, an "uninformative cue" does not distinguish between a signal designed to mislead and a cue that contains no information at all. Third, it is apparent that we are frequently concerned with the reliability and error associated with potential social and asocial sources of information, for which our use of "reliable or unreliable information" can be taken as shorthand.

reveal that social learners adopting a pure strategy of random copying would have higher fitness than asocial learners only when copying is rare, that is, when most potential "demonstrators" of new behavior would be asocial learners who have acquired accurate information by directly sampling the environment (Boyd and Richerson 1985, 1995; Rogers 1988; Giraldeau et al. 2002). As the frequency of social learners increases, the value of using social information typically declines, as the proportion of individuals demonstrating accurate personal information decreases. At the extreme, with all individuals exhibiting random copying, no one would have acquired accurate personal information by sampling the environment. In order for it to be adaptive, individuals must use social learning selectively and engage in the collection of accurate personal information some of the time (Galef 1995; Laland 2004).

Despite rapid growth in the field of animal social learning, the circumstances under which individuals rely on alternative sources of information remain relatively unexplored. What rules have evolved in animals to specify how they should exploit personal and social information? Do animals copy the behavior of others when they are uncertain how to solve a problem, or, perhaps, when it is easy to do so? Do they have rules dictating from whom they should copy—for example, high-status or apparently successful individuals? Is social learning a last resort when asocial learning has failed, or first port of call? Following Laland (2004), the term "social learning strategies" is used here to equate evolved learning heuristics with those strategies commonly analyzed using evolutionary game theory (Maynard Smith 1982) and to encourage theoretical analysis. Naturally, animals need not be aware that they are following a strategy, nor understand why such strategies may work.

In this chapter we review the predictions arising from theoretical models and outline the current empirical support for several social learning strategies, focusing largely on our own experimental studies and other recent work (Laland 2004; Kendal et al. 2005; Galef 2006). We draw attention to adaptive trade-offs in the use of social and personal information. Laland (2004) distinguished between two classes of social learning strategy: "when" strategies, which dictate the circumstances under which individuals copy others, and "who" strategies, which specify from whom individuals learn. We address each in turn.

13.2. "When" strategies

13.2.1. COPY WHEN ASOCIAL LEARNING IS COSTLY

Trial-and-error learning is often both costly and error prone. Direct interaction with the environment may entail fitness costs, such as injury, sick-

ness, and predation, as well as "missed opportunity" costs, such as the loss of time or energy that could be allocated elsewhere. These costs are expected to restrict an animal's investment in asocial learning, resulting in consequent reliance on social learning, which may lead to "errors" such as a failure to perform an adaptive behavior or the retention of a suboptimal variant. Where these costs are substantive, we anticipate that selection may plausibly have favored shortcuts to adaptive solutions, notably copying others (Boyd and Richerson 1985).

13.2.1.1. *Theoretical background*
Several theoretical analyses conclude that reliance upon social information should increase as the costs associated with acquiring personal information increase (Boyd and Richerson 1985, 1988; Feldman et al. 1996; but see section 13.2.2.3). Boyd and Richerson (1985) propose a "costly information hypothesis," which depicts an evolutionary trade-off between acquiring accurate but costly information versus less accurate but cheap information. While this trade-off may manifest itself at different levels, for our purposes it can be summarized as the idea that when information is too costly to acquire or to utilize personally, individuals will take advantage of the relatively cheap information that can be learned from others. A similar argument was proposed by Bandura (1977, 12), who stated that "the more costly and hazardous the possible mistakes, the heavier is the reliance on observational learning from competent examples." Although the costly information hypothesis lays emphasis on the costs of acquiring personal information, the same reasoning holds with respect to the costs of using personal information.

13.2.1.2. *Empirical evidence*
Laland and Williams (1998) provide an experimental example in which fish were seemingly prepared to pay the costs of using suboptimal foraging information provided by conspecifics in order to avoid the risk of predation associated with the isolated learning of a more efficient foraging route. Small groups of "founder" guppies (*Poecilia reticulata*) were trained to take either an energetically costly circuitous route to a feeder or a less costly direct route. In a transmission chain design, these founders were gradually replaced with naive conspecifics, one individual being replaced each day for a week. Three days after all the trained individuals had been removed, the groups of fish whose founders were trained to swim the circuitous route continued often to use this route to reach the feeder, despite its cost relative to the available direct route. In addition, individuals in groups with founders trained to take the circuitous route took significantly longer to switch to the short route than did otherwise-
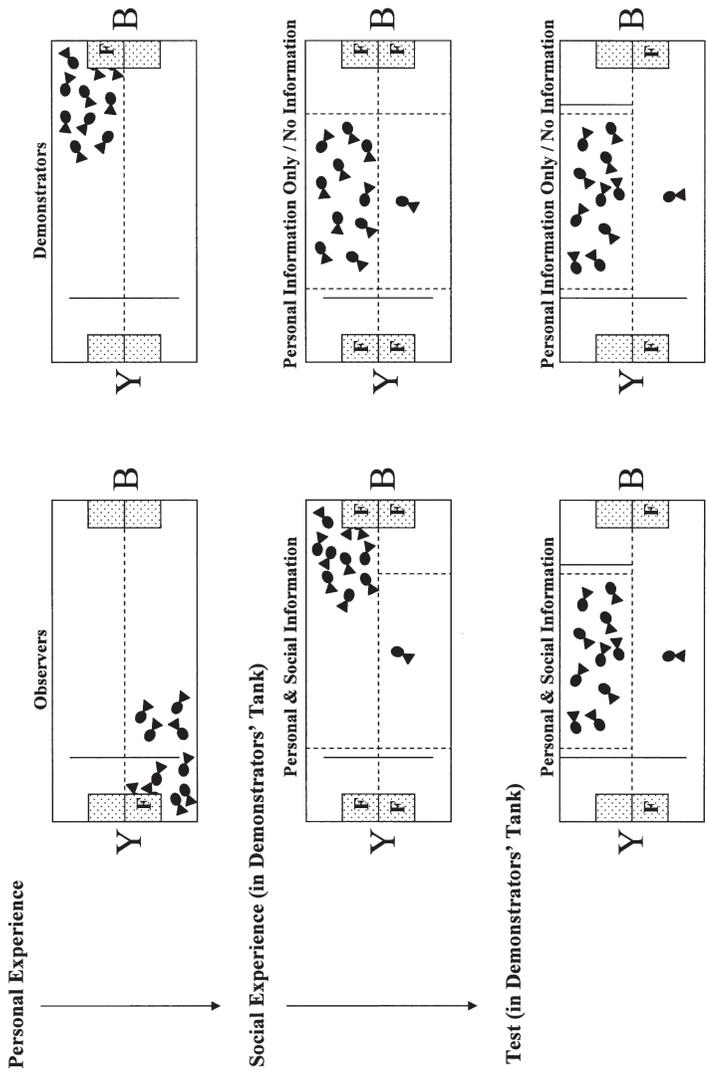
FIGURE 13.1. Experimental procedure, showing the personal experience training of observer guppies to feed (food designated as F) from either blue (B) or yellow (Y) feeders behind an opaque barrier, and demonstrators to feed at the open end of the tank; the social experience procedure for guppies in all conditions (prior personal and social information, personal information only, and no information); and the identical test period for all conditions, in which observers must lose visual contact with the constrained demonstrator shoal in order to feed at the trained feeder. Solid lines indicate opaque partitions and dashed lines indicate transparent partitions. From Kendal et al. 2004.

equivalent solitary fish. It is well established that guppies are reluctant to leave conspecifics and forage alone due to predation risk (see Day et al. 2001); thus, the perpetuation of a suboptimal behavioral tradition in these fish can be explained by the relative cost of acquiring personal information.

Losing visual contact with shoal[2] members is potentially costly to small fish like guppies, since isolation leaves them vulnerable to predation (see Day et al. 2001 and references therein). Kendal et al. (2004) exploited this observation to manipulate the cost of using previously acquired personal information in a social foraging experiment, in the process providing a second illustration of animals utilizing a "copy when asocial learning is costly" strategy. Individuals were allocated to one of three conditions in which they received either (1) prior personal information only, (2) prior personal and social information, or (3) no information (see fig. 13.1). Individuals in the first two conditions had the opportunity to learn through direct experience that food was located in only one of two differently colored feeders at the ends of their tanks. The feeder that contained food was located behind an opaque barrier while the one that did not was in open water. In the next stage of the experiment, one group was then provided with conflicting social information. The fish in the condition that received both personal and social information (2) observed a shoal of demonstrators feed at the feeder in the open water, which their personal experience had indicated never contained food, whereas fish in the other two conditions, (1) and (3), were constrained in the central section of the tank, facing nondemonstrating fish. Following this observation period, there was a test in which the demonstrator shoal was restricted to the center of the tank, both feeders were baited with food, and the fish were released to investigate where each fed. Fish with both sources of information faced a choice between using personal information (i.e., feeding at the feeder that had consistently contained food but that necessitated losing visual contact with conspecifics) and using the social information (i.e., feeding at a feeder that had never previously contained food but did not necessitate loss of contact with conspecifics). Fish in all conditions fed at the feeder in the open water rather than the one behind the opaque partition, supporting the assumption that swimming behind the opaque barrier to feed represented a cost that guppies would avoid if possible. However, fish with both sources of information ignored their personal information and fed at the feeder in the open water more rapidly, and with less variability, than did fish with personal information alone (fig. 13.2);

2. A shoal of fish is a loose aggregation of individuals formed largely for social reasons. When members of a shoal school, they move in a highly coordinated and synchronized fashion. The experiments discussed in this chapter all involve loosely aggregating "shoaling" fish.
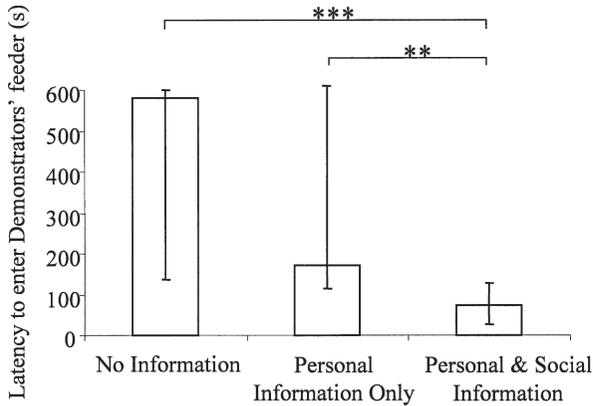
FIGURE 13.2. The latency (median and interquartile range) of guppies to enter the demonstrators' (no barrier) feeder in the "no information," "prior personal information only," and "prior personal and social information" conditions (**$P < 0.01$, ***$P < 0.001$). From Kendal et al. 2004.

hence, it would appear that the former used the social information provided in preference to their personal information. An otherwise-equivalent prior experiment with no visual barrier, in which the use of personal information did not necessitate loss of contact with conspecifics, found that, at test, fish with both sources of information, but not those in other conditions, continued to use their personal information and ignored the conflicting social information (Kendal et al. 2004). As social information outweighed contradictory personal information only where the latter was costly to use, it appears that the guppies were employing a "copy others when asocial learning is costly" strategy.

Further support for this strategy is provided by Coolen et al. (2003), who examined the propensity of wild-caught three-spined *Gasterosteus aculeatus* and nine-spined *Pungitius pungitius* sticklebacks to use public information about the profitability of food patches. In a laboratory test, individual fish were restricted to a central compartment of an aquarium from where they could see two equivalent-sized shoals of conspecifics each feeding at one of two identical but spatially separate feeders. The feeders were designed such that observers could not directly see the food, which was dispensed at different rates, but could use cues indicating the feeding rates (here, the frequency with which individuals pecked at the feeder as the food sank through it) (fig. 13.3). Following observation, the demonstrators and all food were removed from the tank, and the observer was released and its choice of feeder monitored. Solely on the basis of the demonstrators' success, observers were required to choose the richer of the two feeders. At test, nine-spined sticklebacks preferentially

chose the goal zone that had formerly held the rich feeder, suggesting that they were able to exploit public information, an interpretation supported by Coolen et al.'s other experiments. However, three-spines swam with equal frequency to the former locations of rich and poor patches (fig. 13.4). This reluctance or inability of three-spines to use prior public information was confirmed by Webster and Hart (2006) in a study involving the acquisition of subhabitat preferences. In Coolen et al.'s final experiment, observers were provided during demonstration with optional use of vegetative cover, which nine-spines, but not three-spines, used. The collection of personal information in open water is costlier for nine-spines than for three-spines because nine-spines have inferior structural antipredator defenses and are consumed preferentially by piscivorous fish (Hoogland et al. 1957). Because of these costs, nine-spines may forgo the opportunity to collect reliable personal information and favor vicarious assessment of foraging opportunities through observational learning. Thus, public information use in sticklebacks can be regarded as an adaptive specialization in learning, reflecting the differential costs of personal information acquisition.

In the first explicit test of flexibility in the social learning strategies of Norway rats (*Rattus norvegicus*), Galef and Whiskin (2006) assessed reliance on social information while foraging in risky situations. Following a 30-minute interaction with a demonstrator rat that imparted cues on its breath as to whether it had been eating either cinnamon- or cocoa-flavored food, naive rats were provided with both cinnamon- and cocoa-flavored food in a single location that afforded them little cover/refuge and entailed traversing an open space (from the safety of the nest box) to reach it. The potential cost of consuming
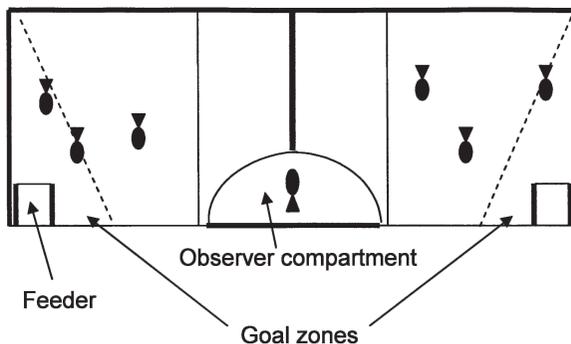

Observer compartment

Feeder

Goal zones

FIGURE 13.3. Diagram of the experimental tank setup allowing single sticklebacks to observe conspecifics feeding at two feeders. Thick lines represent opaque partitions, thin lines represent transparent partitions, and dashed lines represent goal zone virtual delimitations. From Coolen et al. 2003.
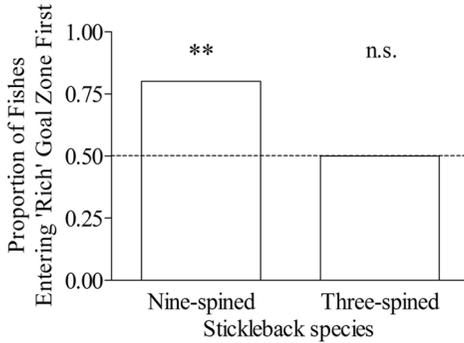
FIGURE 13.4. The proportion of three-spined and nine-spined sticklebacks that entered first the goal zone corresponding to the feeder that appeared "rich" rather than "poor" during the demonstration period ($n = 20$ for each species). The dashed line indicates the proportion expected at random (**$P < 0.01$, n.s. = not significant). From Coolen et al. 2003.

these unfamiliar foods was increased for the rats by placing two cats in a cage in the housing room for either (*i*) 4 or (*ii*) 24 hours or by (*iii*) allowing the cats to roam freely. Contrary to Galef and Whiskin's expectation, rats did not eat more of the diet eaten by their demonstrator as potential predation risk increased; indeed, individuals under potential predation risk were less influenced by the social information than controls, who faced no predation risk. Galef and Whiskin interpreted this finding as contrary to the prediction that, as the costs of acquiring personal information increase, so should the reliance on social information. However, this interpretation is open to question. The cost the rats were facing was largely in traveling, over open ground, to the food site (where both foods were presented in close proximity), rather than in acquiring personal information pertaining to the foods. In contrast to control rats, those under stress of potential predation may have chosen a food at random without taking the time to either (*i*) collect personal information or (*ii*) use their previously acquired social information.

The cost of acquiring personal foraging information, represented by the difficulty of asocial learning, was also manipulated in a study of social foraging in callitrichid monkeys, involving three lion tamarins (*Leontopithecus* sp.), two tamarins (*Saguinus* sp.), and two marmosets (*Callithrix* sp.). Day (2003; Day et al. 2003) presented a series of novel artificial-fruit tasks, requiring the extraction of preferred food items, to zoo-housed groups of monkeys. Judging by the time to learn, as well as the amount of food extracted, the tasks varied significantly in difficulty. For each task there were two options (doors or holes) by which monkeys could extract food, with the alternatives being equivalent except in location and color. While the monkeys learned all of the tasks, a detailed statistical analysis revealed that the difficult, but not the easier, tasks were learned socially (Day 2003). For the difficult, but not the easy, tasks there was a significant tendency for individuals within a group to extract food using the same colored option as others, suggesting nonindependent learning.

Presumably, the personal information required to solve the easy tasks could be acquired at little cost, while the solutions of the more complex tasks were associated with a sufficiently large time or energy cost to render social learning adaptive. Similarly, Baron et al. (1996) reported that human subjects were found to imitate more as task difficulty increased.

In summary, although there is little explicit experimentation, that which exists provides strong support for animals exploiting a "copy when asocial learning is costly" strategy. This is probably the best-supported social learning strategy.

13.2.2. COPY WHEN UNCERTAIN

13.2.2.1. *Copy when have no relevant information*
Theoretical background. Boyd and Richerson (1988) considered a model exploring the advantages of reliance on social and asocial learning in a temporally variable environment in which animals have to make decisions as to which of two environments they are in and choose the appropriate behavior. Behavior 1 is appropriate in environment 1, behavior 2 is appropriate in environment 2, while performing the alternate behavior results in a fitness cost. The animals base their decision on the magnitude of a continuous parameter (x) representing the outcome of direct observation. At one extreme, if x has high values, above a threshold value d, the animals "know" they are in environment 1 and perform behavior 1. At the other extreme, if x has low values (below $-d$), they "know" they are in environment 2 and perform behavior 2. However, if x has intermediate values ($-d < x < d$), animals are uncertain as to whether they are in environment 1 or 2, and it is assumed that they will copy the behavior of others.

We note a (*i*) broad and a (*ii*) narrow interpretation of Boyd and Richerson's assumption. Individuals may be predisposed to rely on social information (*i*) if they lack relevant prior knowledge to guide their decision making, or (*ii*) if they are uncertain as to which of several established behavior patterns is appropriate given the information at hand. We are aware of considerable, albeit often inadvertent, empirical evidence for the former, whereby totally naive individuals use social information, for example, pertaining to the location of food, but none for the latter, whereby individuals would be faced with the choice, given some social information, of using previously acquired personal information, for example, pertaining to the location of food depending upon which laboratory "environment" they believed themselves to be in.

Empirical evidence. In an experiment related to that described in section 13.2.1.2, Kendal et al. (2004) tested in three conditions the propensity of guppies to use social information concerning the availability of food at two

differentially colored feeders, although this time the use of personal and social information did not differ in cost. One group was provided first with personal and then with conflicting social information, a second group was given solely social information, and a control group was provided with no personal or social information at all. They found that fish that were provided with social information only, and that lacked relevant prior information, fed at the feeder indicated by conspecifics significantly more often than chance expectation. In contrast, individuals with both sources of information ignored the social information and continued to feed according to their personal information. This finding holds even when the order in which personal and social information are experienced is reversed (i.e., social first, personal second) (Laland, unpublished data). Similarly, Coolen et al. (2003; see section 13.2.1.2) found that nine-spined sticklebacks that did not have personal information copied the patch choices of others, whereas van Bergen et al. (2004; see section 13.2.2.2), testing the same species in an identical setup, found that fish would ignore social information when they had relevant personal information.

Social learning may occur as a result of an individual collecting information either directly, by observing a particular behavior in others (public information), or indirectly, by inferring possible causes of a given behavior pattern (social cues). In an extension of the 2003 study, Coolen et al. (2005) examined the use of direct and indirect social foraging information by nine-spined sticklebacks. The number of demonstrators present at each patch varied (two vs. six fish), supposedly indicating a poor and a rich patch, respectively. This indirect information either conflicted with the demonstrators' feeding rate at each patch (feeding respectively six times vs. twice in the 10-minute demonstration) or was the only information available. The sticklebacks were capable of using both direct and indirect information to make choices about where to forage, but when these contradicted each other, they relied on the direct information provided by feeding rate (see fig. 13.5). These findings are consistent with "copy when have no relevant information," since fish copied their demonstrators' patch choices in both conditions, but also indicate what type of social information individuals prefer to use. Direct information tends to be associated with greater accuracy, whereas by copying the decisions of others (indirect information), one may also copy their mistakes. By relying preferentially on direct information, nine-spines may avoid potentially maladaptive informational cascades (Giraldeau et al. 2002).

Galef et al. (2008) also provide support for a "copy when uncertain" strategy being deployed. They created conditions whereby Norway rats were either certain or uncertain as to the causal relationship between ingesting an
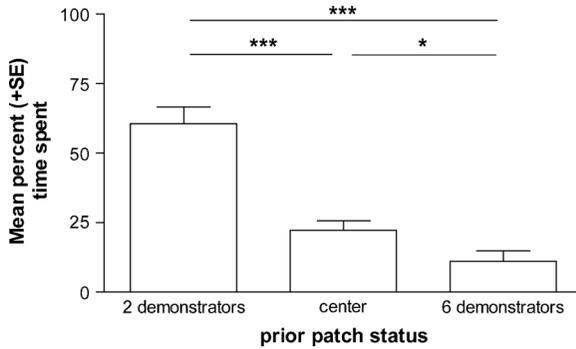
FIGURE 13.5. The mean percentage (+ SE) of time nine-spined stick-lebacks spent in each patch (*n* = 20) after they collected both direct (demonstrators' feeding rate) and conflicting indirect information (shoal size) about relative patch quality during the observation period (*P* < 0.05, ***P* < 0.001). From Coolen et al. 2005.

unfamiliar flavor and gastrointestinal upset. Thus, "certain" rats were fed cinnamon-flavored food and immediately afterward were injected with lithium chloride, and "uncertain" rats were fed a food containing both cinnamon and cocoa flavors prior to experiencing toxicosis. After a 24-hour recovery period, these rats, having learned that sampling unfamiliar foods can be dangerous, were exposed to a demonstrator that had eaten another unfamiliar food (either anise or marjoram flavor). Following this, when exposed simultaneously to anise- and marjoram-flavored foods for 24 hours, "uncertain" rats ate significantly more of the food eaten by their demonstrator than did "certain" rats.

Galef et al. interpret this study as a test of a response to having "ambiguous prior personal information." However, given that the social information individuals received pertained to different flavors than those experienced during personal information, we posit that the rats were not faced with "ambiguous personal information" but rather lacked personal information relevant to the social information received. While the elevated copying in the "ambiguous" social information condition supports the "copy when uncertain" interpretation, the observation that copying occurs in both conditions to some degree might also be interpreted as consistent with a "copy when asocial learning is costly" strategy; rats may have learned as a result of their poisoning that asocial learning is dangerous in this environment. However, a previous study (Galef and Whiskin 2006) showed that rats experiencing toxicosis after ingesting variously 1, 2, and 4 different foods did not differ in their subsequent use of social information pertaining to unfamiliar foods.

13.2.2.2. *Copy when prior information is unreliable*

Theoretical background. We now consider scenarios where, for whatever reason, personal information is actually less reliable than social information. Boyd and Richerson (1985, 1988) modeled the use of social information in a spatially heterogeneous environment where individuals experience different environments. The average quality of information available from demonstrators enables individuals to weight their use of asocial and social learning according to the likelihood of acquiring erroneous information from each source. As environmental heterogeneity increases and personal information becomes more error prone, the optimal amount of social learning from local residents increases, while as the rate of dispersal between environments increases, social information becomes increasingly unreliable (since individuals will increasingly copy "outsiders"), and the optimal amount of social learning decreases.

Giraldeau et al. (2002; see Bikhchandani et al. 1992, 1998) proposed that individuals may use social information not only because their personal information is in itself unreliable but because the accumulated knowledge of conspecifics potentially represents a source of information with even greater reliability. In spite of this, they predict that, in specific instances, reliance on the decisions of others can lead to arbitrary or even maladaptive traditions in animals (Giraldeau et al. 2002; see also section 13.2.2.1). Theoretical work regarding reliability and the value of information in communication and mating systems (Sirot 2001; Koops 2004) suggests that, even if the costs of misinformation are high, animals should still use information, provided that it is usually reliable. This requires animals to be able to assess the relative reliability of personal versus social information correctly.

Empirical evidence. In a study of nine-spined sticklebacks, van Bergen et al. (2004) manipulated the reliability of personal information concerning the profitability of two foraging patches, using a similar experimental design to that of Coolen et al. (2003; see section 13.2.1.2 and fig. 13.3). Fish were allocated to one of three conditions, where they received 100%, 78%, or 56% reliable personal information as to which of two feeders was "rich" and which "poor." Following this training period, fish were tested individually for their feeder preference. Those in the 100% and 78% reliable conditions significantly preferred the "rich" feeder. Subsequently, the profitability of the two feeders was reversed, and fish were presented with (now conflicting) public information in which they observed demonstrators feeding at the two feeders, with what was according to their earlier sampling the poor feeder now the rich feeder, and vice versa. Following this demonstration, only fish in the 100% reliable condition continued to prefer the feeder that was "rich" according to their
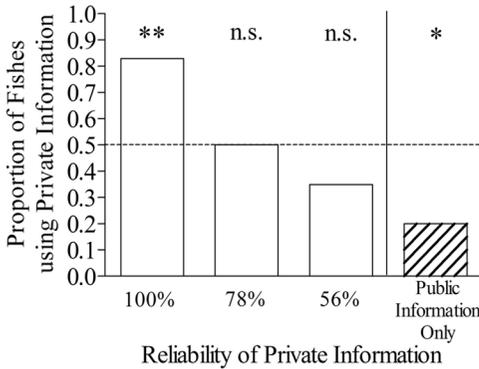
FIGURE 13.6. The proportion of nine-spined sticklebacks that, after receiving personal information of varying reliability followed by conflicting public information, entered first the goal zone of the feeder that was "rich" according to personal information. The dashed line indicates the proportion expected at random, and the hatched bar represents data from Coolen et al. 2003 (*$P < 0.05$, **$P < 0.005$, n.s. = not significant). From van Bergen et al. 2004.

personal information; fish in the other conditions exhibited no preference (fig. 13.6). Since fish with 56% reliable information probably had not acquired private information (they did not prefer the rich feeder immediately after their training period), this experiment does not provide unequivocal evidence that fish increasingly relied on the social information provided by their demonstrators as the reliability of their personal experience diminished, although it is consistent with this interpretation. It does, however, demonstrate that fish with completely reliable personal information will ignore conflicting social information.

13.2.2.3. *Copy when prior information is outdated*

Theoretical background. Boyd, Richerson, and colleagues (Boyd and Richerson 1985, 1988; Henrich and Boyd 1998) have modeled the use of social information in temporally fluctuating environments, finding that intermediate levels of fluctuation will be most likely to favor social learning. Here individuals can acquire relevant information without bearing the costs of direct interaction with the environment associated with asocial learning but with greater phenotypic flexibility than if the behavior was unlearned (Boyd and Richerson 1985, 1988). Consequently, as socially transmitted information becomes increasingly outdated, we might expect individuals to become less likely to rely on it.

In other theoretical analyses, Doligez et al. (2003) predicted that strategies based on public information use (here the breeding success of conspecifics on particular patches) perform best when fluctuation in patch quality is of intermediate or high temporal predictability. Similarly, Moscarini et al. (1998) have looked at the effect of a changing world on the likelihood of informational cascades and predict that blind copying may occur for some limited time if the state of the world changes stochastically but will not happen anymore

when the environment changes too unpredictably (or randomly). Kameda and Nakanishi (2002) reported that in a fluctuating environment, increasing costs of asocial learning initially result in an increase in social learning, a concomitant reduction in fresh information, and thus an outdated "cultural knowledge pool." They predict that natural selection will act against reliance on social learning based on such flawed information, ensuring cultural knowledge tracks environmental change.

These models predict that individuals should acquire personal information and ignore social information when the latter is likely to be outdated. Equally, individuals should opt to frequently update information if the use of their current information, whether acquired asocially or socially, is likely to be outdated.

Empirical evidence. Van Bergen et al. (2004) manipulated the degree to which personal information regarding the relative profitability of two foraging patches was outdated, and they explored how this prior experience affected individuals' subsequent acquisition of public information. Nine-spined sticklebacks were allocated to one of four conditions, where they received personal information as to which of two feeders was "rich" and which "poor" 1, 3, 5, or 7 days prior to receiving conflicting public information and a test of preference. Fish with only a 1-day delay between receiving personal and public information ignored the social information and first visited the feeder that was "rich" according to their personal information. Fish with delays of 3 and 5 days showed no feeder preference, and those experiencing a 7-day delay preferred the feeder that was "rich" according to the public information (see fig. 13.7). Accepting van Bergen et al.'s arguments that personal information was not forgotten after 7 days, comparison with results from Coolen et al. (2003), where fish received public information only, appeared to indicate that
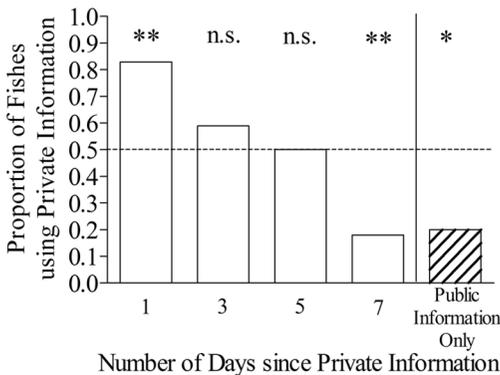

FIGURE 13.7. The proportion of nine-spined sticklebacks that, after receiving personal information followed at varying time lags by conflicting public information, entered first the goal zone of the feeder that was "rich" according to personal information. The dashed line indicates the proportion expected at random, and the hatched bar represents data from Coolen et al. 2003 (*$P < 0.05$, **$P < 0.005$, n.s. = not significant). From van Bergen et al. 2004.

fish in the 7-day condition ignored their personal information in favor of the public information. As personal information becomes increasingly outdated, nine-spined sticklebacks become increasingly reliant upon socially acquired information.

In summary, experimental data support the prediction that animals utilize a "copy when uncertain" strategy, although this strategy can be interpreted in various ways.

13.2.3. COPY WHEN DISSATISFIED

13.2.3.1. *Theoretical background*

Schlag (1998) explored an imitation rule that he termed "proportional reservation" but that might be called "copy when dissatisfied," finding that it is a highly effective learning rule. Here, the size of the payoff to its current behavior determines an individual's satisfaction, as a linear function. The individual retains its current behavior with a probability equal to this satisfaction and otherwise copies the action of a randomly chosen demonstrator. This strategy has the advantage that it is potentially simple to implement, because it does not require individuals to assess the payoff to a demonstrator or to make any judgment as to the relative profitabilities of alternative behavior patterns. Because "copy when dissatisfied" requires evaluation only of one's own success (e.g., in terms of satiation), not of the relative success of oneself and others, "copy when dissatisfied" seems more likely to have evolved than "copy when better" (Laland 2004), which Schlag found to be equally effective.

13.2.3.2. *Empirical evidence*

Galef et al. (2008) manipulated rats' dissatisfaction with their diet (experiment 1) or environment (experiment 2). In the first experiment, rats were maintained for 1 week on either an unpalatable low-caloric diet, requiring increased handling time to maintain their health (dissatisfied condition), or a palatable relatively high caloric diet (satisfied condition). Following this, the subjects were exposed for 30 minutes to a demonstrator rat carrying cues on the breath as to whether it had eaten either a marjoram- or an anise-flavored diet. In the following 24 hours the subjects were exposed to both diets, and "dissatisfied" rats ate more of the food that their demonstrator had eaten than did "satisfied" rats. In the second experiment, rats, essentially crepuscular burrowing animals, were housed either on a hard substrate with no cover, constant light, and an overly warm ambient temperature (1: dissatisfied condition) or with bedding, cover, a 12:12 light:dark cycle, and appropriate ambient temperature (2: satisfied condition). Again, "dissatisfied" subjects ate more of the diet indicated by their demonstrator than did "satisfied" rats.

In summary, Galef et al.'s experiments are consistent with the strategy of "copy when dissatisfied," although the latter experiment exemplifies "dissatisfaction" more broadly than the former. In experiment 2 rats appear to be generally dissatisfied with their lot, while in experiment 1 they are specifically dissatisfied with their feeding regime—that is, dissatisfied in the same domain as the social information. There is, perhaps, a case for characterizing these as two separate strategies, although it is interesting to note that both types of dissatisfaction translate into the same result with respect to socially induced food preferences.

13.3. "Who" strategies

13.3.1. THEORETICAL BACKGROUND

Boyd and Richerson (1985) proposed a number of cultural transmission biases. For example, a "frequency-dependent bias," in which the most popular variant in a population is disproportionately more likely to be adopted, may be translated into the social learning strategy of "copy the majority" ("conformist bias"). The opposite, negative frequency-dependent bias for rare variants can likewise be characterized as "copy if rare." Henrich and Boyd (1998) established that the range of conditions that favor conformist transmission is likely broader than that for cultural transmission. However, Eriksson et al. (2007) have challenged the theoretical grounds and the empirical evidence for a conformist bias; they claim that the assumptions of previous models may be unrealistic. Hence, whether animals are expected to use a "copy the majority" strategy is very much a controversial point among theoreticians and awaits relevant experimentation.

With "direct bias," individuals adopt cultural variants based upon an assessment of the value of the trait itself, a bias that could be translated into a strategy such as "copy if better" (requiring an individual to evaluate the relative payoffs of the actions of itself and others; Laland 2004). In contrast, with "indirect bias," traits exhibited by successful or high-status individuals may be preferentially adopted, even where the trait in question has absolutely nothing to do with the individuals' success or status. Indirect bias then can be portioned into strategies such as "copy individuals that are successful, high-status (prestige bias), older, or good social learners" (Laland 2004). Indeed, the strategy of "copy older individuals" has been assumed in theoretical analyses (M. Kirkpatrick and Dugatkin 1994) on the basis of reports of mate choice copying in female guppies. Finally, where the adoption of a trait is random with respect to its apparent utility transmission is said to be "unbiased." This is different from "indirect bias," as there is no assumed cor-

relation between the "type" of individual (e.g., high-status) and the adaptiveness of the trait he or she exhibits. Here, individuals would randomly choose a "role model" and copy the trait he or she exhibits. Note, the existence of "random copying" at a population level is perfectly consistent with individuals pursuing directed strategies, provided individuals do not all exhibit the same behavior such that they sum up to generate a population-level bias. Hence, "unbiased transmission" processes may be translated into strategies such as "copy kin" or "copy friends," where the specifics of who is copied vary from one individual to the next. Any kin bias may reflect nothing more than the fact that individuals spend considerably more time in the presence of kin than non-kin. However, there are two reasons to suspect that selection may have favored a disproportionate degree of learning from kin. First, social learning, particularly in a variable environment, is of use only to the extent that demonstrator and observer experience the same environment and reap the same rewards (Boyd and Richerson 1985, 1988). This may be more likely among kin than non-kin because, by virtue of their shared genes (and other sources of similarity), kin may be more likely than non-kin to reproduce similar behavior variants and to experience the same affective sensations in reinforcement. Second, in situations where information transmission is costly, kin may have more to gain by providing reliable information to fellow kin, and less to gain from deceiving them, than non-kin. Witness, for example, teaching among worker ants (Franks and Richardson 2006) and bees (von Frisch 1967). Similarly, if friends are regarded as individuals with whom one trades altruistic acts (Trivers 1971), by similar lines of reasoning we might expect more social learning among friends than nonfriends, in a "copy friends" strategy.

In accordance with mathematical theory, Coussi-Korbel and Fragaszy (1995), after observing the relation between social dynamics and social learning in nonhuman primates, stressed directed social learning. Here, the social rank, sex, age, patterns of association, and other characteristics of demonstrator and observer critically affect the probability of social learning. As a result, information may be transmitted through subsections of animal societies at different rates.

13.3.2. EMPIRICAL EVIDENCE

13.3.2.1. *Frequency-dependent bias*

Following Boyd and Richerson (1985), we treat a conformist bias as entailing a disproportionate tendency to copy the majority. We do not review here recent empirical studies pertaining to a broader interpretation of "conformity" (see Whiten and van Schaik 2007; Galef and Whiskin 2008).

Day et al. (2001) found evidence for conformity in a series of experiments investigating how shoal size affects foraging efficiency in fish. Hidden food was presented to shoals of guppies, and large shoals were found to locate food faster than small shoals, consistent with similar findings in other fishes. This is probably because fish in large shoals have more shoal mates from whom to acquire information, and in open water large numbers of individuals at a food site will attract conspecifics more rapidly than small aggregations. However, in a second experiment, the fish had to swim through a hole in an opaque maze partition to get to a food source, and in this situation the opposite result was found: smaller shoals located food faster than larger shoals. The seemingly conflicting findings of these experiments make sense in the light of the observation that guppies prefer to join large, rather than small, shoals, which implies that individuals ought to be more willing to leave smaller shoals than larger shoals. Swimming through an opaque partition to locate food involved breaking visual contact with, and hence effectively leaving, the shoal. Under such circumstances, conformity, or a strategy of "copy the majority," resulting from the natural shoaling tendency of these fish, results in greater reluctance to acquire a novel behavior in large shoals than in small shoals, at least early in the diffusion process. This interpretation was supported by the findings of a third experiment, which replicated the second except for using a transparent partition: individuals in large shoals once again located the food faster than those in small shoals. Here visual contact between fish was maintained because the partition was transparent, so fish passing through it behaved as if they were not leaving the shoal. Here, social transmission of foraging information was not hindered by conformity, and large shoals were again advantaged.

McElreath et al. (2005) had groups of people repeatedly play a computer-based task (planting one of two crops that gave different yields), either (*i*) where asocial learning alone was possible, (*ii*) with the opportunity to view the previous choice of one randomly selected group member (allowing social learning), or (*iii*) with the opportunity to view the previous choices of all group members (allowing conformity). The use of social information increased when individual learning was relatively inaccurate, thus confirming the strategy of "copy when uncertain" (see section 13.2.2). Similarly, although models indicated that conformity was the better strategy under all conditions, it was used only when the environment fluctuated—hence, when there was a cost to individual learning. Similarly, Efferson et al. (2008), in another computer-based study, found considerable, as yet unexplained, heterogeneity in the extent to which humans follow a strategy of "copy the majority," even when doing so would be in their interests. In accordance with these findings are those of

Eriksson et al. (2007) indicating that the likelihood of conforming is highly context dependent. People reported that, when presented with vignettes pertaining to either a scenario of novel food choice (different soups) or one of punishment of social defectors (defection being the undertaking of large print jobs on a communal machine), they would conform in regard to the former but not the latter.

In summary, empirical evidence for utilization of a "copy the majority" strategy is surprisingly weak, given the emphasis on conformity in the social science literature.

13.3.2.2. *Indirect bias*

Mesoudi and O'Brien (2008) provide the first attempt to simulate the cultural transmission of prehistoric artifacts in order to determine whether theoretical predictions can explain patterns observed in the archeological record. They examined a previously observed pattern in which the attributes (e.g., length and width) of arrowheads dating to AD 300–600 were poorly correlated with each other in eastern California but were well correlated in central Nevada. The pattern in California was thought to be due to cultural transmission involving "guided variation" (individual trial-and-error experimentation of attributes) and that in Nevada due to "indirect bias" (wholesale copying of a successful individual's design) (Bettinger and Eerkens 1999). Mesoudi and O'Brien's study involved participants playing a computer game whereby they tested "virtual projectile points" in "virtual hunting environments." Consistent with "indirect bias" and a strategy of "copy the most successful individual" they found that individuals chose to copy the arrowhead design of the single most successful demonstrator. In addition, where individuals were allowed to adapt their culturally acquired arrowheads via individual trial-and-error learning ("guided variation"), the resulting arrowheads were less uniform in design than those of individuals allowed only to choose which individual to copy arrowhead attributes from (their hunting success being indicated on screen). Consistent with the adaptiveness of a strategy of "copy if asocial learning is costly" (see section 13.2.1), participants who could engage in indirectly biased cultural transmission outperformed those engaging in individual learning, particularly when the latter was costly (modifications incurred a caloric penalty).

13.3.2.3. *Unbiased transmission*

Many fish express preferences for shoaling with familiar individuals (Griffiths 2003), and we may interpret a strategy of "copy familiar individuals" in the same light as "copy friends" or "copy kin." Guppies have been reported to

acquire foraging information faster when in groups of familiar individuals than when in groups of unfamiliar individuals (Swaney et al. 2001). A meta-analysis by Reader (2000) found disproportionate numbers of reports of learning from mothers in nonhuman primates. Galef and Whiskin (unpublished data) have explicitly attempted to examine the influence of both familiarity and kinship on the transmission of food preferences in rats. Following a similar protocol to that outlined above, they found that both familiar-kin and familiar-non-kin had an equivalent social influence as unfamiliar-kin and unfamiliar-non-kin, respectively. However, when considering only studies where observer rats interacted simultaneously with familiar and unfamiliar individuals, regardless of relatedness, they found unfamiliar individuals to have the greatest social influence over subsequent food preferences. Galef (personal communication) suggests that the peculiarities of rat social life, where interaction with a strange conspecific takes precedence over social interaction with a known individual, may override any strategy of "copy kin or familiar individuals."

13.4. Evolutionary implications

An individual animal's use of social learning strategies may generate specific population-level effects on evolutionary processes. For instance, theoretical analyses suggest that a strategy of "copy the majority" may underlie widespread cooperation generated by cultural group selection, while a strategy of "copy successful individuals" may generate runaway prestige markers that become exaggerated in a similar manner to runaway sexual selection (Boyd and Richerson 1985). Maladaptive cultural traditions may result from the (asocial learning) costs of breaking a convention or from informational cascades (Giraldeau et al. 2002) where individuals base behavioral decisions on a prior decision of others without observing the cue upon which that decision was based (akin to personal information). When "asocial learning is costly" or "uncertainty" reigns, animals and humans may be more likely to engage in erroneous or maladaptive informational cascades (e.g., Cavalli-Sforza and Feldman 1981; Boyd and Richerson 1985; Laland and Williams 1998).

Consideration of social learning strategies may explain why social learning abilities appear to reflect ecological (environmental and social) rather than taxonomic affinities among species. There may be a greater reliance on social information in species that use complex foraging skills or must overcome challenging prey defenses than in species that do not (e.g., folivorous vs. frugivorous species: Fragaszy and Visalberghi 1996; extractive vs. nonextractive foragers: Day et al. 2003; Zentall 2004); but see Lefebvre and Giraldeau 1996 for caution regarding inferences based on comparative studies of social learn-

ing. Although our findings cast doubt on the widespread belief that social learning is particularly important to large-brained species, Sol (chapter 7 in this volume) argues for a positive correlation between innovation, the starting point of any socially learned trait, and brain size.

In fact, the accumulating evidence for social learning strategies may guide researchers in the difficult task of assessing the plausibility of social learning being involved in any observed patterns of behavioral variation in the wild (see Laland et al., in press). For example, given the theoretical and empirical support for a "copy when asocial learning is costly" strategy, researchers might reasonably question the plausibility of putative cultural traits that are relatively simple and cheap to acquire asocially. Similarly, a growing understanding of the contexts in which social learning is used may enhance our understanding of factors that may have influenced the evolution of cultural capacities. For example, several empirical findings (e.g., Coolen et al. 2003; Kendal, unpublished data) indicate that the costs associated with acquiring or using personal information may promote the evolution of increasingly complex social learning processes. If replicated in our closest ancestors, these findings may shed light on the evolution of the potent cultural capacity of humans. Theoretical studies indicate that an individual's ability to adopt a strategy of "copy if better" may be more important for the evolution of a cumulative culture than either conformist transmission or imitation (Eriksson et al. 2007; Enquist and Ghirlanda 2007). Thus, a "cognitive deficit" in evaluating the relative payoff of actions performed by the self and by others, preventing animals from discriminating between cultural variants (or "adaptive filtering"), may explain why cumulative culture appears to be virtually unique to humans. Incidentally, a similar line of reasoning, regarding cognitive abilities (e.g., theory of mind) required to cope with increasingly complex social life, may be important in the apparent distribution of social intelligence and deception in human and nonhuman animals (see Federspiel, chapter 14 in this volume). Indeed, for some, a theory of mind is deemed necessary for both imitation and cumulative culture (Tomasello 1990).

In contrast, several of the proposed social learning strategies may actually hinder the cultural transmission of information. As we have seen, a strategy of "copy the majority" may hinder the adoption of novel information in large groups (Day et al. 2001), and a recent theoretical study (Eriksson et al. 2007) indicates that it may also hinder the development of cumulative culture. In addition, a strategy of "copy high-status individuals" may inhibit the spread of novel information where the innovator, as is often the case in primates, is of low status (Reader and Laland 2003). The apparent failure of most animal innovations to spread (Reader and Laland 2003) has a profound influence on

species' evolution and survival, not least because the ability to adopt innovations is implicated in invasion success and the ability to respond to anthropocentrically altered environments (Lee 1991; Sol et al. 2002; Sol, chapter 7 in this volume).

13.5. Summary and future directions

In summary, we report good support for several "when" strategies, particularly "copy when asocial learning is costly," "copy when uncertain," and "copy when dissatisfied." However, in many cases the precise strategy employed is ambiguous, conditional, and context specific. In contrast, support for the existence of "who" strategies is weaker, and even the comparatively well established "copy the majority" strategy remains contentious in the absence of unambiguous support.

It is early days in the study of social learning strategies, and clearly further research is necessary before a deep understanding is gained of how and when acquired social information is used. We would like to encourage further empirical research in this area, particularly as there is a paucity of direct investigation, in nonhuman animals especially. Of particular interest is investigation into whether there is a hierarchy in the implementation of strategies (Laland 2004). For example, individuals might practice unbiased transmission (e.g., copy kin) unless they have access to relevant biased transmission information (e.g., copy high-status/successful individuals) or can afford to invest in the time, energy, or cognition required for individual learning/direct bias. We note also that many of the studies investigating "who" strategies hint at the existence of conditional strategies. For example, both of the reviewed conformist transmission studies (Day et al. 2001; McElreath et al. 2005; section 13.3.2.1) and, to a certain extent, the results of another study in guppies (Kendal et al. 2004; see section 13.2.1.2) appear to indicate a mixed strategy of "copy the majority when asocial learning is costly." Individual characteristics of observers, favoring the overriding of social learning strategies, and the continued acquisition of personal information (as reported by Efferson et al. 2008 and Kendal et al. 2004 with regard to conformity), may be influential in determining the innovatory capacities of individuals.

In parallel, we argue that there is considerable potential for fruitful integration of empirical and theoretical work, particularly game-theoretical analyses (Laland and Kendal 2003; Laland 2004). We hope that consideration of the trade-offs inherent in the adaptive use of social and asocial learning will contribute to an increased understanding of the observed pattern of social learning and behavioral traditions in the animal kingdom, especially as the use of

social information may lead to cultural evolution, which may in turn affect biological evolution (Boyd and Richerson 1985; Feldman and Laland 1996; Danchin et al. 2004).