

Review

Exploring the costs and benefits of social information use: an appraisal of current experimental evidence

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Research on social learning has focused traditionally on whether animals possess the cognitive ability to learn novel motor patterns from tutors. More recently, social learning has included the use of others as sources of inadvertent social information. This type of social learning seems more taxonomically widespread and its use can more readily be approached as an economic decision. Social sampling information, however, can be tricky to use and calls for a more lucid appraisal of its costs. In this four-part review, we address these costs. Firstly, we address the possibility that only a fraction of group members are actually providing social information at any one time. Secondly, we review experimental research which shows that animals are circumspect about social information use. Thirdly, we consider the cases where social information can lead to incorrect decisions and finally, we review studies investigating the effect of social information quality. We address the possibility that using social information or not is not a binary decision and present results of a study showing that nutmeg mannikins combine both sources of information, a condition that can lead to the establishment of informational cascades. We discuss the importance of empirically investigating the economics of social information use.

Keywords: social information; public information; social information costs; social learning; informational cascade

1. INTRODUCTION

Using the behaviour of others as a means to acquire novel behavioural techniques by social learning has been the focus of a considerable number of empirical and theoretical studies [1] (see also [2] for an example of an empirical study). More recently, the focus of social learning research has diverged slightly from just the acquisition of novel motor patterns to the acquisition and updating of information about the value of alternative options, social sampling of a sort [3–7]. In this review, we address specifically cases of the latter: social information use or social sampling.

Social sampling information is important because it is argued to afford the first building block for the evolution of traditions on the one hand, and to provide an advantage to group living on the other. As a result, considerable theoretical and empirical research has been directed to the ecological and cognitive requirements for its evolution [8–11]. Empirical research on the subject has focused on exploring whether animals do indeed acquire and use social information

generated by the behaviour of others [1]. A number of empirical findings suggest social sampling is taxonomically widespread, observed in fish, birds and mammals and useful in various ecological settings such as group foraging, anti-predatory behaviour, agonistic interaction, migration, dispersal, mate choice and breeding habitat selection. Moreover, it has been reported in both intra- and interspecific social interactions [5,12–18].

Evidence of social information use comes usually in the form of ‘copying’: adopting the same option others are observed to choose. Research on copying focuses on the circumstances under which an animal copies rather than selects an option on the basis of its own personal information. Theoretical studies have explored the different rules that animals may adopt when faced with the decision of whether to copy others or learn by themselves [19]. These rules can take forms such as ‘copy the majority’ or ‘copy if others are more successful’, and which is best depends on the costs and benefits of social learning in a given ecological setting. Such an economic approach to social learning has enjoyed some empirical success (e.g. see [20] in this issue for an extensive review of social learning in fish). Empirical evidence arising mostly from the field of human culture (i.e. see the chapter entitled ‘Culture is maladaptive’ in [21])

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suggests that socially acquired information can sometimes be incorrect and still spread within groups. This raises the issue that animals that use social information should perhaps use it with some caution, paying attention to the specific circumstances and the pay-offs associated with social and asocial acquisition of information [19,22].

Our objective in this four-part review is to summarize the research that has been dedicated to the study of the costs associated with the use of social information. In the first section, we deal with the cost linked to the possibility that animals are incapable of simultaneously gathering social and asocial information. When this happens, they must choose which type of sampling they will engage in and the economic value of each alternative depends on how many individuals choose to sample socially. The more social samplers there are in a population, the fewer the asocial samplers. As a consequence a combination of asocial and social learners is expected [19,22,23], a situation which is similar to the producer–scrounger scenario [24,25]. In the second section, we argue that if social information can be risky, then there should be evidence of this in studies providing subjects with a choice between both social and personal information that differ in reliability. The third section reviews experimental studies that explore the circumstances under which animals could use incorrect social information and consequently decide wrongly to adopt maladaptive behaviour. The fourth presents a recent experimental study that shows how the persuasiveness of social information can influence individuals to the point where they disregard highly reliable personal information to copy the erroneous behaviour of others. Finally, we use these results to discuss the informational cascade, a phenomenon that has been reported to be widespread in human societies.

2. ONLY A FRACTION OF ANY GROUP PROVIDES SOCIAL INFORMATION

Almost all evolutionary models of social information use assume that within a group of animals engaged in searching for some resource, food, water, mates and nesting material, all individuals are actively occupied by exploration and search. During this exploratory process, each searching individual would be generating inadvertent social information and the success of each could be summed to provide a more representative corporate sample of current resource levels in that habitat. This idyllic view of the advantage of social information, however, is questionable because it assumes that all individuals in a group are engaged in searching for the resource while concurrently monitoring the success of others. If individuals cannot obtain both types of information concurrently, then they will have to choose which of the two to use. When this happens, at any instant the population is composed of pure asocial and pure social learners, a situation that was originally modelled by Rogers [23]. The gains of social learning depend on how many asocial learners there are to copy. Social learners initially do very well but as they spread and replace asocial learners in the population, their

benefits decline as they become increasingly likely to copy a social learning individual whose information may be outdated. The incompatibility predicts an evolutionarily stable mixture of social and asocial learners within a population, a situation akin to a producer–scrounger game [19,24–26]. That means that at best, in any group, only a fraction of its members are actively generating useful inadvertent social information, Kendal *et al.* [19] going as far as predicting that the expected social learning rule is the one that forms an equilibrium with the fewest asocial learners as possible.

Although the claim for frequency-dependent pay-offs associated with the social learning strategy can be traced as far back as Rogers [23] and is found in a number of recent studies [19,22], there is yet no convincing empirical evidence for it. No study for instance has ever experimentally demonstrated that groups with increasing numbers of social learning strategists do more poorly than others. To date, no study has addressed whether the collection of social and asocial information are incompatible activities. Such an incompatibility could be sensory or include higher neural processes. Such studies remain dearly needed.

3. WHEN ANIMALS CAN CHOOSE BETWEEN SOCIAL AND ASOCIAL LEARNING

Giraldeau *et al.* [22] suggested that social information may not be universally reliable and predicted that animals should be more discerning of its value before using it (see also [19,27]). A recent study based on the results of a social learning tournament [28,29] suggests instead that social learning is widely beneficial, showing that individuals do increasingly better in a changing world the more they use social as opposed to asocial learning, so long as asocial learners are present in the population. This theoretical result, which appears insensitive to the accuracy of social learning, is partly at odds with a large number of studies showing that animals use social information primarily as plan B, or a backup when personal information is too costly to obtain, unreliable or outdated. Many of those studies are devoted to considering the ecological circumstances under which animals choose socially over asocially acquired information. Such studies have been conducted on social insects, fishes, birds and mammals and relied on the use of experimental designs that allow precise control of the source of information available, creating situations where social and personal information are incompatible or in conflict [30–36].

Templeton & Giraldeau [31], in an experimental study on European starlings (*Sturnus vulgaris*), reported that birds relied on only public information (i.e. a specific type of inadvertent social information based on performance that provides indication about the quality of a resource [4,37]) when personal information about the quality of different food patches was either difficult or costly to obtain. These results combined with findings from a previous study of Templeton & Giraldeau [30] suggest that starlings mostly use information obtained from their own sampling of the environment rather than social

information when both types of information are not available concurrently. Starlings, it seems, are unwilling to forgo collection of any personal information in order to obtain public information. Since then, several other studies have explored the situations under which animals may use preferentially one source of information over the other.

Many studies have been devoted to the question of fish's propensity to rely on social information [20]. For instance, van Bergen *et al.* [35] in a study where nine-spined sticklebacks (*Pungitius pungitius*) were provided with conflicting asocial and social information found a preferential use of personal information over social information when fish had access to highly reliable personal information. However, as personal information became out-of-date, fish relied mostly on social information. Van Bergen *et al.* [35] argue that sticklebacks can assess the reliability of both sources of information and choose to exploit the most reliable such that reliance on either social or personal information may vary according to circumstances.

Fletcher & Miller [38] also reported an effect of social information reliability on its use during offspring production of female cactus bugs (*Chelinidea vittiger*). This hemipteran is known to form foraging and reproductive aggregations on the prickly pear cactus (*Opuntia* spp.) where the prior presence of conspecific nymphs or eggs may provide social cues about the quality of a patch. Female bugs exposed to different sources of social information about the quality of the resource (the presence of juveniles was assumed to be more informative than the sole presence of eggs) were found to rely mostly on a recent and accurate type of social information than on outdated prior information. This, therefore, provides experimental support for the theoretical assumption that current information (either socially or personally acquired) should be used preferentially over prior knowledge because reliability of prior information is expected to degrade over time [16,39,40].

The costs of acquiring personal information may be a key determinant in an animal's decision to use social information. Boyd & Richerson [41] proposed that social learning will be favoured whenever personal information becomes costly to acquire directly; individuals should take advantage in this case of the cheaper source of information. From this formulation of the 'costly information hypothesis' [41], Laland [42] suggested that individuals could possibly adopt a 'copy when asocial learning is costly' social learning strategy. The nature of these asocial learning costs is multiple. They can arise from energetic, time or opportunity losses induced by the direct sampling of the environment or from an increasing vulnerability to predation when, for instance, gathering personal information interferes with anti-predator vigilance. Moreover, such asocial learning costs may also depend on the ecological context that an individual is facing. For instance, Bouliner *et al.* [43] argued that if estimating the overall quality of a food patch could be done quasi-instantaneously by a forager, this is clearly not the case when animals have to assess the quality of a breeding site where acquiring personal information requires at least that the

individual experiences a complete reproductive event. As a consequence, one may expect that in some contexts, where asocial information is highly costly to obtain, such as choosing a breeding habitat and perhaps even a mate, individuals will be expected to rely on social rather than asocial information.

Empirical support for the 'copy when asocial learning is costly' hypothesis is accumulating. Webster & Laland [44] tested the hypothesis directly in European minnows (*Phoxinus phoxinus*), by giving these social fish a foraging patch choice under different levels of simulated predation risk (presence or not in the experimental tank of a life-sized dummy perch, *Perca* sp.). The minnows' propensity to rely on social information was mediated by the level of predation risk; under simulated situations of high danger, both naive fish and those provided with social information that conflicted with their reliable personal information choose to rely more on social information. Minnows, it seems, adopt a copy when asocial learning is costly strategy. In another shoaling species, Kendal *et al.* [34] reported that guppies (*Poecilia reticulata*) were willing to gather personal information rather than copy group members' decisions until it required losing visual contact with the rest of the shoal; a situation that is expected to reduce the security benefits provided by swimming in a group.

4. USING INCORRECT SOCIAL INFORMATION

While evidence that animals can gather adaptive information about the outside world and learn from others is becoming common, social learning can, under some specific circumstances, also promote the diffusion of maladaptive decisions throughout a population [22,32,45]. Under a rapidly changing environment, information diffused socially can lag behind environmental changes and so result in the transmission of outdated and perhaps maladaptive information [45]. In such a situation, individuals that decide only on the basis of their own personal information should be favoured, and so using socially learned information may not be universally adaptive [45].

Laland & Williams [32] tested this prediction with the guppy using a transmission chain design experiment. In such an experiment, a founder group of demonstrators is initially trained to access a floating feeder using either a long circuitous route or a short direct route, a pilot study having previously confirmed that guppies spontaneously prefer the short, more direct route. Founders are gradually replaced one by one by naive fish in each group throughout the experiment, until no founder eventually remains within either group. Not surprisingly, when placed with founders that use the short direct route, the preference persists in the group even when no founder remains within the group. Similarly, preference for the long route persists even when no founder remains within the group. Maladaptive information, using a long instead of a short route, therefore, can be socially transmitted throughout a population and promote the establishment of suboptimal traditions [32].

Bates & Chappell [33] argued that an anti-predatory component could account for the persistent

preference for the long route even when no founders remain within the group; when fishes are shoaling, the security benefits of remaining with swimming mates can outweigh any energetic benefit associated with choosing the shorter route. To control for this anti-predatory benefit, Bates & Chappell [33] conducted an experiment where fish that have acquired the founders' preference for the suboptimal long route via social learning were tested individually when given a choice between long and short routes to a feeder. Under such conditions, fish that previously swam with long-route founders prefer the long route when tested in a shoaling condition, but clearly prefer the short route when tested alone [33]. The preference switch between the group and solitary conditions suggests a trade-off between anti-predatory and energetic benefits.

Experimental evidence of maladaptive choice following exposure to social information remains sparse and begs the development of stronger experimental procedures that control the quality of the social information provided to subjects. In a field experiment investigating breeding habitat choice of first-time breeding natal dispersing birds of the solitary Nelson's sharp-tailed sparrow (*Ammodramus nelsoni*) and social bobolink (*Dolichonyx oryzivorus*), Nocera *et al.* [46] provide strong evidence that only young inexperienced bobolinks rely on social information (location cues) provided by visual models and audio playbacks of adult males to choose a breeding habitat. Interestingly, they report that erroneous social information (i.e. when audio playbacks and visual models were played and placed in suboptimal habitats) induces young bobolinks to settle in and even defend these suboptimal territories the following spring. Nocera *et al.*'s [46] work is compelling because of the experimental technique that was adopted: audio playback. In such a situation, the experimenter controls the quality of the social information and as a result provides a convincing demonstration of the potential effect of false social information use directly and in field conditions.

5. CHANGING THE QUALITY OF SOCIAL INFORMATION

Animals can use the number of demonstrators performing a given task as a warrant of social cue quality. Such a conformity effect was highlighted in experiments using groups of fishes in a context of food patch choice [34,47] or escape route preference [48]. An observer will be more willing to follow a demonstrator group's decision the greater the number of individuals within the group. However, if such a conformity effect is handy for naive individuals because they can thus obtain information rapidly and at low cost, more experienced individuals with reliable and accurate personal knowledge seem more insulated from its effects [34].

Giraldeau *et al.* [22] argue that social information based on the actual quantitative value of a reward, public information, would be more reliable than information obtained from simply observing an individual's decision, a social cue. Public information that is more directly related to the actual state of the world

should therefore be preferred when available concurrently with less informative social cues [49,50]. A clever series of experiments with nine-spined sticklebacks provides the first empirical support for this preference [51]. A social cue in this experiment consists in observing a large and a small group of conspecifics each visiting a feeding location that has no food and so provides no public information about food quality. With these cues, the observer fish prefers to go where more fish had been observed [51], showing that they relied on social cues to choose a feeding location. However, when provided concurrently with social cues and public information, naive fish relied preferentially on public information, always choosing the location where the demonstrators were feeding, independently of the demonstrator group's size. Coolen *et al.* [51] concluded that when available, public information is preferred over social cues, providing the first empirical support for Doliguez *et al.* [49] and Koops' [50] prediction. Following up on Coolen *et al.*'s [51] work on preference for public information, Kendal *et al.* [27] show that sticklebacks use public information adaptively, switching their prior preference for a feeder only when the observed outcomes of a demonstrator fish at another feeder exceeded their own outcomes.

Up to now, the decision to use social as opposed to asocial learning has been approached as a dichotomous choice. When asocial information is outdated, costly to obtain or otherwise doubtful, the animal is predicted to use social information. Economists Bikhchandani *et al.* [52] break with this view and assume that individuals should always combine both asocial and social information when having to come to a decision about options. They argue that the best way to choose what to do is to combine personal cues obtained from one's own sampling to the combined social cues provided by the sequence of earlier decisions of other group members. Social information may be of little consequence when it is redundant with accurate and unambiguous asocial information. However, as asocial information is increasingly ambiguous, the contribution of social information on decision increases. This Bayesian combination of asocial and social information can generate a phenomenon known as an 'informational cascade', characterized by the explosive spread of a decision, whether correct or not [52]. Once an informational cascade is engaged, the weight of social information is such that it completely outweighs the value of asocial information and individuals appear to totally disregard their own personal experience. Informational cascades have been proposed as a possible explanation for a number of large-scale explosive copying events in humans, such as market crashes in economics and panic rushes in crowds as well as flock alarm flights, night roost selection in colonial birds or mate-choice copying in animals [22]. Even though establishment of informational cascades has been found in laboratory experiments involving human participants [53,54], clear experimental evidence of an informational cascade in non-humans is still lacking.

One intriguing aspect of informational cascades is that animals may be called to disregard their current,

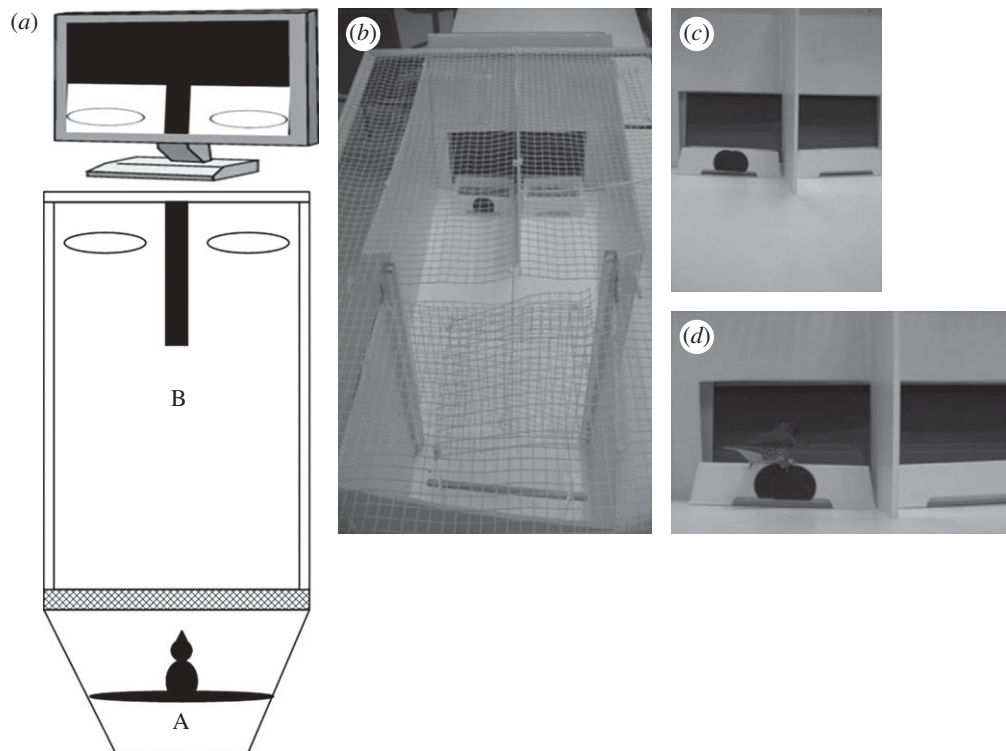


Figure 1. (a,b) Representations of the apparatus: each bird is individually introduced in the observation compartment A where it can observe the video sequences through the transparent partition. (c) Once in compartment A, the focal bird cannot see the content of the feeders in compartment B, and once let into compartment B by remote raising of the partition between compartments A and B, it can choose its feeder using the visual cue on one of the feeders with which it had previous experience or/and the social information that had been provided by a video playback of companions behind one of the feeders (d).

asocially acquired information to conform to contradictory social information provided by a sequence of group mates. This may appear unlikely given the quantity of research previously reviewed which shows that animals are circumspect about social information, using it only as a backup for inaccurate or outdated personal information. However, few studies have explored whether the apparent high quality of social information when combined with reliable but contradictory asocial information can induce individuals to disregard their asocial information as predicted by the theory of informational cascades.

One earlier study explored whether budgies (*Psittacus undulatus*) foraging in groups would combine both personally acquired and socially acquired information about the distribution of seed patch quality [55]. The results indicated that the birds relied exclusively on their asocially acquired information (personal patch-sample information combined with prior knowledge of food distribution) and were apparently incapable of or unwilling to integrate socially acquired information into their foraging decisions. More recently, Rieucau & Giraldeau [36] provide some experimental evidence to suggest that nutmeg mannikins (*Lonchura punctulata*), small social estrildid finches from Southeast Asia, could be induced to integrate social and asocial sources of information in their assessment of the best foraging patch. Twenty food-deprived birds were individually given a choice to feed from one of two feeders that differed in their quality. One dish was filled with a large quantity of their highly preferred millet seeds and provided

rapid access to a palatable source of food. The other contained only a thin layer of seeds covered by a thick layer of a non-edible substrate, forcing them to search through the substrate in order to access the food. The birds never knew ahead of time which of the right or the left feeder was the better one.

Before testing, half of the birds were provided with asocial information about dish quality by training them to recognize that a dish with a coloured dot always had more food. The other half of the birds had no asocial information about which was the better dish because they were trained in such a way that the dot had no predictive value for them. Once trained, birds from both groups were placed singly in a choice apparatus and were provided with social information. The birds were first confined to an observation compartment that contained no food and shown a video playback of birds feeding from one of two dishes in the adjacent feeding compartment (figure 1). For each trial, only one of the dishes bore a dot and the playback could show companion birds at the marked dish or at the other. Once the video playback ended and conspecifics could no longer be seen, the bird was allowed into the feeding compartment where it could choose to feed in one of the dishes.

The quality of social information was manipulated in two ways: behaviourally and numerically. Behavioural persuasiveness depended on whether the companions were seen feeding or not. We assumed feeding birds were more persuasive than non-feeding

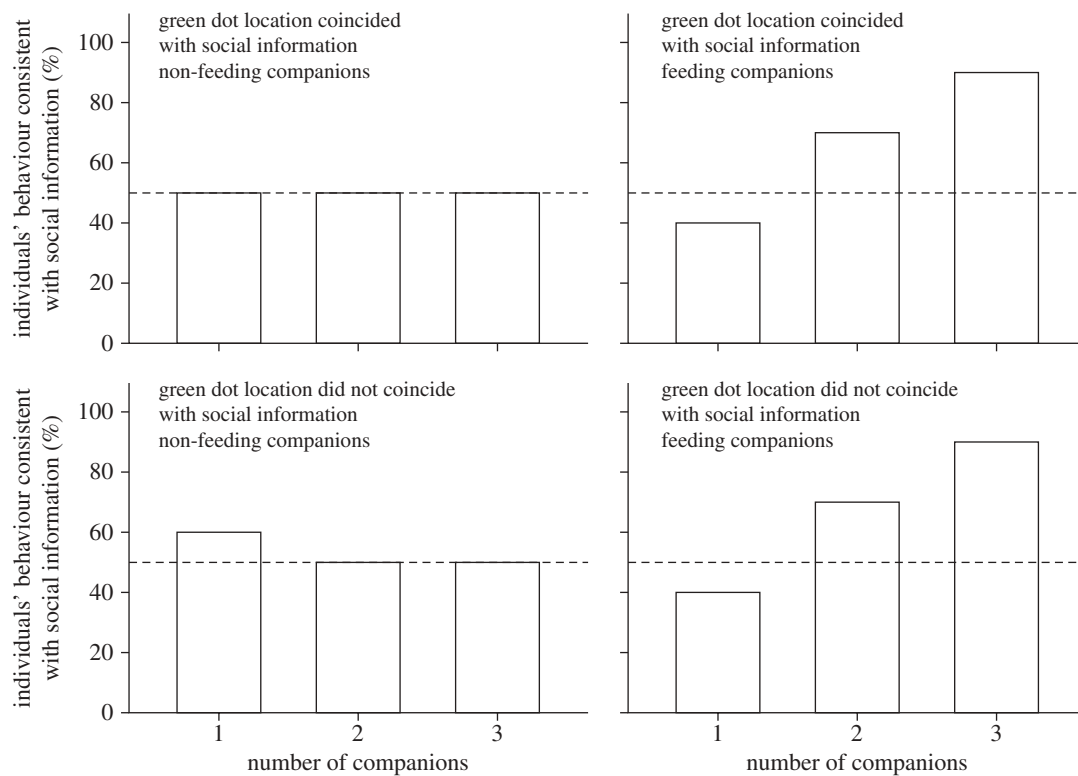


Figure 2. Proportion of focal birds ($n = 10$) for which prior training was such that the green dot failed to predict the location of the fast feeder that relied on social information to choose their feeder, expressed according to the number and the behaviour of virtual companions and whether the social information coincided or not with the location of the green dot. (Reproduced with permission from [36].)

birds. Numerical persuasiveness was based on the number of companions, assuming the more birds were in the playback, the more persuasive the social information. As expected, birds with no asocial information consistently chose the feeder according to the social information they had obtained irrespective of the number of companions or whether they were feeding or not (figure 2). Companions did not so easily influence birds with asocial information. The birds continued to choose dishes according to their asocial information when companions did not feed, no matter how many there were. The result was quite different, however, when the playbacks showed feeding companions. In that case, the number of birds with asocial information that chose to copy the companions' choice of going to the poor-quality feeder increased as the number of companions increased (figure 3). This result shows that the persuasive social information was probably combined with the bird's reliable asocial information, leading to a decision suggestive of individuals disregarding their reliable asocial information in a way that is entirely consistent with the establishment of informational cascades [22,52]. This use of video playback provides a powerful and effective way of tackling questions of social information use. More laboratories should consider developing the technique further. Future research concerning cascades should consider situations where asocial information is more ambiguous than the experimental situation tested so far. If cascades can occur, their duration, their rate of establishment and risk of being incorrect should all

depend crucially on the uncertainty associated with asocial information.

6. CONCLUSION

Social information use in a sampling context and social learning of new motor skills are increasingly amalgamated under the topic of social learning. While both imply the use of social information, they differ in important ways. Social sampling, for instance, appears to be more common and taxonomically widespread, reported in species ranging from invertebrates to primates, than social learning of new motor patterns. It may be important in the future to pay more attention to the differences between the two. Our review of studies devoted to social information in the context of sampling among foraging alternatives leads us to a number of conclusions. First of all, although the claims for the frequency-dependent nature of the value of social information are increasing, empirical evidence is suspiciously lacking. We cannot argue more forcefully for the pressing need to investigate the frequency dependence of social information empirically. More specifically, it would be important to establish the extent to which the collection of both asocial and social information is incompatible. Second, the results of a recent and already widely cited social learning tournament [29] indicate that, while some asocial learners still persist in the population, increasing the use of social learning, irrespective of the informative nature of social information on which it is based, provides the best strategy in a

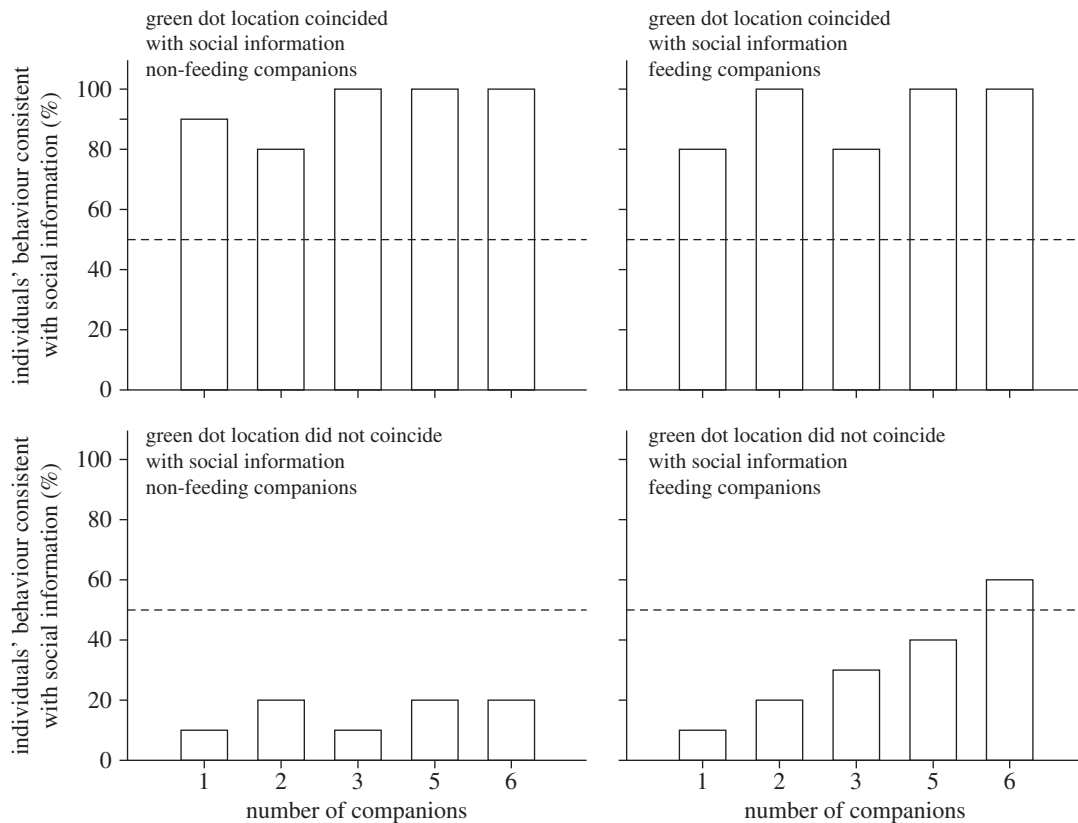


Figure 3. Proportion of focal birds ($n = 10$) for which prior training was such that the green dot provided a strong predictor of the location of the fast feeder that relied on social information to choose their feeder, expressed according to the number and the behaviour of virtual companions and whether the social information coincided or not with the location of the green dot. (Reproduced with permission from [36].)

changing world. This result is somewhat surprising given the impressive number of empirical studies which show that when given a choice between asocial and social information, animals tend to rely primarily on asocial information and only use social information as a backup when asocial information is unsatisfactory. This discrepancy between the results of the social learning tournament and reported caution exercised by animals that use social information now needs to be addressed. One possibility is that the tournament simulates a situation of adopting novel motor patterns rather than a case of merely sampling alternatives. This issue deserves further investigation. Third, we have highlighted that up to now the use of social versus asocial learning has been presented as a more or less dichotomous decision. Animals are predicted to use social information or not. Some theoreticians have pointed out the superiority a Bayesian combination of both social and asocial information in the evaluation of the quality of alternative options. We showed the results of one study in which individuals provided with strong asocial information were increasingly led to choosing the incorrect option when increasingly convincing social information contradicted their asocial information. This combination of the two sources of information paves the way to the establishment of informational cascades. Researchers should now turn to investigating whether informational cascades, whether for correct or incorrect decisions, can actually be induced within animal groups. We encourage researchers to develop further the playback

approaches, whether auditory, video or involving any other relevant modality, as a means to control experimentally the social information provided to subjects. In the end, we encourage all those engaged in social learning research to consider more seriously whether the economics of using social information in a sampling context differ from those presiding over the social learning of novel motor patterns and hence technical traditions such as food-handling techniques in orang-utans [56] or over-imitation [57].

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