
Trade-Offs in the Adaptive Use of Social and Asocial Learning

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I. INTRODUCTION

A common assumption by ethologists, behavioral ecologists, and anthropologists, albeit rarely made explicit, is that the acquisition of learned information from others (henceforth “social information”) is *inherently* adaptive. Individuals are deemed to gain fitness benefits by copying others on the assumption that they acquire adaptive information while avoiding some of the costs associated with learning for themselves (the costs of “personal information”). Social learning is known to enable naïve animals to acquire information relevant to many life skills, including when, where, what, and how to eat (Galef and Giraldeau, 2001), with whom to mate (White, 2004), or fight (Peake and McGregor, 2004), as well as which predators to avoid and how (Griffin, 2004). The unspoken supposition is that the acquisition and exploitation of such information will inevitably confer fitness benefits on the learner, since individuals will save themselves the costs, for instance, of searching their entire home range, sampling all potential foods, or learning to escape predators for themselves.

In fact, the use of social information does not guarantee success (Boyd and Richerson, 1985; Laland, 2004). Individuals face evolutionary trade-offs between the acquisition of costly but accurate information and the use of cheap but potentially less reliable information (Boyd and Richerson, 1985). Theoretical models investigating the adaptive advantages of different forms of learning conclude that social learning cannot be employed in a blanket or indiscriminate manner, and that individuals should adopt flexible strategies that dictate the circumstances under which they copy others (Laland, 2004). Such theoretical analyses reveal that social learners would have higher fitness than asocial learners only when copying is rare, when most potential demonstrators would be asocial learners who have acquired and display accurate information about the environment (Boyd and Richerson, 1985, 1995; Giraldeau *et al.*, 2002; Rogers, 1988). As the frequency of social learners increases, however, the value of using social information would decline, because the proportion of individuals demonstrating accurate personal information would decrease. At the extreme, with all individuals copying, the population would have to rely upon unreliable and possibly inaccurate information¹ as no one would have acquired accurate personal information by sampling the environment. In order for the use of social learning 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).

The circumstances under which individuals might switch between reliance on different sources of information remain relatively unexplored. What context-dependent rules have evolved in animals dictating how they exploit both personal and social information? Do animals copy the behavior of others when they are uncertain how to solve a problem? Do they copy others when it is easy to do so and only learn asocially when copying is not an option? Or is social learning a last resort when asocial learning has failed? Following Laland (2004), the term “strategies” is used here to equate such learning heuristics with those strategies commonly analyzed using evolutionary game theory (Maynard-Smith, 1982). Of course, animals

¹Some 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.

need not be aware that they are following a strategy, nor need they understand why such strategies may work.

Until relatively recently, the existence and characteristics of social learning strategies have not been allotted a great deal of empirical attention, despite assumptions and predictions pertaining to such strategies in theoretical models. However, experimental support is now emerging for the existence of two broad classes of strategies, dictating both *when* animals will use social information and from *whom* they will learn (Laland, 2004). In this article, we will focus on *when* strategies, reviewing the current empirical support for the putative strategies of *copy others when asocial learning is costly* and *copy others when uncertain*.

We hope that by emphasizing consistent findings in a range of species, including fishes, birds, and mammals, the prevalence of trade-offs in the use of social and asocial learning will become apparent, and will be taken into account in future studies of social learning. A further aim is to encourage the integration of theoretical and empirical work in animal social learning, where there is considerable potential for combining laboratory experiments and game theoretical analyses (Laland and Kendal, 2003; Laland, 2004).

II. EVIDENCE THAT ANIMALS EXPLOIT SOCIALLY TRANSMITTED INFORMATION WHERE ASOCIAL LEARNING WOULD BE COSTLY

A. THEORETICAL FOUNDATION

Several theoretical analyses have reached the conclusion that reliance upon social information should be increasingly favored as the costs associated with acquiring personal information increase (Boyd and Richerson, 1985, 1988; Feldman *et al.*, 1996; but see Section III.C.1). Trial-and-error learning is often both costly and error prone. Personal interaction with the environment may entail costs that directly influence survival, such as risk of injury, poisoning or predation, as well as “missed opportunity” costs, such as the loss of time or energy that could be allocated elsewhere. The existence of these costs restricts an animal’s investment in asocial learning, and may lead to “errors” such as a failure to perform an adaptive behavior or the retention of a sub-optimal variant. When these costs are substantive, selection ought to favor shortcuts to learning, such as copying others (Boyd and Richerson, 1985). On the basis of an extensive theoretical investigation, Boyd and Richerson (1985) proposed their “costly information hypothesis,” which proposes an evolutionary trade-off between acquiring accurate but costly information versus less accurate but cheap information.

While this trade-off manifests itself at various different levels, for our purposes this hypothesis 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. An identical argument had earlier been put forward by Bandura (1977, pp. 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 places emphasis on the costs of *acquiring* personal information, the same reasoning holds when considering the costs of *using* personal information. As highlighted by Galef (1995), once an individual has acquired a behavior pattern, whether through social or asocial learning, its continued use depends primarily upon the consequences of the behavior relative to the available behavioral alternatives. Moreover, it also follows that as the costs associated with acquiring or using social information increase, we might expect increasing reliance on personal information. For example, on the basis of a theoretical model in which individuals’ only source of social information is the decisions of others (i.e., without seeing the cues upon which such decisions are based), Giraldeau *et al.* (2002) state that the greater the costs of engaging in an erroneous “informational cascade” (Bikhchandani *et al.*, 1992, 1998), the greater the selective pressure to ignore the decisions of others and rely upon personally acquired information.

B. EMPIRICAL EVIDENCE

We will summarize empirical support for the costly information hypothesis in fishes, birds, and mammals. Our primary focus will be on the relatively well-studied topics of foraging and mate-choice, but we also dwell on other subject matters of interest, such as aggressive encounters in fish. Although learning about predators would seem an obvious context where it can be very costly to learn asocially, we are unable to present any data on the costs of direct experience with predators. Thus, we cannot yet judge whether the apparent importance of social learning on predator recognition “reflects an evolutionary trend favoring acquisition of risky information from others, rather than at one’s own peril,” as asserted by Griffin (2004, pp. 131).

1. Foraging

a. Fish Laland and Williams (1998) provide an experimental example in which fish were seemingly prepared to pay the relatively trivial costs of using suboptimal foraging information provided by conspecifics in order to

avoid the potentially more substantive cost of vulnerability to predation associated with the asocial learning of more efficient foraging. 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 naïve 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 longer to switch to the short route than did otherwise equivalent solitary fish. It is well established that guppies are reluctant to leave conspecifics and forage alone due to predation risk (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 regarding the least costly foraging route and the benefit of conforming to the majority for predator defense.

Kendal *et al.* (2004) exploited the fact that losing visual contact with shoal members is potentially costly to guppies to manipulate the cost of using previously acquired personal information in a social foraging experiment. Individuals were allocated to three conditions in which they either received (1) prior personal information only, (2) prior personal and social information, or (3) no information (Fig. 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, while fish in the other two conditions, (1) and (3), were constrained opposite 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) or 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

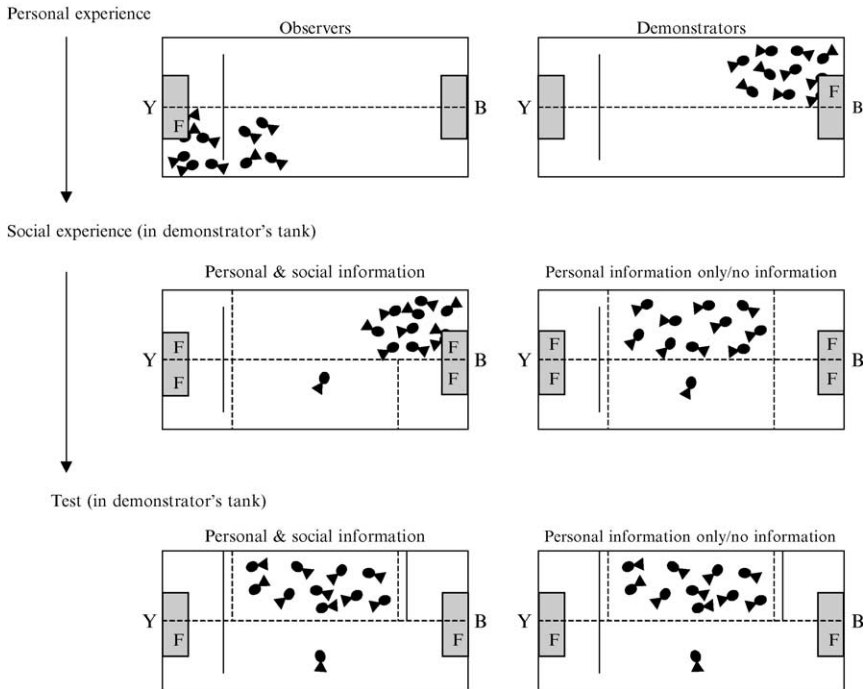


FIG. 1. (Fig. 3 from Kendal *et al.*, 2004) Experimental procedure, showing the personal experience training of observer guppies to feed (food designated as F) from either blue (B) or yellow (Y) feeders, behind an opaque barrier and demonstrators to feed at the open end of the tank; the social experience 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 transparent partitions (Kendal, R.L. *et al.*, 2004; role of conformity in foraging when personal and social information conflict. *Behav. Ecol.* used with by permission of Oxford University Press).

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. 2); 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

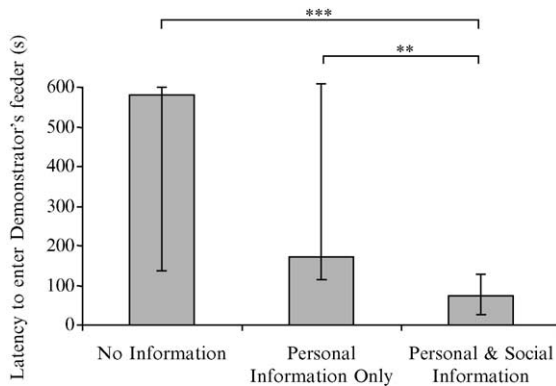


FIG. 2. (Fig. 7 from Kendal *et al.*, 2004) The latency (median and interquartile range) of guppies to enter the demonstrators' (no barrier) feeder in the no information, personal information only, and personal and social information conditions (** $p < 0.01$, *** $p < 0.001$) (Kendal, R.L. *et al.*, 2004; used with permission of Oxford University Press).

conditions, continued to use their personal information and ignored the conflicting social information (Kendal *et al.*, 2004). As social information only outweighed contradictory personal information where the latter was costly to use, it appears that the guppies were employing a strategy of “copy others when asocial learning is costly.”

Theory and experiments suggest that *public information use*, which refers to the ability to assess the quality of a resource, such as a food patch, by observing the relative success or failure of others, could lead to faster, more accurate assessment than private information alone, and that a flexible combination of these sources of information potentially provides for adaptive decision making (Valone, 1989; Templeton and Giraldeau, 1996; Valone and Templeton, 2002). However, assumptions about when animals gather and exploit these different types of information have only recently been tested explicitly. A good illustration of how and why the use of public information is not always adaptive is provided by a series of experiments on public-information use in two closely related species of sticklebacks that differ in their anti-predator defenses (Coolen *et al.*, 2003).

Coolen *et al.* 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. Individual fish were restricted to a central compartment of an aquarium from where they could see two equivalent-sized shoals of conspecifics feeding at one of two identical but spatially separate feeders dispensing food at different

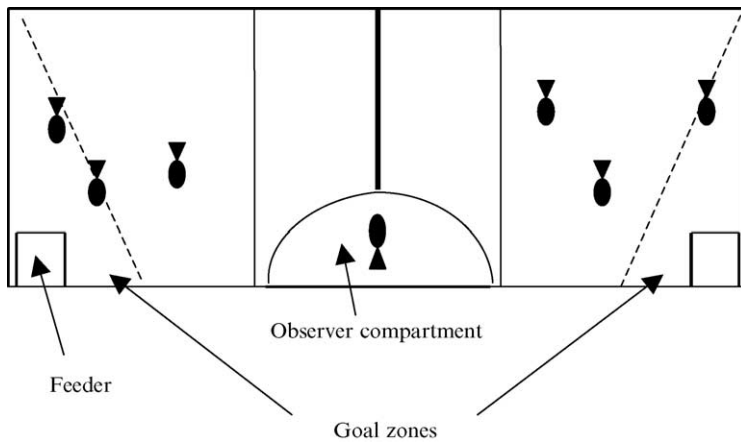


FIG. 3. (Fig. 1 from [Coolen *et al.*, 2003](#)) Diagram of the experimental tank set up allowing single sticklebacks to observe conspecifics feeding at two feeders. Thick lines represent opaque partitions; thin lines represent transparent partitions, and dashed lines represent goal zone delimitations (Coolen, I. *et al.*, 2003; used with permission of the Royal Society of London).

rates (Fig. 3). Food was delivered to the demonstrators down a tube that was transparent at the front but opaque at the sides, hence visible to demonstrators but not observers, and consumed from a “hopper” at the base of the tube. Following a 10-minute observation period, the demonstrators and all food were removed from the tank and, after a brief pause, the observer was released and its choice of feeder monitored (as measured by the goal zone to which the fish swam first, and in which it spent most time). Thus, solely on the basis of the demonstrators’ success, observers were required to choose the richer of the two feeders.

Coolen *et al.* found that, at test, nine-spined sticklebacks preferentially chose the goal zone that had formerly held the rich feeder, indicating that they were able to exploit public information. The experimental design ensured that this preference could not be attributed to residual olfactory cues, direct observation of the food in the feeder, or local enhancement. However, three-spines, when subject to the same test, swam with equal frequency to the former locations of rich and poor patches. This species difference held, regardless of whether individuals observed conspecific or heterospecific demonstrators (Fig. 4), and in spite of good power in the statistical analysis.

Previous studies have indicated that the two species exhibit subtle habitat-partitioning as nine-spines use weeded areas more than three-spines,

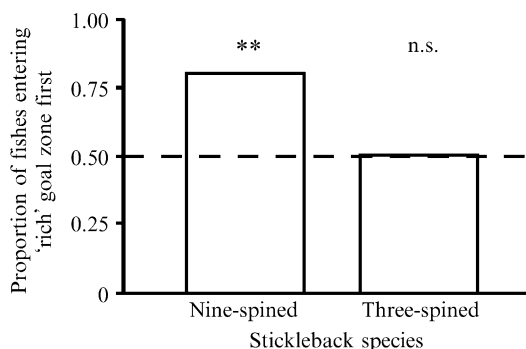


FIG. 4. (Fig. 3A from Coolen *et al.*, 2003) The proportion of three-spined and nine-spined sticklebacks that entered first the goal zone corresponding to the feeder that appeared “rich,” rather than “poor” during the demonstration period ($n = 20$ for each species). The dashed line indicates the proportion expected at random (** $p < 0.01$, n.s., not significant) (Coolen, I. *et al.*, 2003; used with permission of the Royal Society of London).

even when food is present only in open water (FitzGerald and Wootton, 1996; Hart, 2003). In a final experiment, observers were provided with optional use of vegetative cover during the demonstration and, as expected, in the course of collecting public information, nine-spines observed the demonstration from within the vegetation, while three-spines did not. In fact, the three-spines did not appear to observe each demonstrator shoal equally, as in each trial they would spend more time near one shoal than the other. This latter finding was thought by Coolen *et al.* to reflect the preference of three-spines for physical sampling of the environment, consistent with Gotceitas and Colgan’s (1991) findings, and with the collection of personal information. Previous studies have shown that when allowed to join conspecifics and sample directly, three-spines will join the shoal feeding at the richer food patch (Krause, 1992). In contrast, the collection of personal information in open water is costlier for nine-spines than for three-spines because nine-spines have inferior structural anti-predator defenses (e.g., lack of girdle and body armor and shorter dorsal spines). Indeed, piscivorous predators are known to preferentially consume nine-spines over three-spines (Hoogland *et al.*, 1957). Because of these costs, nine-spines may forego the opportunity to collect reliable personal information and favor vicarious assessment of foraging opportunities.

More generally, public-information use may be an adaptation that allows animals vulnerable to predation to acquire valuable foraging information at low risk. However, individuals that do not incur such costs would be

expected to acquire and utilize personal information, since this is typically more reliable. Public-information use is often thought to require more complex cognition than assessment of the mere presence or absence of a resource (Valone and Templeton, 2002). Coolen *et al.*'s finding that three-spines could acquire the latter, but not the former, type of information suggests that increases in the complexity of the information gathered may favor the evolution of advanced cognition. This finding is consistent with the assumption that "the value of public information may depend upon the cost of acquiring sample (personal) information" (Valone and Templeton, 2002, pp. 21; parentheses added).

b. Birds In a study involving the use of personal and public information, regarding patch quality, Templeton and Giraldeau (1996) demonstrated that starlings preferentially use public information when it is easy to acquire but use personal information otherwise. Naïve starlings were paired with "low information" or "high information" demonstrators who respectively sampled few or many holes in an artificial foraging patch. As the observers' patch contained few or no baited holes, they had to sample several holes before deciding whether the patch was empty and departing it, but could also use the simultaneous foraging behavior of their demonstrator. When patches were arranged in a linear array and thus personal information was easy to collect, naïve starlings ignored the public information. Observers sampled an equal number of holes before departure for another patch, irrespective of whether they were paired with a high- or low-information demonstrator. However, when the foraging patch comprised a square array of holes, it was simultaneously more difficult for birds to keep track of which holes they had personally sampled and easier for them to observe the demonstrators. Here, the number of holes observers sampled before patch departure decreased as the amount of information provided by demonstrators increased. In accordance with theoretical predictions, this indicates an increased use of public information as the cost of acquiring accurate personal information increased. Here, relative reliance on personal or public information appeared to depend on the difficulty of acquiring personal (and social) information (see also Templeton and Giraldeau, 1995a).

c. Mammals Galef and Whiskin (1998) found that the food intake of rats exposed to novel food sources of equal palatability (cayenne- or cinnamon-flavored rat chow) was significantly influenced by exposure to a demonstrator that had recently eaten one or other of the food sources. For example, rats exposed to a demonstrator that had eaten cayenne-flavored food ate more of this flavored food when subsequently exposed to both flavored foods

simultaneously. However, where there was no difficulty in discriminating between the palatability of food sources, either because one was made relatively unpalatable (increased cayenne: experiment 1) or relatively more palatable (addition of sugar to cinnamon: experiment 2), the effect of demonstrator rats on the observer's food intake diminished. One interpretation of these findings is that the rats only use social information when it would be too time consuming (costly) to distinguish between the two food sources.

The cost of acquiring personal foraging information was manipulated in a study of social foraging in callitrichid monkeys, involving seven lion tamarin (*Leontopithecus*), tamarin (*Saguinus*), and marmoset (*Callithrix*) species. 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 latency between the first contact of the task and successful food extraction, as well as by the total number of food items 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 means of opening the difficult, but not the easier tasks, were learned socially. 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 personal cost, in terms of time and energy, while the solutions of the more complex tasks were associated with a sufficiently large cost to render social learning adaptive. Similarly, Baron *et al.* (1996) reported that human subjects were found to imitate more as task difficulty increased.

2. *Mate Choice*

Assessing and choosing potential mates is thought to be a demanding task, requiring the acquisition and processing of a variety of information indicating mate quality. Several researchers have proposed that the costs associated with mate assessment, such as increased vulnerability to predation, search costs, opportunity costs, and errors, will favor reliance on mate-choice copying (see review by White, 2004). As the costs of mate choice increase, personal sampling will decrease with a concomitant increase in vicarious sampling (Gibson and Höglund, 1992).

a. Fish Female guppies possess a heritable preference for orange body coloration in male mates (Houde, 1988). In a mate-choice experiment in which "observer" females choose between two males, Dugatkin (1996)

pitted this personal information concerning coloration against conflicting social information, by constraining “demonstrator” females in such a way as they appeared to the observer to choose the male with the least orange coloration. He found that, when the orange coloration of the two males differed by 24% or less, females used the social information provided by demonstrators. Thus, when females could potentially make an erroneous decision based upon personal assessment, plausibly representing a cost in terms of reproductive success, females appeared to disregard their personal information in favor of social information. However, when male coloration differed by 40% or more, the personal preference overrode the social information, as females chose the male with the greater orange body coloration. The empirical evidence for this phenomenon is not unequivocal, however, as Brooks (1996) found that females’ ease of discrimination of males based upon ornamentation did not influence the incidence of mate-choice copying in guppies.

Briggs *et al.* (1996) explicitly tested whether mate-choice copying of laboratory-housed guppies was affected by the cost of potential predation from a piscivorous fish. They found that guppies disregarded their personal preference and chose males according to the apparent preference of another female in the absence of an immediate threat of predation. However, there was no evidence for copying under threat of predation, possibly because observer females choose between males with less discrimination under such risks. As other studies (e.g., Dugatkin, 1992; Dugatkin and Godin, 1992) used guppies originating from low-predation sites, and did not compare guppies originating from low and high predation sites, to our knowledge researchers have not tested whether predation costs influence the extent to which individuals rely on social information in mate choice. Similarly, studies currently provide no evidence to support an avoidance of search costs explanation for the use of social over personal information in fish mate assessment. On the contrary, Dugatkin and Godin (1998) found that food-deprived guppies, who would presumably face high energetic costs in collecting personal information due to lost foraging time, did not show an enhanced tendency to use social information, in their mate choice, compared to satiated females. In fact, the guppies were less likely to use social information as food deprivation increased, possibly because females do not prioritize mate choice when hungry.

b. Birds Gibson *et al.* (1991) examined the mating distributions of wild sage grouse (*Centrocercus urophasianus*) at two leks, and suggested that although females assess males directly, they also take advantage of the opportunity to copy the decisions of conspecifics. They argue that this indicates that personal assessment of potential males may be costly to females, and copying may allow them to make greater investment in

foraging or nest-site defense. However, a subsequent study by Gibson and Bachman (1992) reported that sage grouse incur only trivial increases in energetic expenditure and predation risk, and no reduction in foraging time or nest defense, when repeatedly sampling males at leks versus visiting once, suggesting there may be little opportunity to reduce costs by copying. One potential explanation is that copying may increase the reliability of decision making over the use of personal information alone, rather than reducing costs. A second possibility is that these birds are locked into “information cascades” (Giraldeau *et al.*, 2002). Moreover, it is also possible that copying itself entails some costs to females due to inaccurate identification of preferred male traits and the possibility that females waiting in line for a particular male risk reduced fertility through sperm depletion (Gibson and Bachman, 1992; Gibson and Höglund, 1992). Sirot (2001) proposed that mate-choice copying may incur a cost whereby offspring of the preferred male may be disadvantaged due to increased competition among offspring of the same father.

Finally, in a series of experiments (reviewed by White, 2004) with Japanese quail (*Coturnix japonica*), White and Galef show that social information overrides prior personal preferences for mates in both males and females, although the costs of using personal information have yet to be explicitly manipulated in this system.

c. Mammals In many lekking species of mammals, females often join males that have the largest harems (Clutton-Brock *et al.*, 1989). However, after a series of experiments, McComb and Clutton-Brock (1994) determined that, for fallow deer (*Dama dama*) at least, this did not reflect mate-choice copying but a tendency of estrus females to follow each other's movements due to the costs of predation and of harassment by males in mixed-sex groups. Here, the costs of using personal information to join a preferred male may indirectly cause social information to be used in mate choice.

3. Aggression

The benefits of fighting may include gaining or maintaining access to limited resources, such as food, mates, or shelter, while the costs include injury, increased risk of predation, and time and energy costs (Huntingford and Turner, 1987; Neat *et al.*, 1998). As fights are costly for both interactants (Neat *et al.*, 1998), but more so for losers, it may pay for individuals not directly involved in aggressive interactions to gather social information about the quality of future opponents (Johnsson and Akerman, 1998; Peake and McGregor, 2004).

a. Fish Male Siamese fighting fish (*Betta splendens*) monitor aggressive interactions between neighboring conspecifics and use the information on relative fighting ability in subsequent aggressive interactions with the males they have observed (Oliveira *et al.*, 1998). Similar observations have been made in rainbow trout (Johnsson and Akerman, 1999). This exploitation of communicated signals in a network has become known as “eavesdropping” (McGregor, 1993). Oliveira *et al.*’s findings suggest that the level of aggression that eavesdroppers observe in interactions between a pair of demonstrators strongly affects their subsequent agonistic interactions. We suspect that it is no coincidence that the exploitation of social information concerning fighting ability has evolved in a species for which the asocial gathering of equivalent information (i.e., by fighting all parties) would be extremely costly, as these fish frequently fight to the death. We anticipate that this ability may not be found in other Gourami species in which the costs of agonistic encounters are lower, and encourage research comparing species differing in the cost of agonistic encounters.

In sum, a large amount of empirical evidence has amassed in support of the hypothesis that animals will show greater reliance on social learning as the costs of acquiring or using asocial information increase. This evidence is all the more compelling, as it spans a variety of species and behavioral domains covering costs of predation, injury, lost opportunities, or energy and reproductive success. There still remains, however, a paucity of experiments designed specifically to test whether animals adhere to a strategy of *copy others when asocial learning is costly*, especially outside of the foraging domain and in the obviously costly domain of anti-predator behavior.

III. EVIDENCE THAT ANIMALS EXPLOIT SOCIAL INFORMATION WHEN UNCERTAIN AS TO WHAT TO DO

A. UNCERTAIN BECAUSE THEY HAVE NO RELEVANT INFORMATION

1. Theoretical Foundation

In 1988, Boyd and Richerson published a model exploring the advantages of reliance on social and asocial learning in a temporally variable environment, in which hypothetical animals have to make a decision as to which of two environments they are in and choose the most appropriate behavior. Behavior 1 is appropriate in environment 1, behavior 2 in environment 2, and 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. If x has high values, above a threshold value d , the animals “know” they are in environment

1 and perform behavior 1; if x has low values (below $-d$) they “know” they are in environment 2 and perform behavior 2; while if x has intermediate values ($-d < x < d$), they are uncertain and copy the behavior of others. The model consequently assumes that animals adopt a *copy when uncertain* strategy (Boyd and Richerson, 1988; Laland, 2004). Thus, when prior personal experience leaves individuals certain as to how to behave, it is assumed that they will ignore social information. However, when their prior experience leaves them uncertain as to which pre-established behavior pattern is appropriate in a given context, animals are expected to attend to the behavior of others. Note, Boyd and Richerson present no data in support of this assumption, and at the time it was unclear whether animals were more likely to use social learning when they were uncertain.

We note a (i) broad and a (ii) narrow interpretation of Boyd and Richerson’s (1988) 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 two or more established behavior patterns is appropriate. There is considerable empirical evidence (detailed in the following section) for the broad assumption, albeit often inadvertent and circumstantial, but none that we know of for the narrow assumption, which must be regarded as the strict interpretation of Boyd and Richerson’s assumption.

2. Empirical Evidence

As before, we will now summarize empirical support, in fishes, birds, and mammals, for Boyd and Richerson’s hypothesis.

a. Foraging

i. *Fish* In an experiment related to that described previously, Kendal *et al.* (2004) tested the propensity of guppies in three conditions 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 with both prior personal and conflicting social information; a second was solely given social information, and a control group had no personal information. They found that fish that were provided with social information only, and lacked relevant prior information, fed at the feeder indicated by conspecifics significantly more 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, irrespective of the order in which personal and social information are experienced (Laland, unpublished data). Similarly, Coolen *et al.* (2003; see Section II.B.1.a) found that nine-spined sticklebacks that did not have personal information

copied the patch choices of others, whereas [van Bergen *et al.* \(2004; see Section III.B.2.a\)](#), testing the same species in an identical set-up, found that fish would ignore social information when they had relevant personal information.

ii. *Birds* An illustration of how animals may sometimes ignore social information is provided by [Dorrance and Zentall's \(2002\)](#) study of imitation in pigeons. These researchers conducted a series of experiments involving a conditional discrimination foraging task whereby, in order to receive access to grain, pigeons learned to step on a treadle in the presence of one light (either white or green) and to peck at the treadle in the presence of the other light. Although the study was designed to investigate aspects of imitation in these birds, the experimental design sheds light upon the trade-off between personal and social information. First, they found that social information was ignored in the initial acquisition of the conditional discrimination. Second, pigeons ignored a single demonstration that was contradictory to their previously acquired personal information relating to which behavior (peck or step) should be performed in the presence of which light (white or green). In order to say that the social information was ignored, one must be able to show that the social information was actually acquired. They found that where birds were required to learn the reverse of their conditional discrimination, those pigeons provided with demonstrations that were consistent with the current reinforcement regime (e.g., grain provided if *peck* on treadle in presence of green light) learned to reverse their prior conditional discrimination more rapidly than did those provided with a demonstration that was inconsistent with the current reinforcement regime (e.g., grain provided if *step* on treadle in presence of green light). Thus, it appears that the pigeons ignored social information when they had the relevant personal information available to them but were predisposed to use social information, rather than personal information, when uncertain of what to do.

The importance of social information for those individuals who lack personal information is highlighted by experimental work on the developmental basis of social learning in chickens. [Nicol \(2004\)](#) reports that sensitivity to social information, which is very high in chicks, reduces as chickens mature. For example, day-old chicks avoided pecking at an aversive stimulus after observing the “disgust” response of another chick ([Johnston *et al.*, 1998](#)), whereas 9-week-old, adult hens showed no avoidance of a food that had previously elicited “disgust” in their demonstrators ([Sherwin *et al.*, 2002](#)). It appears that a lack of personal information, in this case ingestive experience, regarding food preferences in young chickens may foster reliance upon social information ([Nicol, 2004](#)). However, as these birds gain greater experience, their reliance on social learning seemingly diminishes.

It is possible also that foraging mistakes are more costly for day-old than for 9-week-old chicks, hence a greater reliance on social learning at earlier ages (see [Section II](#)).

[Templeton and Giraldeau \(1995a\)](#) found that when opaque barriers prevented starlings from watching foraging conspecifics at the same time as they acquired personal information by probing for food, they ceased to acquire social information. When the opaque barriers were absent, the same individuals behaved as if they were combining personal and social information. Thus, this study provides further support for the hypothesis that asocial learning is the preferred source of information, and social information will only be acquired or used if personal information is inadequate. A second study involving starlings ([Templeton and Giraldeau, 1995b](#)) showed that individuals ignored conflicting social information when they possessed personal information as to the location of food (according to a color association), but used it when they had no such personal information.

iii. *Mammals* Galef and colleagues (see review by [Galef and Giraldeau, 2001](#)) have repeatedly demonstrated that Norway rats (*Rattus norvegicus*) use various sources of social information to decide whether to consume novel foods. [Galef et al. \(2001\)](#) further highlighted contexts in which rats appear to use social information only when they lack relevant personal information. Here, a series of experiments were conducted to determine when individuals steal food (kleptoparasitism) from conspecifics, despite the presence of a surplus of food. In one experiment, rats were divided into two conditions, each being fed a different type of food (food type 1 and 2). Pairs of rats, from the same condition, were then placed in a test arena, containing 10 pellets of food type 2, for 10 minutes. Significantly less food stealing was observed in the pairs that had been pre-exposed to food type 2 than in those that had not. Seemingly, rats lacking prior personal experience with a food will ignore personal sampling opportunities in favor of using social information to discern the safety of a food item.

In a subsequent experiment, rats were assigned to three conditions according to their relative ages; (1) both “old,” seven to eight weeks; (2) both “young,” four to five weeks; and (3) one “young” and one “old.” Although the total number of food stealing instances did not differ between conditions ([Fig. 5A](#)), in the young-old condition, young rats attempted to, and succeeded in, stealing from older rats more frequently than did old rats from young rats ([Fig. 5B](#)). This corresponds to the findings with guppies and chickens that young individuals who lack personal experience may rely more heavily on social information than their elders.

[Visalberghi and Fragaszy \(1995\)](#) reported enhanced consumption of novel, but not familiar, foods among capuchin monkeys (*Cebus apella*) in

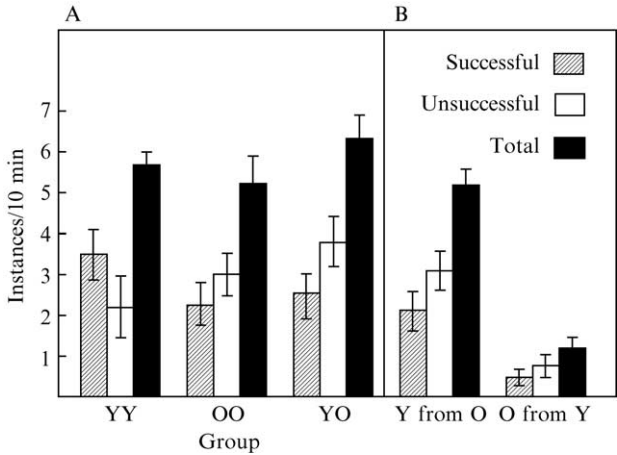


FIG. 5. (Fig. 4 from Galef *et al.*, 2001) The mean (\pm SE) total number of successful and unsuccessful instances of food stealing by rats during a 10-minute test, for (A) rats assigned to groups YY (young-young), OO (old-old), and YO (young-old); and (B) within group YO, young rats stealing from old rats (Y from O) and old rats stealing from young rats (O from Y) (Galef, B. G. Jr. *et al.*, 2001. Copyright © 2001 by the American Psychological Association. Reprinted with permission).

the presence of conspecifics, compared with when alone. However, in a subsequent study (Fragaszy *et al.*, 1997), involving many novel and familiar foods, infant capuchins showed no evidence of selective use of social information from older or more experienced individuals. Similarly, Queyras *et al.* (2000) found that young common marmosets were as likely to favor personal information, regarding food palatability, despite contrasting social information provided by older conspecifics, as were older individuals paired with younger demonstrators. In contrast, several studies of callitrichid monkeys suggest that young animals seek out social information regarding novel but not familiar food. For instance, studies of captive family groups of lion tamarins have reported that infants are less willing to take novel food items from food bowls themselves than they are to take familiar items (Price and Feistner, 1993). Furthermore, young golden lion tamarins were found to be less likely to reject novel foods acquired from other group members than they were to reject foods that they had obtained independently (Rapaport, 1999), a process that may be enhanced by emission of vocalizations in adults when “offering” foods (Snowdon, 2001; Roush and Snowdon, 2001).

b. Mate Choice

A theoretical model by Stöhr (1998) reports that mate-choice copying is likely to evolve when young females discriminate poorly among males and need to learn what high-quality males look like. Similarly, in considering mate-choice copying in a public information (see Section II.B.1.a) framework, Nordell and Valone (1998) predict that copying behavior should increase as the discrimination task becomes more difficult for an individual.

i. *Fish* Prior to these models, Dugatkin and Godin (1993) designed an experiment in which female guppies observed the apparent mate choice decision of females who were either bigger (experiment 1) or smaller (experiment 2) than the observer. They assumed that smaller fish were younger than their larger counterparts and that larger females had had more experience of choosing mates than younger ones. Dugatkin and Godin reported that, following the observation period, smaller females spent more time in proximity to the male that had seemingly been chosen by larger demonstrators, whereas larger females chose mates randomly with respect to the mate choice of smaller demonstrators. If this finding proves robust, it would appear that guppies rely upon social information in mate choice decisions where relevant personal information is lacking. However, alternative explanations must be ruled out. For example, smaller females may be more vulnerable to predation than larger ones, and they may rely on social information to avoid comparatively large sampling costs.

In sum, there is ample empirical evidence that animals will ignore social information unless they lack requisite personal information. Although not true for all species studied, there is evidence that young animals appear to be more reliant on social learning than older animals.

B. UNCERTAIN BECAUSE PRIOR INFORMATION IS UNRELIABLE

1. Theoretical Foundation

In relatively spatially homogenous environments, animals may be expected to rely on genetic inheritance of pertinent information, while learning is likely to be of utility in situations that are more changeable. Boyd and Richerson (1985, 1988) modeled the use of social information in a spatially *heterogeneous* environment where individuals of the same age cohort experience different environments, resulting in the possibility of observers and demonstrators having differing experiences. 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 (Boyd and Richerson, 1985). In other words, as environmental heterogeneity increases

and personal information becomes more error prone (or less reliable), the optimal amount of social learning from local residents increases, while as the rate of dispersal between environments increases, social information becomes increasingly unreliable, and the optimal amount of social learning decreases (Boyd and Richerson, 1988).

Giraldeau *et al.* (2002; see Bikhchandani *et al.*, 1992) proposed that individuals may use social information not 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. For instance, where an individual witnesses a sequence of individuals responding to the environment in the same manner, it may conceivably be optimal for that individual to ignore its own personal information and use the more prevalent social information, particularly where individuals can detect the decisions of others but not the cues on which such decisions are based. They suggest such reliance on social information concerning the decisions of others can lead to arbitrary or even maladaptive traditions in animals (Giraldeau *et al.*, 2002; see also Section IV). Despite this, current theoretical work regarding the reliability and value of information in communication systems (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. Finally, using a mate-choice model, Sirot (2001) found that females should use personal information if male phenotypic value is a reliable indicator of reproductive success, but as this reliability decreases, they should use public information and copy the choices of other females.

In summary, a variety of theoreticians have proposed that animals should use social information, either when their personal information is unreliable or when it is merely less reliable than the social information available to them.

2. Empirical Evidence

a. Foraging

i. *Fish* 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 as Coolen *et al.* (2003; see Section II.B.1.a and Fig. 3). Fish were allocated to three conditions, where they received (1) 100%, (2) 78%, or (3) 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% reliable condition significantly preferred the “rich” feeder, as did those in the 78% condition,

although to a lesser extent. Individuals in the 56% reliable condition showed no feeder preference. 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 personal information, as fish in the other conditions exhibited no preference. As shown in Fig. 6, only fish with completely reliable personal information (100%) ignored the public information. 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

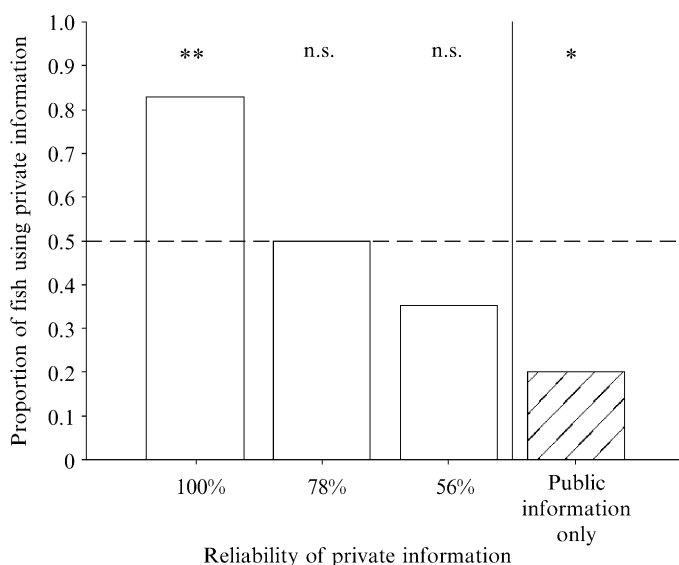


FIG. 6. (Fig. 2A from van Bergen *et al.*, 2004) The proportion of nine-spined sticklebacks that, after receiving personal information of varying reliability followed by conflicting public information, entered first the goal zone of the feeder that was “rich” according to personal information. The dashed 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. indicates not significant (van Bergen, Y. *et al.*, 2004; used with permission of the Royal Society of London).

fish with completely reliable private information will ignore conflicting social information.

ii. *Birds* Starlings (*Sturnus vulgaris*) have been found to value social information in an unpredictable, but not in a predictable, environment (Rafacz and Templeton, 2003). The birds were assigned to four conditions: predictable environment with an informative demonstrator, predictable environment with an uninformative demonstrator, unpredictable environment with an informative demonstrator, and unpredictable environment with an uninformative demonstrator. The “environment” consisted of three wooden wells covered with paper circles, of differing colors or patterns, which could be pierced to retrieve a mealworm. In the predictable conditions, a demonstrator bird would always locate a mealworm beneath the same colored/patterned circle (regardless of hole position), whereas in the unpredictable conditions, a demonstrator was seen to obtain food from each of the three colored/patterned circles an equal number of times. In the informative conditions, demonstrators and observers were provided with the same combination of colored/patterned circles and acquired a mealworm from the same colored/patterned well. However, in the uninformative conditions, the demonstrator was provided with three white circles, representing irrelevant information to the observer, who was subsequently provided with a consistent combination of three colored/patterned circles. Following each of 30 demonstration periods, observers were provided with three wells, and the color/pattern of the circle they first pierced was noted.

As expected, birds in the predictable conditions discovered more mealworms than those in the unpredictable conditions. Although in the unpredictable environment foraging success was greater for birds with informative, rather than uninformative, demonstrators, no such effect was found in the predictable environment (Fig. 7). These results are consistent with theoretical predictions that the value of social information increases as the reliability of personal information decreases.

This study may allow assessment of the interpretation of Boyd and Richerson’s (1988) assumption: that animals will tend to use social information when uncertain as to which pre-established behavior pattern is appropriate in a given context (see Section III.A.1). As can be seen in Fig. 7, for birds in an unpredictable environment, there was a time delay (of 20 trials or 2 days) before the foraging success of birds with an informative demonstrator exceeded that of those with an uninformative demonstrator. Rafacz and Templeton (2003) argued that this delay reflects the fact that birds with the informed demonstrator were initially relying upon their personally acquired information, despite their low foraging success, and it took them time to recognize the value of the social information. Birds in

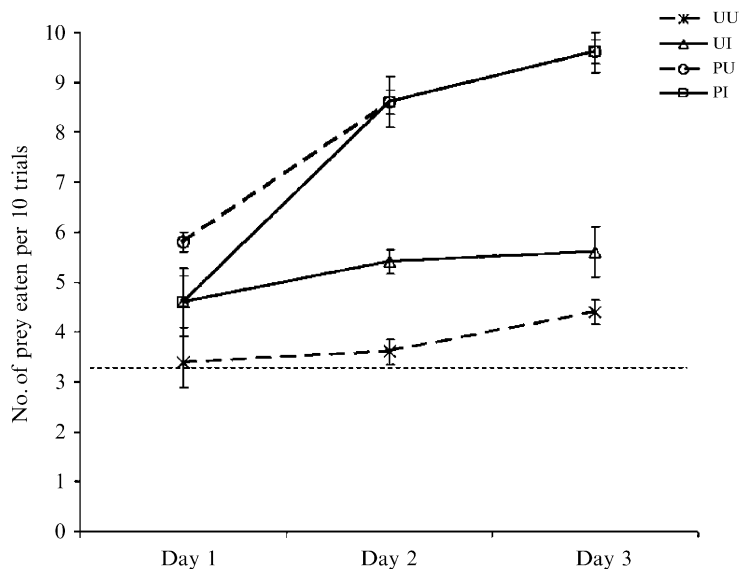


FIG. 7. (Fig. 2 from Rafacz and Templeton, 2003) The mean number of prey items eaten by starlings in four environment/demonstrator treatment groups over three days of testing. UU = unpredictable/uninformative, UI = unpredictable/informative, PU = predictable/uninformative, PI = predictable/informative (Rafacz, M. *et al.*, 2003; used with permission of Blackwell Publishing Ltd).

unpredictable environment conditions were always provided with the same three colored/patterned wells (although the food was not reliably associated with any one) and over several trials may have learned, through personal sampling, that food may be associated with either of two colors or patterns. Thus, the delayed use of social information by these birds may represent indirect confirmation of the narrow version of Boyd and Richerson's (1988) assumption, to the extent that learned preferences for the two colors or patterns equate to "pre-established" behavior patterns.

iii. *Mammals* Dewar (2003a) developed a *cue reliability approach* to elucidate when foragers should accept or reject a novel food. The basic principle states that, when the average payoff for consuming familiar foods is high relative to other payoffs (here the consumption of novel foods), foragers subsequently require more reliable personal or social information that a new food is beneficial or safe to consume. In Dewar's terms, these animals have a HIGH reliability threshold and hence a low probability of eating a further novel food. Conversely, animals that experience novel foods of higher caloric value than their familiar food will develop a LOW

reliability threshold and a high probability of eating further novel foods. An initial experiment provided empirical support for this proposal (Dewar, 2004). Norway rats were familiarized with encapsulated food of moderate caloric value (marjoram flavor), and all experienced the same probability that encapsulated food had a positive caloric value (i.e., 10/12 capsules). The rats were then split into two groups that received either 10 novel foods with an average caloric value that was *higher* than the familiar food or 10 novel foods with an average caloric value that was *lower* than the familiar food.

The resulting reliability thresholds acquired by the rats were then tested by simultaneously presenting both groups with two foods of moderate caloric value, one being completely novel and the other familiar (marjoram flavor). For the group that received novel foods of higher caloric value than the familiar food, the probability that the novel food was eaten, rather than the familiar food, was dictated by a LOW reliability threshold; and hence they were expected to consume more of the novel food. This occurred because their prior experience had been that novel foods were on average of higher caloric value than familiar foods, resulting in a requirement for relatively little information, indicating that a novel food has a higher payoff than a familiar one. In contrast, the group that received novel foods of lower caloric value than the familiar food had a HIGH reliability threshold, as their prior experience indicated that novel foods were on average of lesser caloric value than familiar foods, and they were expected to eat less of the novel food. These rats require greater confidence than the other group that consumption of a new food will be more profitable than that of a familiar food. Indeed, Dewar reports that rats in the LOW, but not HIGH, reliability threshold group consumed more of the novel, than familiar, food in the test phase. This is presumably because the personal information is reliable for LOW threshold rats (the 10 novel foods and the test novel food all had a positive caloric value) but not for HIGH threshold rats (the 10 novel foods had a negative caloric value, and the test novel food did not). Indeed, the high caloric value of LOW threshold rats' diet yielded a reliability threshold below the probability that encapsulated food had a positive caloric value and was thus reliable. In contrast, rats in the HIGH threshold group had unreliable personal cues; the low caloric value of their diet generated a reliability threshold that exceeded the probability that novel food had a positive caloric value.

According to Dewar's theory, rats with a HIGH reliability threshold require additional information indicating that a novel food will have a higher payoff for them than a familiar food, compared to LOW reliability threshold rats. Thus, Dewar proposed a *social cue dependency hypothesis* whereby foragers should show increasing dependence on social cues as asocial cues become less reliable (i.e., as their reliability threshold

increases). In a second experiment, Dewar presented HIGH and LOW reliability threshold rats with two completely novel foods, one of which a demonstrator had recently eaten (socially marked via the breath of the demonstrator) and one that the demonstrator had not eaten (socially unmarked).² As expected, rats in the LOW threshold group ate more of the socially unmarked food than did rats in the HIGH threshold group, indicating that rats with low expectations about the value of novel foods (HIGH threshold group) required the additional information provided by the demonstrator. This therefore indicates that individuals with reliable personal information (LOW reliability threshold), as to the expected profitability of novel foods, do not ignore the opportunity to acquire personal information in the presence of conflicting social information. However, as rats in the HIGH threshold group (who have unreliable personal information) did not eat more of the socially marked food than did rats in the LOW threshold group (Gwen Dewar, personal communication.), the findings are not completely consistent with the prediction that animals will use social information when their personal information is unreliable.

b. Social behavior

i. *Mammals* Dewar (2003b) demonstrated that female macaques (*Macaca mulatta*) discriminate between reliable and unreliable social information, providing further support for the *cue reliability approach*. Here, an observer macaque may obtain reliable social information, pertaining to the relative social rank of an unfamiliar individual, if she observes the unfamiliar individual being outranked by a familiar individual who is subordinate to herself. In contrast, the observer can obtain unreliable social information, pertaining to the relative rank of an unfamiliar individual, if she observes the unfamiliar individual being outranked by a familiar individual who is dominant to herself. This is the case because the unfamiliar individual may either have a rank lower than the observer or intermediate to the observer and the familiar dominant. Thus, in this scenario, for social information to be considered reliable, it must provide evidence that the observer's attempt to dominate the unfamiliar individual will succeed with a probability exceeding the reliability threshold. In addition, the reliability threshold increases, requiring information indicating an increasing probability of success, as the costs (i.e., injury) of failing to outrank an unfamiliar individual increase.

²As socially marked novel foods may be considered safer to consume than unmarked novel foods, Dewar attempted to make the willingness of rats to eat each of the novel foods equivalent. Thus, the socially marked food was further away and less abundant than the unmarked food.

Mid-ranking female observers were exposed to three conditions, where unfamiliar individuals appeared subordinate to a familiar subordinate, a familiar dominant, or an unfamiliar female. The behavior of the observer towards the unfamiliar female was subsequently tested. As expected, observers were more assertive towards unfamiliar individuals in the familiar subordinate condition than either the familiar dominant or unfamiliar conditions. This finding is consistent with the hypothesis that macaques are capable of discriminating between unreliable and reliable social cues, although it is difficult to be certain that “reliability” underpins this discrimination. It is possible that the macaques are not making a discrimination based on cue reliability but are rather making differential use of cues that vary in their informativeness.³

c. Anti-predator behavior

i. *Mammals* Among yellow-bellied marmots (*Marmota flaviventris*), which produce individually distinct alarm calls, Blumstein *et al.* (2004) report that caller reliability is negatively associated with the amount of time allocated to personal assessment of the level of threat. In an initial experiment, individual marmots appeared to conspecifics to be “reliable” or “unreliable” alarm callers through the pairing of their calls with the presence of a predator or non-predator, respectively. In playback tests, group members allocated more time to vigilance behavior following the alarm call of an “unreliable” than “reliable” individual, consistent with their gathering personal information when social information is unreliable. In a second experiment, marmots were presented with degraded and non-degraded alarm calls, representing distant and adjacent alarm callers, respectively. The degraded calls were considered unreliable, as alarm calls from distant individuals were assumed to represent a lesser certainty of risk than those emitted by adjacent individuals. Again, during playback of calls, marmots responded to the “unreliable” rather than “reliable” social information with increased vigilance and collection of personal information. This second experiment may well be better considered in the following section, where a trade-off in the use of information is assumed when one or other source is likely to be outdated or inappropriate.

In a review of social learning about predators, Griffin (2004) argued that social learning might be expected to be faster and more robust in species in which social information (here alarm behavior) reliably predicts a high

³Inevitably, many of these examples could have been discussed under different strategies. For instance, the Dewar (2003b) macaque example could fit equally well with a strategy such as “copy others when uncertain what to do because have no relevant information” rather than “when personal information is unreliable.”

predator threat than in other species (e.g., fish versus birds and mammals; [Griffin, 2004](#)). There is, as yet, little evidence to assess the validity of this argument.

In sum, although the empirical evidence that animals copy others when their personal information is unreliable is somewhat limited, it does cover several different species, and it includes situations where information pertaining to food, conspecifics, and predators is unreliable. Dewar's cue reliability approach and the domain of anti-predator behavior offer promising sources of greater evidence for a trade-off in animal decision making according to the relative reliability of social and personal information.

C. UNCERTAIN BECAUSE PRIOR INFORMATION IS OUTDATED

1. *Theoretical Foundation*

[Boyd, Richerson, and colleagues \(1985, 1988; Henrich and Boyd, 1998\)](#) have modeled the use of social information in temporally *fluctuating* environments, where individuals in different age cohorts experience different environments, resulting in the possibility of observers acquiring social information from models who are demonstrating optimal behavior for an earlier state of the environment. The analyses suggest that species living in an environment of intermediate levels of fluctuation will be most likely to use social learning. Conversely, those experiencing the extremes of a highly fluctuating environment or, alternatively, a stable environment, would have less to gain from observing others and should rely to a greater extent upon asocial learning or genetic inheritance of information, respectively ([Boyd and Richerson, 1985, 1988; Laland et al., 1996](#)). Social learning is thought to be favored at intermediate rates of change, as 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 were 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 and more likely to evaluate it through personal sampling.

In another theoretical analysis, [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 it will not happen anymore when the environment changes too

unpredictably (or randomly). In a more recent theoretical analysis, based upon an earlier model by [Henrich and Boyd \(1998\)](#), [Kameda and Nakanishi \(2002\)](#) reported that in a fluctuating environment, increasing costs of asocial learning initially results in a concomitant increase in social learning, a lesser amount of fresh information, and thus an outdated “cultural knowledge pool.” However, they predict that natural selection will act against reliance on social learning when doing so is based on such flawed information. Thus, when acquisition of personal information is costly (see [Section II](#)), conformity, or frequency-dependent social learning (see [Boyd and Richerson, 1985](#); [Day et al., 2001](#)), should be weaker in fluctuating than in stable environments, ensuring that 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 costly due to its being outdated.

2. Empirical Evidence

a. Foraging

i. *Fish* In another experimental study of nine-spined sticklebacks, [van Bergen et al. \(2004\)](#) manipulated the degree to which personal information, regarding the profitability of two foraging patches, was outdated and explored how this prior experience affected individuals’ subsequent acquisition of public information. Again, a similar experimental design as [Coolen et al. \(2003\)](#); see [Section II.B.1.a](#) and [Fig. 3](#)) was used. Fish were allocated to four conditions, where they received personal information as to which of two feeders was “rich” and which “poor,” either 1, 3, 5, or 7 days prior to receiving conflicting public information individually. Immediately following the conflicting demonstration and the removal of demonstrators, the fish were tested to see which feeder they visited first. 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 three and five days since acquiring their personal information showed no feeder preference, and those experiencing a 7-day delay first visited the feeder that was “rich” according to the public information ([Fig. 8](#)). 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 fish in the 7-day condition instead ignored their personal information in favor of the public information. Thus, in accordance with the theory, as personal

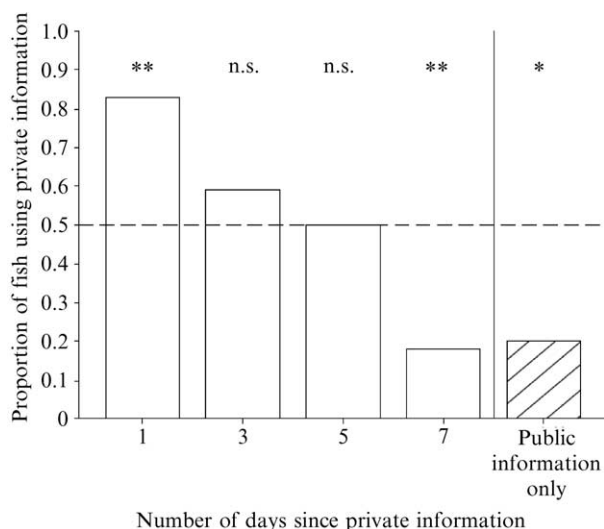


FIG. 8. (Fig. 3A from [van Bergen *et al.*, 2004](#)) The proportion of nine-spined sticklebacks that, after receiving personal information followed at varying time lags by conflicting public information, entered first the goal zone of the feeder that was “rich” according to personal information. The 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. indicates not significant (van Bergen, Y. *et al.*, 2004; used with permission of the Royal Society of London).

information becomes increasingly outdated, nine-spined sticklebacks become increasingly reliant upon socially acquired information. Although not specifically tested, this reliance upon the more recently acquired source of information could equally apply if personal information follows social information.

ii. *Mammals* In a study involving several species of domestic dogs, [Pongrácz *et al.* \(2003\)](#) trained dogs to acquire a food reward through a door in a fence. Upon closing of this door, which prevented dogs from using their personal information, those dogs that saw a demonstrator detour around the fence learned to do the same to obtain the reward, and they learned more quickly than did those with no such demonstration. Confirmation of theoretical predictions was not the authors’ aim, and although the study demonstrates that social information was used when personal information was no longer useable, hence outdated, it lacks a condition enabling assessment of the extent to which dogs would have used the social detour information when their personal information was a concurrently available alternative to social information.

Galef and Whiskin (2004) assessed Boyd and Richerson's (1988) prediction that animals will show greater reliance on social learning in relatively stable, rather than rapidly changing, environments. Observer rats were assigned to a variable-environment group, where over 12 days they experienced random variation in time, location, duration, and type of food presented; and a stable-environment group, that each day received the same food in the same location, at the same time, and for the same length of time. On the 13th day, a demonstrator rat that had eaten either cinnamon- or cocoa-flavored food (both novel to observers) was placed in each observer's cage for 30 minutes. Following this, observers were provided with equal amounts of cinnamon- and cocoa-flavored food for 22 hours. Although observers in both the variable- and stable-environment groups consumed more of the food that their demonstrator had eaten, those in the stable-environment condition did so to a significantly greater extent than those in the variable-environment group. As this study did not pit personal information against social information, both cinnamon and cocoa flavor being novel to observers, it is not possible to fully assess whether the rats relied more heavily on personal or social information in environments of differing variability. Nonetheless, the behavior of the rats is consistent with their increasing reliance on copying as the expected reliability of transmitted information increases. We do not have, however, any evidence to suggest that rats in the stable-environment condition would have favored social over personal information to a greater extent than did those in the variable-environment condition. In fact, the reverse may well have occurred, were variable-environment rats to consider their personal information to be outdated relative to the social information gleaned from the breath of the demonstrators.

b. Mate choice

i. *Birds* There is some circumstantial evidence that Japanese quail are sensitive to the possibility that their social information regarding mate choice is outdated. In this species, there appears to be a sex difference in the extent to which sources of information become outdated. Although we refer to the value of outdated social information here, rather than personal information, it is interesting to note that males avoid a female they just saw mating, most likely because of sperm competition. However, 2 days later, males no longer avoid females they saw mating earlier; at this point, first male precedence, in sperm competition, is thought to give way to last male advantage (Birkhead *et al.*, 1995), and social information regarding female unsuitability becomes outdated (White and Galef, 2000). Until empirical tests are carried out, however, we cannot rule out the possibility that males simply forget social information concerning females after 2 days. In contrast, for females, social information regarding a male's quality remains

valuable in the future (over 2 days; [White and Galef, 2000](#)). The fact that female quails can remember social information about mate quality after two days hints at a similar capacity of information retention in males of the same species, and it suggests that the discarding of 2-day-old social information by males is due to a decision to do so rather than mere forgetting.

c. Monetary reward

i. *Mammals* Using human subjects, [Kameda and Nakanishi \(2002\)](#) tested their prediction that, in a variable environment, individuals will be less likely to conform (or copy the majority) to the behavioral decisions of others with increasing costs of acquiring personal information (see [Section III.C.1](#)). A fluctuating environment was created through the use of a computer game where subjects had to guess whether a rabbit was located in one of two holes, over 60 trials. As the rabbit had a non-perfect tendency to remain in the same hole over time, the location of the rabbit corresponded to the current state of the fluctuating environment. The subjects were told that they would earn money for every trial in which they guessed the location of the rabbit correctly. Each individual played the computer game in isolation but at the same time as five others, and they could use personal or social information. Social information was free and always visible. It consisted of a random selection of three of the other players' decisions in the previous trial. Personal information through assistance from a "rabbit search machine" had to be paid for. Depending upon condition, acquisition of personal information cost either 50% (high cost condition) or 16.7% (low cost condition) of the reward for successfully locating the rabbit in that trial. A table of accumulated rewards, of all six players, was displayed to players after every five trials, thereby enabling adaptive learning of strategies.

As expected (see [Section II](#)), individuals used personal information to a lesser extent when it was costly to acquire than when it was relatively cheap. In addition, under these changeable conditions, conformity to the majority decision of the previous trial in the current trial choice was greater when personal information was cheap to acquire than when it was costly; due to the increased cost of acquiring personal information, fewer players acquire it, and thus the prior majority decision would constitute unreliable information. This was true, irrespective of whether the majority decision matched the individual's decision in the previous trial. These results support the theoretical prediction that social information will be valued to a lesser extent in contexts where it is likely to be outdated, in this case as everybody is attempting to avoid the cost of acquiring personal information, and thus contributes less to the renewal of social information. However, in this experiment, individuals did not make an active choice to

acquire social information, merely as to whether to *use* it; thus, it is questionable that this study can be directly compared to the theoretical analyses of [Boyd and Richerson \(1985, 1988\)](#). In addition, the experiment does not evaluate the degree of conformity, with regard to the cost of acquiring personal information, in a non-fluctuating or less-changeable environment, which we might expect to increase with the costs of asocial learning.

In sum, it appears that empirical evidence indicating that individuals rely increasingly heavily on social information as personal information becomes outdated is, as yet, rather limited. What evidence there is, however, does cover several different species, including humans, and pertains to the domains of foraging, mate-choice, and monetary reward. Considering how widely researchers cite the benefits of social learning in variable environments, there is a surprising lack of experiments designed explicitly to test this prediction.

IV. IMPLICATIONS FOR SOCIAL LEARNING RESEARCHERS

This review has surveyed a rapidly growing field of empirical study that supports the existence of “social learning strategies” ([Laland, 2004](#)), corresponding to trade-offs in animals’ reliance on social and asocial sources of information. In the following sections, we consider the broad implications of the reliance of animals on such strategies for researchers studying social learning processes.

A. COPY WHEN ASOCIAL LEARNING IS COSTLY

1. *Plausibility of Social Learning in the Wild*

The accumulating evidence for a strategy of *copy others when asocial learning is costly* may guide field researchers in their expectations as to which behavior patterns, observed in the wild, are likely to have been learned socially. As stated by [Byrne \(1999; Byrne and Russon, 1998\)](#) there are some behavior patterns for which asocial learning may appear to be a contrived alternative to social learning. For example, [Byrne and Russon \(1998\)](#) proposed that certain food-processing skills, seen in gorillas, are too complex and costly for an individual to acquire asocially. Here, the costs of time, energy, and physical discomfort, involved in acquiring personal information as to how to process physically and chemically defended plants successfully, point towards the use of social information. Such reasoning is now bolstered by empirical support for the tenet that reliance on social

learning increases with the costs of asocial learning, and by the findings of theoretical analyses. However, this support merely enhances the probability that a plausibility argument is correct, and it does not negate the need for experimental evaluation (Galef, 2004). For example, reproductive information may be particularly costly to acquire asocially (as a whole breeding year may be lost), and social information use may allow circumvention of these costs. In fact, several species of birds have been reported to rely on the observed reproductive success of conspecifics to make their breeding habitat choice (Brown *et al.*, 2000; Doligez *et al.*, 1999), an observation confirmed through experimental manipulation (Doligez *et al.*, 2002). Such findings also point to the validity of the converse argument. It follows that researchers might question the legitimacy of putative cultural traits that are relatively simple and cheap to acquire asocially.

Several of the empirical findings reviewed here appear to indicate that the costs associated with acquiring or using personal information may promote the evolution of increasingly complex social learning processes. In Coolen *et al.*'s (2003) study of foraging in sticklebacks, public information use, which is often regarded as cognitively more complex to acquire and utilize than other types of social information such as local enhancement (Valone and Templeton, 2002), was reported for nine-spines but not for three-spines, which was interpreted as reflecting the greater cost of acquiring personal information for nine-spines. Similarly, in an attempt to account for the relative lack of evidence for imitation in frugivorous monkeys compared to birds, Zentall (2004) argues that birds may face greater costs associated with asocial learning because they are generally smaller and have higher energetic needs than monkeys, and because their seed-based diet requires learning of complex extractive foraging techniques. In discussing the evolution of human culture, Castro and Toro (2004) suggested that the greater the difficulty or cost of developing a behavior through asocial learning, the greater the selection pressure in favor of the development of imitative processes, ensuring rapid information acquisition. This argument might also generalize to the process of "emulation," where the observer duplicates the results of others' behavior, but not the means of achieving them (Tomasello, 1990), and perhaps to other social learning processes. Note: implicit in this argument is Castro and Toro's assumption that imitation allows the learning of behavior patterns for which indirect social learning processes (e.g., stimulus enhancement, response facilitation) are insufficient, and that imitation facilitates more rapid learning than alternative processes.

A pragmatic stance would be to assume that behavior patterns are unlikely to be cultural in cases where asocial learning is "cheap" enough to accomplish the task in question, but plausible in cases where asocial

learning is costly. However, we guard against reliance on subjective impressions of the difficulty or cost of asocial learning, which can be misleading. For example, in a study of grubbing in woodpecker finches (*Cactospiza pallida*), [Tebbich *et al.* \(2001\)](#) demonstrate that the use of cactus spines, as extractive foraging tools, is not socially learned but instead develops by trial-and-error learning during a sensitive period of development. Rather, we wish to encourage the evaluation of the costs of asocial learning through direct experimentation. Such experiments will not only add weight to arguments concerning the plausibility of putative cases of culture but also generate data that can be employed to determine the probability of social learning statistically (see [Laland and Kendal, 2003](#)).

2. *Suboptimal Cultural Traditions*

Where the acquisition or use of personal information is costly compared to the acquisition or use of social information, the use of social information may be adaptive for an individual, even where that information results in suboptimal traditions. In game theory terms, traditions may be Nash equilibria if it never pays anyone to abandon them unilaterally. Individuals may be locked into conventions by virtue of their being penalized by the (asocial learning) costs of breaking the convention, resulting in traditions tracking changing environments less efficiently than individual learners, and only slowly, or never, converging on the global optimum. Such maladaptive traditions have been reported in animals and humans ([Boyd and Richerson, 1985](#); [Cavalli-Sforza and Feldman, 1981](#); [Laland and Williams, 1998](#); see also [Section II.B.1.a](#); [Pongrácz *et al.*, 2003](#)) and may have evolutionary implications. Similarly, [Giraldeau *et al.* \(2002\)](#) discuss a number of possible cases where maladaptive behavior may spread as a result of informational cascades, where individuals base behavioral decisions on the prior decisions of others. They proposed that the propensity to use social information depends upon the costs of engaging in erroneous cascades. For example, they posit that in the case of birds learning how to evade a predator, the cost of an erroneous cascade may be small (loss of time that could otherwise be allocated to foraging) relative to its benefits (successful evasion of a predator). However, were the costs of an erroneous cascade to be increased, for instance if birds were seriously food deprived, such that the risk of death by starvation approaches predation risk, animals might be expected to pay less attention to their companion's decisions to flee and to require a stronger, more predictive personally acquired cue to pass up on a foraging opportunity.

It is conceivable that where the costs of personal mate choice are extremely high, most individuals will copy others, potentially resulting in maladaptive mate choice due to erroneous informational cascades, based

upon the initial choice of one or a small number of individuals (Losey *et al.*, 1986). In a study of lekking sage grouse, Gibson *et al.* (1991) reported that the decisions of females using personal information to decide whom to mate with were more closely correlated with male phenotypic traits indicating quality than were the decisions of individuals using social information. This was thought to be due to females copying the mate choice of other females who had not themselves assessed male quality directly (i.e., an informational cascade). As mate-choice copying resulted in increased variance in male mating success and a reduced correlation between male quality and male reproductive success, Gibson *et al.* (pp. 178) stated that “the variance in male mating success on leks is inversely related to the strength of sexual selection on male traits.” Similarly, Gibson and Höglund (1992) predict that where mate-choice copying is primarily a cost-reduction strategy, the relationship between male quality and mating success will be noisier, resulting in unpredictable “fads” in the characters that females find attractive and a lowering of the intensity of sexual selection. This occurs because most individuals will use social information, and males will rarely be directly sampled, resulting in mate choice becoming increasingly divorced from male quality. In contrast, where mate-choice copying is due to uncertainty on the part of females, or an inability to discriminate between males, copying should increase the intensity of sexual selection (see Section IV.B.2).

B. COPY WHEN UNCERTAIN

1. *Plausibility of Social Learning in the Wild*

Dewar (2003a, 2004) argued that her proposed cue reliability approach (see Section III.B.2.a) has two important implications for the study of social learning: (1) it encourages researchers to consider why animals might try a novel behavior for the first time; and (2) it provides a new test for identifying behavioral traditions in the wild. The latter is based on the hypothesis that, if convergent asocial learning can be “ruled out” because individuals lack reliable asocial cues, a case can be made that a widespread behavior is traditional, since social cues are the *only* cues that exceed the reliability thresholds constraining individuals. Conversely, where personally acquired information is reliable, foragers do not need to use social information in order to decide what is safe to eat. Thus, a unique shared dietary preference in one population, which is absent in other populations, cannot always be assumed to be a cultural tradition. In an argument akin to the ecological independence of population-level differences in chimpanzee behavior patterns (Whiten *et al.*, 1999), Dewar (2003a, 2004) proposes that the possibility that reliability thresholds vary across environments must be

eliminated before cultural differences can be assumed. She states (2004, p. 87) that the case for a behavior being cultural is “strongly supported if social cues are the only reliable cues available. If, however, asocial cues are also reliable, more caution is warranted.” This novel approach may well result in new insights. It does not require direct observation of social transmission, which may make it a practical method for determining whether behavior seen in the wild is traditional. In addition, its strongly quantitative emphasis allows evaluation using conventional statistical tools. However, the approach is restricted to situations where individuals must decide whether to treat unfamiliar stimuli as profitable or safe, and it is of little use for the study of traditions involving complex behavioral sequences. It also remains to be shown whether the complex environments of natural populations make it realistic to collect the data necessary to calculate payoffs and reliability thresholds and indeed whether the model itself provides a close fit to the real world (Dewar 2003).

2. *Sub-Optimal Cultural Traditions*

Giraldeau *et al.* (2002) proposed that the point at which an informational cascade begins (i.e., when an individual adopts the behavioral “decisions” of others despite the absence of the cue, or “signal,” to which they responded) may depend upon the uncertainty involved in the signal. For example, the moving of a branch is a signal only loosely associated with the approach of a predator, compared to the sight of the predator itself. In the former case, an informational cascade may take longer to begin, involving the prior decisions (fleeing) of more individuals, than the latter case. Indeed, Blumstein *et al.* (2004) found yellow-bellied marmots responded more strongly to an equivalent number of alarm calls apparently emitted by two individuals than by one. As discussed in Section III.B.2.c, Blumstein *et al.* (2004) found that the necessity of avoiding missed opportunities, for activities other than antipredator behavior, requires an assessment of the reliability of social information provided by alarm callers and thus may have promoted the evolution of individually distinctive alarm calls. The growing body of literature concerning the responsiveness of individuals to alarm calls of different individuals (see Blumstein *et al.*, 2004 and references therein) merits further discussion in consideration of social learning strategies dictating from *whom* individuals learn (see Laland 2004).

Rafacz and Templeton (2003) in their study of starlings, outlined in Section III.B.2.a, reported an example of an arbitrary, personally acquired behavior. Of the birds assigned to conditions of varying environmental predictability and demonstrator informativeness, only those in the unpredictable environment and uninformative demonstrator condition developed arbitrary color aversions and color preferences. Those individuals in

the predictable environment and uninformative demonstrator condition did not develop such biases, despite the fact that their demonstrators also provided irrelevant information pertaining to the utility of color cues in locating food. This occurs because it is only in the unpredictable environment that the birds required social information to assist their foraging decisions. The use of social information in unpredictable environments may prevent the development of erroneous personal behavior.

The apparent delay before which individuals in the unpredictable environmental condition with informative demonstrators exhibited greater foraging success than those with uninformative demonstrators led [Rafacz and Templeton \(2003\)](#) to assert that individuals may need to learn to recognize when social information is more valuable to them than personal information. This is consistent with [Kendal *et al.*'s \(2004\)](#) finding that individuals appear preferentially to rely on personal over social information. Both the characteristics of a species and the predictability of the environment that it inhabits will influence to what extent animals value social information. For example, [Klopfer \(1959, 1964\)](#) found that dietarily conservative greenfinches (*Chloris chloris*) relied on social over personal information in a foraging experiment, whereas more opportunistic great tits (*Parus major*) did not. As indicated by [Coussi-Korbel and Fragaszy \(1995\)](#), highly social species might have greater social tolerance (e.g., tolerance of close proximity of others during foraging), which may conceivably favor placing a higher value on social information than do less social species ([van Schaik, 2003](#)). Conceivably, there will be a delay before animals recognize the altered value of different sources of information, in response to a change in environmental predictability.

In contrast to when mate-choice copying functions to reduce the cost of mating decisions (see [Section IV.A.2](#)), [Gibson and Höglund \(1992\)](#) predict that where it functions to reduce the uncertainty of mating decisions (e.g., due to an inability to discriminate accurately between males), copying should increase the intensity of sexual selection. The argument here is that erroneous informational cascades would not be expected, as only those individuals who were unable to discriminate accurately (e.g., due to inexperience) will copy the choices of others, and a substantial proportion of the female population will directly sample the males and choose mates according to personally acquired information.

C. IMPLICATIONS FOR THEORETICAL MODELS OF SOCIAL LEARNING

These findings have several implications for mathematical models of social learning. First, as individuals appear to switch between reliance on social and asocial sources of information in a flexible and facultative

manner, theoretical models of social transmission would benefit from the routine incorporation of both asocial and social learning processes, rather than treating each as an entirely separate process, as they often do (Galef, 1995). Second, models would benefit from assuming variation in (1) the reliability of social and asocial information, and (2) individual and species differences in the propensity to exploit these two types of information. These two factors will depend on the costs associated with acquiring and using social and asocial information, as well as the level of noise associated with information acquisition and the rates of change of relevant features of the environment. Third, evidence is emerging that animals may not weight social and asocial information equally, as has frequently been assumed in social foraging models (e.g., Clark and Mangel, 1984; Valone and Giraldeau, 1993; Templeton and Giraldeau, 1995a, 1996). By highlighting these current issues concerning potential trade-offs between reliance on social and asocial information, it is hoped that further empirical work testing the assumptions and predictions of theoretical models of social learning will be forthcoming.

V. GENERAL DISCUSSION

A. THE EVOLUTION OF SOCIAL LEARNING ABILITIES

Many researchers have suggested that social learning abilities may be more strongly associated with ecology than taxonomy (Coolen *et al.*, 2003; Fragaszy and Visalberghi, 1996; Klopfer, 1959; Lefebvre and Palameta, 1988; Zentall, 2004), a position that we endorse. Yet the belief that social learning is particularly important to large-brained species, or to animals closely related to humans, remains widespread. Consideration of the *social learning strategies* outlined in this review may help to explain why social learning is more prevalent in some populations, and in some species, compared with others. If individuals use social information when personal information is costly, unreliable, or easily outdated, then there may be differing propensities for social learning in populations for which survival demands vary along these dimensions. For example, populations at greater risk of predation when they collect personal information will be more likely to use social information than others less at risk (e.g., sympatric sticklebacks; Coolen *et al.*, 2003). Dietarily conservative species are exposed to the kind of slowly changing environmental conditions that favor reliance on social learning, whereas generalists are exposed to the kind of rapidly changing and spatially heterogeneous conditions that favor asocial learning (e.g., Klopfer, 1964; but see Dall and Cuthill, 1997, for theoretical evidence

indicating that generalists may be more reliant on social learning than specialists in order to reduce sampling costs). Among food-caching species, there may be a greater reliance on social information in those that cache perishable, rather than non-perishable, foods, as information relating to the edibility of personally cached foods is likely to be outdated relative to the recently observed caches of others (e.g., Clayton and Dickinson, 1998). There may also be a greater reliance on social information in species that use complex foraging skills or must overcome challenging prey defenses, compared to those that do not (e.g., folivorous vs. frugivorous species: Fragasy and Visalberghi, 1996; extractive vs. non-extractive foragers: Day *et al.*, 2003; Zentall, 2004). However, as highlighted by Lefebvre and Giraldeau (1996), there are many problems inherent in drawing general inferences on the basis of comparative studies of social learning. The majority of empirical evidence reviewed here avoids these issues by assessing whether the use of social information is an adaptive specialization to specific ecological conditions within a species.

Consideration of social learning strategies may also help to explain why social learning is more prevalent in some populations than others. For example, it is possible that there is a greater propensity for social learning in populations exposed to “risky” environments compared to benign ones (e.g., guppies living in high predation sites; Reader, 2000), where the costs of individual assessment of these risks are likely to be high. Similarly, populations at the periphery versus the center of their species range or those exposed to greater climatic variability may have a greater need for social learning to enable them to cope with the increased demands of these environments (Reader and MacDonald, 2003). In a similar vein, it is interesting to note that “social release” of conformity to a socially learned escape route is more readily achieved in domesticated guppies tested in the laboratory (Brown and Laland, 2002) than wild guppies tested in the wild (Reader *et al.*, 2003). Wild guppies may be under stronger selection to shoal and minimize predation risk than are domestic guppies (Reader *et al.*, 2003). Consequently, it is conceivably more costly for wild guppies to acquire personal information about alternative escape routes than to use social information and conform to the majority, while this balance is tipped the other way in domestic strains.

B. FUTURE DIRECTIONS

There are several social learning strategies for which empirical evidence is, as yet, lacking. Even those strategies that have been subject to attention are largely supported by circumstantial rather than direct evidence. As noted by Peake and McGregor (2004) and Griffin (2004), the use of social

information in communication, aggression, and anti-predator behavior is relatively understudied; and it would seem ripe for tests of costs and uncertainty involved with the acquisition and use of personal information. Similarly, there is a paucity of data regarding the strict interpretation of [Boyd and Richerson's \(1988\)](#) assumption that animals copy others when they are uncertain as to which pre-established behavior pattern is appropriate in a given context. In addition, despite the fact that social learning researchers commonly introduce their subject matter by quoting Boyd and Richerson's predictions regarding the costs of outdated information, very few studies have addressed this issue empirically.

More specifically, there are many outstanding questions that would make interesting avenues for future research. First, we have not touched upon social learning strategies regarding from *whom* individuals should learn (see [Laland, 2004](#)), partly because this topic remains relatively unexplored. It is quite probable that such strategies as copy the majority, copy successful individuals, copy kin or familiar individuals, and copy older individuals, will interact with the *when* strategies outlined in this review. (Indeed the *who/when* division breaks down in some cases, for instance, where individuals copy any other that is reaping greater benefits than they.) We may ask whether the expected strategy of using social information if, and only if, personal information is costly, unreliable, or outdated, is violated when social information is provided by individuals with the characteristics listed above. For example, many of the studies reviewed here (e.g., [Kendal et al., 2004](#); [van Bergen et al., 2004](#)) could be extended through replication with conditions of varying demonstrator characteristics.

A second avenue of research is the possible interaction of observer characteristics and social learning strategies. To what extent do state-dependent factors (such as social status, hunger, age, and sex), and individual differences (in for example, neophilia/neophobia and mental abilities) influence the use of social learning strategies regarding both when individuals use social information and from whom they acquire it? For example, in [Kendal et al.'s \(2004\)](#) study (see [Section II.B.1.a](#)), a small proportion of trained-observer fish continued to use their personal information, despite its apparent cost and the availability of social information. It would seem likely that there are individual differences in the tendency of guppies to weight one source of information over the other, as seen in foraging great tits ([Marchetti and Drent, 2000](#)). Characteristics of observers favoring the overriding of social learning strategies and the continued acquisition of personal information may be influential in determining innovatory capacities of individuals.

While social learning strategies have provided a useful framework with which to structure this review, some potential limitations to the framework

are considered briefly here. First, in most instances, it remains to be established whether animals are actually employing these strategies and whether they do so consistently. There may not be uniform patterns in animals' reliance on unlearned and learned behavior, or on asocial and social information. All that can be claimed is that an animal's behavior is (or is not) consistent with one or more of the proposed social learning strategies. Second, we do not know what specific cues animals attend to when their behavior appears to be consistent with a social learning strategy. For instance, it may be difficult to distinguish between animals copying successful individuals, animals copying the successful *behavior* of other individuals, or animals responding to some correlated cue that may signal prior success. Third, social learning strategies are potentially not mutually exclusive, and animals may well apply combinations of these strategies. For instance, animals may *copy familiar* individuals *when uncertain* as to what to do because relevant asocial information is lacking. Fourth, at this stage, it is not entirely clear whether the hierarchical approach proposed by Laland (2004), which posits that animals would use social information when asocial learning proves ineffective and only resort to innovation when both social and asocial information leave them uncertain as to what to do, reflects the actual decision-making processes of animals. Such new frameworks must not only be proposed but also tested, employing both theoretical and empirical approaches, if we are to gain new perspectives for future work in the field of social learning.

VI. SUMMARY

Theoretical models investigating the adaptive advantages of social learning conclude that social learning cannot be employed in a blanket or indiscriminate manner, and that individuals should adopt flexible strategies that dictate the circumstances under which they copy others. As highlighted in this review, laboratory and captive-population based evidence is amassing, mostly with regard to foraging and mate choice, indicating that individuals preferentially rely on personally acquired information, but acquire and use social or public information (i) when asocial learning would be costly, or (ii) when asocial learning leaves them uncertain as to what to do. Individuals ignore social cues when they have relevant personal experience but rely on social learning when the costs of acquiring or implementing personal knowledge is high, when they are uncertain of the optimal behavior, when their personal information is unreliable, or when it has become outdated.

We encourage theoreticians to incorporate social learning strategies into their models and empiricists to evaluate and test explicitly the assumptions

and predictions of such models, even where they are already widely accepted. It is hoped 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 processes 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 (Danchin *et al.*, 2004). The hypothesis that individuals increasingly rely on social learning as the costs of asocial learning increase potentially explains the existence of maladaptive cultural traditions in humans and other animals. Furthermore, consideration of social learning strategies may explain why evidence for complex social learning processes appears to be related to ecological rather than taxonomic affinities among species.

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