Potential disadvantages of using socially acquired information

Luc-Alain Giraldeau[1][*], Thomas J. Valone[2] and Jennifer J. Templeton[3]

[1]*Département des Sciences biologiques, Université du Québec à Montréal, Case Postale 8888, succursale Centre-Ville, Montréal, QC Canada H3C 3P8*
[2]*Department of Biology, Saint Louis University, St Louis, MO 63103, USA*
[3]*Department of Biology, Knox College, Galesburg, IL 61401, USA*

The acquisition and use of socially acquired••2•• information is commonly assumed to be profitable. We challenge this assumption by exploring hypothetical scenarios where the use of such information either provides no benefit or can actually be costly. First, we show that the level of incompatibility between the acquisition of personal and socially acquired information will directly affect the extent to which the use of socially acquired information can be profitable. When these two sources of information cannot be acquired simultaneously, there may be no benefit to socially acquired information. Second, we assume that a solitary individual's behavioural decisions will be based on cues revealed by its own interactions with the environment. However, in many cases, for social animals the only socially acquired information available to individuals is the behavioural actions of others that expose their decisions, rather than the cues on which these decisions were based. We argue that in such a situation, the use of socially acquired information can lead to informational cascades that sometimes result in sub-optimal behaviour. From this theory of informational cascades, we predict that when erroneous cascades are costly, individuals should pay attention only to socially acquired cues and not behavioural decisions. We suggest three scenarios that might be examples of informational cascades in nature.

Keywords: public information; informational cascades; social learning; sampling

1. INTRODUCTION

Individuals in groups may learn novel skills, find resources, and estimate resource quality by obtaining information from their own activities, and by collecting information from other individuals. Thus, one advantage that social individuals have over solitary animals is that individuals in groups can acquire information faster, more reliably and at lower cost (Clark & Mangel 1984, 1986; Giraldeau *et al.* 1994; Giraldeau 1997; Galef & Giraldeau 2001). For instance, individuals in groups, much like solitary animals, may learn skills by trial and error. However, they may also observe other group members engaged in their own trial and error learning and use such socially acquired information to learn a skill more quickly (Giraldeau 1997; Galef & Giraldeau 2001). Similarly, individuals may learn about the location of resources by searching on their own, but may also observe when another individual has found a resource patch and then move to the discovered resource; a process known as local enhancement (Thorpe 1963) or area copying (Krebs *et al.* 1972; Pöysä 1992; Giraldeau 1997). In addition, an individual may learn about the quality of a resource, such as a food patch, by noting its own foraging success rate in the patch. It may also make note of the successful and unsuccessful search attempts of other foragers in the same patch and use such socially acquired public information to speed and improve the accuracy of its estimate (Clark & Mangel 1986; Valone 1989; Valone & Templeton 2002).

Evidence for the use of various kinds of socially acquired information in a variety of contexts is growing (see Valone & Templeton 2002 for a review), and includes habitat assessment (e.g. Boulinier & Danchin 1997), foraging (Galef & Giraldeau 2001), opponent assessment (Freeman 1987; Oliveira *et al.* 1998; Johnsson & Ackerman 1998) and mate choice (Gibson & Höglund 1992••3••; Dugatkin 1996; Nordell & Valone 1998; Galef & White 2000). Some attention has been directed to specifying the conditions under which such social information use is adaptive (Boyd & Richerson 1988; Laland *et al.* 1996). Although some studies have presented evidence that the use of social information can often be costly (Beauchamp & Kacelnik 1991; Laland 1996; Laland & Williams 1998; Day *et al.* 2001), in most cases socially acquired information is assumed beneficial.

We examine two new potential disadvantages of using socially acquired information. We begin with an exploration of the consequences of incompatibility between the acquisition of personally, and socially acquired, information. While most work implicitly assumes that individuals can simultaneously collect personal and social information, it may be difficult for some animals to acquire both types of information simultaneously, either because of cognitive or physical constraints (Dukas 1998; Vickery *et al.* 1991). We then examine the consequences

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of informational cascades (Bikhchandani *et al.* 1992)—situations that give rise to behavioural copying based on very little information. Informational cascades are expected to occur when the only socially acquired information available concerns the behavioural decisions of other group members rather than the cues on which these decisions are based.

2. SOCIAL INFORMATION AND PATCH QUALITY

It is often assumed that individuals that forage in groups have the opportunity to use socially acquired information about patch quality by monitoring the behaviour of others, and that doing so is beneficial. For instance, a group of foragers using socially acquired information can more quickly sample a patch and determine its quality faster than a solitary forager (Clark & Mangel 1986). Thus, we assume that the survival value of information can be measured in terms of the rate at which it can be acquired. Groups will provide faster rates of information uptake only if the social foragers gather information about the foraging successes and lack of success of other foragers in the patch, i.e. they must use public information (Valone 1989). For example, imagine an empty food patch in an environment where it is necessary to experience 24 consecutive unsuccessful feeding attempts to know that the patch is most probably to be empty. In this case, a solitary individual foraging in that patch would require 24 consecutive negative probes of the substrate to learn that the patch is probably empty. Therefore, imagine an ideal pair of animals where each pays attention to the unsuccessful probes of their partner. If each individual probes at a similar rate as when it is alone and both probe at the same rate, then they will have a combined total of 24 negative probes in half the time required by a solitary forager. Hence, they have the potential to know that the patch is empty twice as fast while expending only half the probes. For three individuals, we expect the same sample can be achieved in one-third the time and with one-third the number of probes per capita so long as each individual can observe the others without any interference (Clark & Mangel 1986). Hence, animals that forage in groups could acquire sample information more rapidly and efficiently by paying attention to the consequences of other individual's behaviour. Thus, when speed and accuracy of information acquisition have positive influences on an animal's fitness, we expect natural selection to favour those group foraging animals that use socially acquired public information. As a correlate, we expect groups of foragers to generate more foraging information per unit time than solitary individuals.

(a) *Incompatibility and the use of public information*

The above example of public information use assumes a complete compatibility between collection of personal and socially acquired information. It assumes that public information can be acquired at no cost to the acquisition of personal information, i.e. they can occur simultaneously.

In the real world, complete compatibility may not always be the case for a variety of reasons. The central nervous system may simply not be able to cope with pro-cessing personal and socially acquired information simultaneously. It is also possible that the animal has sensory limitations such that it cannot sense both types of information simultaneously. For instance, when small ground feeding estrildid finches forage in groups, it seems they cannot search for their own food and food discovered by others concurrently (Coolen *et al.* 2001). Apparently, they can only find their own food by hopping on the ground with the head pointed down. However, in order to detect a food discovery of another group member they must hop with the head pointed at the horizontal or above. The search modes required to find one's food, and to find a companion's discovery appear to be distinct and incompatible (Coolen *et al.* 2001). Similar incompatibilities may also exist for the acquisition of anti-predator and foraging information (e.g. Lazarus 1979; Lawrence 1985).

The extent of compatibility between the acquisition of both personal and socially acquired information has an effect on the use of public information. In European starlings (*Sturnus vulgaris*), for instance, Templeton & Giraldeau (1996) show that the birds only used public information when accurate information about patch quality was difficult or costly to acquire via personal sampling alone. The result suggests that there is some cost to collecting or using public information. Templeton & Giraldeau (1995) found similar results when the incompatibility between the two sources of information was environmentally imposed. When opaque barriers prevented animals from watching others as they probed for food, individuals ceased to acquire social information (Templeton & Giraldeau 1995). The results suggest that starlings are unwilling to forgo any personal information in order to gain public information. However, when the opaque barriers were absent, the same starlings behaved as if they were combining personal and public information (Templeton & Giraldeau 1995). Hence, it appears that public information in starlings will be used only if it can be acquired cheaply while the animal collects personal information.

The consequence of incompatibility between the two sources of information is worth exploring. In a scenario of complete incompatibility between both sources of information, an animal can collect social information only at the expense of acquiring any personal information. At each moment, therefore, the animal must decide whether to collect personal *or* social information because it can never collect both simultaneously.

For illustrative purposes, we can model the consequences of this incompatibility in the following way. Imagine a flock of 24 birds foraging in the same environment as the one described above where 24 negative probes are required to determine that the patch is empty. Assume that the environment is made up of recognizable potential food patches, most of which are devoid of any food but only some of which contain large amounts of food, enough to provide a meal to all group members. Assume that all the birds are in the same patch and wish to determine whether this patch is empty. If so, the flock should leave. Assume that probing presents a significant cost. This cost could be energetic or represent an increased risk of predation. Finally, assume that the ancestral state of the population is the absence of any ability to use social information about patch quality. This means that each bird

must individually experience 24 negative probes within the patch before concluding that the patch is empty, and it takes each individual 24 units of time to perform 24 cumulative negative probes.

Now imagine a mutant that never probes but instead spends all its time surveying the probes of its 23 companions. It will have obtained the information that the patch is empty once it has observed 24 negative probes. It can obtain this information in almost 1/23rd of the time and at very little cost compared to each of the wild-type birds to obtain the same information. The social information-using mutant, therefore, has a strong advantage over the wild-type birds; it spends no time or energy probing and obtains the necessary information much faster than the non-probing individuals. The social information-use strategy will therefore spread within the population. If the strategy spreads, provided it does better than the alternative, then it is easy to see that the public information strategy will spread until all but one individuals in the group are engaged in the use of public information. At this stage, there are so many individuals using public information and so few generating information that the group has no advantage over the solitary individuals in terms of the rate of information uptake.

Our analysis leads to a situation where the frequency of public information use within a group will be such that it will no longer be useful. It occurs because no individual could improve its sampling efficiency by deciding not to use public information and sample for itself. The state of all but one individual using public information is the Nash Equilibrium and ESS••4•• to the game of public information use under the assumed incompatibility constraint (Giraldeau & Caraco 2000). Therefore, even though individuals in such a group use public information, none of them will have a higher information uptake rate than a solitary forager.

Empirical evidence of such behaviour is lacking for patch estimation. However, Krebs & Inman (1992) present data suggesting such ESSs may occur. Krebs & Inman (1992) placed starlings in an operant device that offered a tracking problem much like that modelled by Shettleworth *et al.* (1988): two food patches, one of variable quality, the other of constant quality. The variable patch is more profitable than the constant patch when it is in its good state, but less profitable than the constant patch when it is in its poor state. Hence, the forager must sample the variable patch in order to detect when it is in the good state.

Krebs & Inman (1992) paired starlings by placing two cages operating on the same schedule side by side. The birds were tested in the sequence alone, in pairs, alone again and then in a signalled condition, where no sampling was required because a light that could be seen from the constant patch signalled when the variable patch was in its good state. The starlings sampled at near optimal levels when tested alone (Krebs & Inman 1992). However, when placed in a group situation (paired in adjacent cages running on the same schedule), typically, one of the pair members continued sampling at the optimal level for a solitary animal while the other considerably reduced its sampling to near zero levels. The individual that ceased sampling in the group condition continued to exploit the patch almost as quickly as the sampling bird, and was

using the feeding behaviour of the sampling individual at the variable patch as a cue for the patch's quality. When the starlings were placed alone again, the individual that had ceased sampling in the group condition resumed sampling, indicating it could still sample when no alternative source of information was available. Finally, both pair members ceased to sample when the condition of the variable patch was signalled by a light without any need for sampling.

Krebs & Inman (1992) argue that the most likely explanation for their result is that once an individual reduces its sampling activity because it learns to use its companion as a source of social information, the other individual is forced into a situation where reducing its own sampling cannot be profitable given that its partner is already providing less information. The outcome is analogous to the outcome in the complete incompatibility game we explored above: the Nash Equilibrium solution is that the socially sampling bird cannot do better by using personal sampling because it cannot acquire both types of information simultaneously. The personally sampling bird cannot do better by using socially acquired information because none is available.

The above results are based on pairs of birds foraging in a two-patch environment. It would be important to replicate these results to see whether having more than two birds also leads to only one of them doing all the sampling or whether the solution is intermediate. The results of that experiment should help shed light on the extent to which we should expect that the production of socially available information will be shared by all group members or not.

The incompatibility between the acquisition of personally and socially acquired information leads to the paradox that groups of individuals capable of using social information acquire no more information on which to base their decisions than solitary individuals that have no access to socially acquired information. This paradoxical outcome, however, may be uncommon in nature because it depends, crucially, on a number of simplifying assumptions made about the conditions under which the information is collected. When there is only partial incompatibility between the two sources of information then we expect that individuals in groups will benefit by acquiring public information. If an individual can collect some public information while collecting its own sample information, it will be able to estimate that the patch is empty faster than if it was in a group in which no individuals use public information or in a group in which only one individual uses public information. For instance, continuing with the same example as above, assume that there is partial compatibility so that while one individual has sampled 20 holes it has also simultaneously observed that its partner has sampled, say, four holes. Thus in only 20 time-units our partial compatibility bird has determined that the patch is empty and has saved four units of time over the non-public information groups or the group with only one bird sampling. Evidence of some compatibility between searching for food and collecting public information is suggested by the results of Lima & Bednekoff (1999) showing that birds that feed with the head down can still detect the approach of an aerial predator. The extent of compatibility between tasks, however, may depend on the difficulty of obtaining the information. For

instance, detecting an approaching predator may be a much less onerous task than focusing attention on companions in order to detect whether they found food or not. Results from estrildid finches suggest that searching for food, and for information from companions, are incompatible activities (Coolen et al. 2001), as are scanning for predators and detecting food-joining opportunities (Coolen & Giraldeau 2002). Clearly more research must be devoted to exploring the incompatibility between various scanning and foraging activities.

Our proposed example was also based on a critical assumption about the distribution of food among patches. We assumed that patches with food contained sufficient food for all to obtain a meal. However, when food in a patch is limited, a premium is placed on being among the first to find it. At one extreme, if the patch contains only one indivisible item, then clearly there is much less advantage in using only public information to estimate its quality. In most cases, however, we expect public information to be beneficial and this is consistent with empirical work (Templeton & Giraldeau 1995, 1996; Smith et al. 1998••5••; Valone & Templeton 2002). In the next section, we examine another potential negative consequence of social information use that may occur more often in nature.

3. DECISION COPYING AND THE RISK OF INFORMATIONAL CASCADES

When a bird probes the substrate, two consequences may result: the presence or absence of food in the animal's beak. These results may lead to an observable behavioural decision, leave the patch or probe again. Both the outcome of the probe and the resulting behaviour can provide information to an observer about the quality of the food patch. We define the outcome of the probe as a 'cue' because it provides direct information about patch quality (the presence or absence of food after a probe). The subsequent action of the prober, a behavioural decision, provides indirect information about patch quality (if the prober leaves, the patch is probably of poor quality; if the prober probes again, the patch is probably of higher quality).

We have only been discussing the use of vicariously acquired cue information (public information) because we assumed that the animals could observe the success or lack of success of other foragers' probes and use this cue information to judge the quality of a patch. However, in some cases, observers may only have access to behavioural decision information and not the cue on which that decision was based. For example, Howell (1979) has shown that in flocks of nectar-feeding bats, individuals will take turns feeding from the same agave inflorescence. The decision to depart appears to be based on the depletion of nectar below some threshold level, a cue that is hidden to all but the individual sampling the flower at that time. The first bat to reach this threshold will leave, resulting in the rest of the flock 'following-the-leader', without confirming the nectar level themselves. This observation of 'blind' trust in the decision of companions without regard to personal cue information is reminiscent of what economists Sushil Bikhchandani et al. (1992) refer to as an informational cascade.

(a) *An informational cascade*

Imagine a scenario where a new type of prey is encountered by a group of social foragers. Assume, for simplicity, that the prey item has an equal chance of being valuable or injurious and that the taste of the prey item, good or bad, accurately reflects its value with some probability p, where $p > 0.5$ (i.e. if the prey tastes good then the probability that it is valuable is p, if it tastes bad then the probability it is injurious is $1 - p$). One individual, call him individual 1, samples the newly encountered prey item, finds it tastes good and decides to eat it. Individual 2 then encounters the prey item, samples it, and finds it tastes good and therefore that it is likely to be valuable. It saw individual 1 eat it, so it was *probably* also deemed valuable by individual 1 (recall that we assume some uncertainty in cues). Faced with these two supporting items of information, and assuming that individuals give equal weights to socially and personally acquired information, individual 2 is now more certain than individual 1 was, that the item is valuable. Consequently, its only rational decision is to accept the food item as valuable and eat it. Another bystander, individual 3, now encounters the prey item. It samples it, finds it tastes bad, and hence is likely to be injurious. However, having seen that both birds 1 and 2 ate the item provides social information that contradicts its own personal cue. In fact, if both sources of information (socially acquired and personal) are given equal weight then individual 3 will be more certain that the item is valuable than injurious, consequently it should eat the prey item. It is in fact best for individual 3 in this specific set of conditions to ignore its own personal cue and behave only according to its socially acquired information because using the social information provides a higher probability of a correct decision than ignoring it (Bikhchandani et al. 1992). Once this happens, that is, once it is better for an individual to ignore its own personal cue, an informational cascade arises. Once the cascade starts, the same reasoning applies to all successive individuals in the queue; in this case to accept the prey irrespective of their own personal cue information. Once the cascade starts, all subsequent decisions provide little additional information because the subsequent decisions are all based on the same first three individuals' behaviour. The example we provided is in the economists' jargon an 'up cascade' because it generates a wave of accepting an item. If the animals had opted to reject the item, it would have been a 'down cascade'. If the item proved particularly valuable then the cascade would have generated a correct response. However, sometimes cascades generate erroneous responses (accepting an injurious item, rejecting a valuable item).

In informational cascades, the first few events are extremely important in determining the population outcome. Depending on the uncertainty of the cue and the likelihood that the encountered alternatives are valuable or not, there exists a chance that cascades generate incorrect responses. Using the same conditions as above imagine now that the first animal encounters the prey item, decides it is valuable and eats it. The second individual encounters the item but believes it tastes bad. Since we assume it gives equal weight to information provided by its predecessor's decision to accept it, it is faced with a situation where the item was

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probably valuable to its predecessor and is probably injurious to it. Given this, its decision to eat the prey or reject it is equiprobable and is decided by the proverbial flip of a coin. Assume that it decides to accept and hence eat the prey item. Individual 3 is now in an identical situation to individual 3 above. It also finds that the prey tastes bad but it has just witnessed two individuals accept the prey item and so concludes that the prey is more probably valuable than injurious and eats it. Bird 4, and all subsequent birds, will then be caught in what is probably an erroneous up cascade. This is because using the social information usually leads to a higher probability of a correct decision. In this specific case, however, it leads to a mistake.

It is important to emphasize that cascades are, in fact, more likely to result in the correct decision and that is why we expect them to occur in nature (Bikhchandani *et al.* 1992). However, the important point is that cascades are extremely sensitive to the initial sequence of events and may occasionally lead to errors. The evolution of the ability to use socially acquired information will not only be driven by the potential benefits that can be derived from it but also the survival costs induced by the occasional errors. The arguments for the evolutionary origin of the capacity to use social information must take this into consideration.

Bikhchandani *et al.* (1998) show that erroneous cascades (decisions that result in less than the best payoffs) are most likely when cues are noisy (i.e. when P is close to 0.5). They also demonstrate that cascades can occur only when individuals have access to the decisions of predecessors and not the cues on which they based their decisions. Cascades cannot occur when bystanders can observe the very same cue that the predecessor experiences before making its decision. Thus, one important lesson we can draw from informational cascades is that the greater the costs of erroneous cascades the greater the selective pressure to ignore others' decisions and rely solely on socially acquired cues in order to reduce the risk of being trapped in an erroneous and costly cascade. We predict, therefore, that when given the choice of sources of socially acquired information, animals should prefer cues to decisions, but may still use decisions, despite the risks, when no other social information is available. The risk of engaging in inappropriate behaviour when using decisions rather than cues will depend on a number of factors such as the chance of erroneously interpreting a cue as well as the frequency of alternative cues in the environment (Bikhchandani *et al.* 1998).

4. EVIDENCE THAT ANIMALS PAY MORE ATTENTION TO CUES THAN TO DECISIONS

There are several instances where animals have been shown to pay attention to cues generated by the behaviour of others rather than to their decisions. However, these only become evident during experiments that specifically test for both cue use and decision-copying responses. In the case of public information and patch assessment, for example, Templeton & Giraldeau (1996) ruled out the possibility that subjects were simply copying the departure decision of the partner bird. In the low public information condition, where the partner bird probed only a few empty holes before departing from the patch, the subject

remained behind and continued to sample the empty patch rather than copying the departure decision of its partner bird. Similarly, in the high public information condition, where the partner bird sampled many empty holes, the subject departed the empty patch first. These different departure decisions of the subjects support the hypothesis that the birds were paying attention to the cues provided by the partner birds and not to the partners' decisions. In this case, the cues were the unsuccessful probes of the partner birds.

Evidence for cue use rather than decision copying has also been found in social learning experiments in which subjects are given the opportunity to learn a discrimination task or a novel motor skill from observing the behaviour of others. For example, Templeton (1998) showed that naïve European starlings were able to acquire a novel discrimination task most rapidly when they observed the demonstrator always selecting the incorrect stimulus and never obtaining food. Instead of copying the demonstrator's decision, the subjects apparently used the cue provided by the demonstrator's lack of success to select the alternative (correct) stimulus.

In the situations described above, an animal can learn that a lack of success (i.e. no food) is a cue because it has already learned that a particular behaviour can be associated both with food and with no food. Unlike problems of patch assessment or discrimination tasks, however, in most studies of social learning that focus on imitation or behaviour copying, a lack of success following a novel behaviour pattern is not an informative cue. Instead, a novel motor act followed by no food is most probably going to be ignored as simply irrelevant. However, an animal that sees food (i.e. eating) after a novel motor act is much more likely to be witnessing a causal link between the behaviour pattern and the food. For example, Giraldeau & Lefebvre (1987) found that pigeons were unable to learn a novel skill if they were given the opportunity to scrounge from the tutor's demonstration, thus preventing the tutor from obtaining a food reward for its behaviour. So, the absence of a feeding cue from a tutor bird inhibited learning in naïve scroungers, though the act of scrounging itself was found to have an additional inhibitory effect (Giraldeau & Templeton 1991).

Interestingly, Palameta & Lefebvre (1985) demonstrated that pigeons were only able to learn a food-finding problem (piercing a paper lid on a box concealing food) when they were exposed to both the decision (pierce) and the cue (eating). Those that saw the demonstrator only pierce the lid but not eat, or that saw the demonstrator eat but not pierce were unable to learn the task during subsequent testing sessions.

5. POTENTIAL INFORMATIONAL CASCADES

The above studies suggest that animals often do in fact focus on cues rather than decisions to estimate various environmental parameters. However, in the final section of the paper, we offer three scenarios of potential informational cascades that may exist in nature.

(a) *False alarm flights*
Our first example involves explosive events in which many individuals quickly adopt the same behaviour. One

such example is when groups of animals take fright and retreat quickly to protective cover, sometimes even in the absence of any obvious source of danger. The use of social information in the context of rapid escape behaviour has been the subject of recent interest (Lima 1994, 1995; Proctor *et al.* 2001). For Lima (1994, 1995), social information about flock departure may be ambiguous because birds may leave for reasons other than alarm or predator detection, such as satiation or aggression. Proctor *et al.* (2001) develop a model from which they estimate Pareto optimal solutions to predict the conditions under which individuals should respond to others' departures when the cause of departure is ambiguous. We propose a different approach to the use of social information in patch departure by portraying it as a potential case of information cascades.

Imagine that within a flock of ground foraging birds, one individual sees a branch move and that this cue could, with some probability, indicate the presence of a predator. That bird responds by initiating a flight response. This behaviour is then witnessed by its nearest companion who, looking at the branch, also sees it move. The companion also decides that danger is imminent and adopts the flight response. A third individual sees the flight responses of its two companions but does not see any branch moving. It may be best for that individual to conclude that danger is imminent too and adopt the flight response simply because if two birds before it decide to flee, the likelihood of danger may be sufficient to take flight whether it sees the danger cue for itself or not. Once this bird decides to flee, even in the absence of any cue indicating danger (other than its two companions' decisions), an informational cascade starts where it becomes optimal for all other birds to follow suite, irrespective of whether they themselves see a danger cue or not.

In our example, the cascade starts again at the third individual but it is important to note that the cascade can start further down the sequence depending on initial conditions, the uncertainty involved with the cue, and the particular sequence of initial events. The cue we used was a moving branch, a cue that is probably only loosely associated with an approaching predator. A much stronger, less ambiguous cue could have been used—the presence of the predator itself. An approaching predator may cue with high certainty the imminence of an attack. While it is approaching, the predator may be visible only intermittently or only from some positions so that some individuals must decide on a course of action, flee versus stay, without seeing the approaching predator directly. The value of copying others in this case becomes obvious. The cascade is the optimal solution because waiting to figure out by oneself whether there is a real source of danger or not is simply too costly. The informational cascade may lead to false alarms, which are erroneous cascades. However, in the case of predator escape, the cost of an erroneous cascade may be small (loss of feeding time) relative to its benefits (avoiding death by predation). Increasing the costs of the erroneous cascade, say by starving birds, such that losing some feeding time may actually increase the chance of death by starvation, may mean that the animals will pay less attention to their companion's decisions and require a stronger, more predictive personally acquired cue to flee. To date, no study has investi-

gated whether individuals can change the weight they place on socially acquired decision rather than cue information as a function of the costs of erroneous cascades (Valone & Templeton 2002)●●6●●.

(b) *Night roost site selection*
Another potential example of an informational cascade that may occur in nature involves the selection of night roosts by birds. Many birds follow each other to night roosts. Indeed the function of these large dormitories has been the subject of considerable debate within behavioural ecology ever since Ward & Zahavi (1973)●●7●● suggested that roosts served as information centres (Richner & Heeb 1995, but see Barta & Giraldeau 2000●●8●●; Dall 2002). An alternative explanation is simply that roost site selection by many individuals is the result of an informational cascade. All individuals must estimate the quality of potential roost sites before adopting one. If the process of site selection is sequential and observed by all in the group then, after a few individuals pick a specific site, perhaps because their cues indicate it to be of higher quality (i.e. low predation risk, a good location for travel to and fro while exploiting food resources), an informational cascade could result with all others adopting the site simply because the social information indicates the site is profitable, independently of whether the animals joining it experience this profitability or not. If a communal roost site follows from an informational cascade, there may be no fitness advantage to being in any one specific social roost over another, or even no necessary advantage of being grouped in a roost at all. Individuals may roost at a site even if their personal cues indicate it is unprofitable to do so, because cascades cause them to ignore these cues and base their decisions on socially acquired information. The roost may exist as a consequence of an informational cascade and not because of the survival value of being in a group.

(c) *Mate choice copying*
An increasing number of studies have demonstrated that mate choice decisions of females are often influenced by the mating decisions of other females (Dugatkin 1996; Galef & White 2000). Such non-independent mate choice has been called 'copying' behaviour. Gibson & Höglund (1992)●●3●● first proposed that mate choice copying may be an example of an informational cascade, especially in leks where many females have the opportunity to view the sequential mating decisions of other females (e.g. Bradbury *et al.* 1985; Gibson *et al.* 1991; Wiley 1991).

While mate-choice decision copying is consistent with an informational cascade model, empirical demonstrations are lacking. Empirical demonstrations will require that copying behaviour occur because females use the mate choice decisions of other females as has been assumed (Dugatkin 1996). However, we know that cascades based on decision copying can also result in erroneous cascades and that the likelihood of such cascades depends on the amount of uncertainty conveyed by the cue concerning the actual value of the option. The cue information is probably the courtship interactions of males with other females. If informational cascades occur, females are expected to ignore their personally acquired cue information and base their mate choice entirely on the

decisions of their predecessors. This means that a female may mate with a male even if her current courtship interactions with him indicate he is of poor quality. To avoid such potentially erroneous cascades, females should attempt to acquire cue information rather than rely only on the mating decisions of other females (Valone & Templeton 2002). To date, little empirical work on mate-choice copying behaviour has attempted to discern the kind of information females acquire while watching the mating decisions of others (Galef & White 2000). Creative empirical experiments will be required to distinguish these alternatives. For example, it may be more costly for females with few mating opportunities to fall into erroneous cascades than females that have many future mating opportunities. If this is so, using another female's mating decision to choose mates may only be present in cases where females have ample future mating opportunities that would allow dilution of the effect of an erroneous decision. Copying may not be advantageous in older females or in females that reproduce just a few times in their lives.

6. CONCLUSIONS

We have described situations in which the use of socially acquired information may not enhance fitness. Our work suggests that future studies need to consider possible incompatibilities between the acquisition of personal and socially acquired information as well as the possibility of informational cascades. Throughout we have focused on the behaviour of birds but the ideas are general and should apply to other social taxa (Pitcher 1986; Laland & Williams 1998; Day *et al.* 2001). We have also focused on socially acquired information about quality. It may be true that incompatibilities between personal and public information are most common when individuals assess quality, but there is no theoretical reason to suggest that incompatibilities might not exist for other kinds of social information. For example, animals involved in acquiring novel skills may be in a situation where trial and error learning of the skills for oneself is incompatible with acquiring the social information required to engage in imitation. Moreover, different sources of social information may compete with each other reducing the efficiency of social information (Lefebvre & Giraldeau 1994). To date, very little attention has been directed towards exploring the trade-off between collecting information from social or non-social sources (Boyd & Richerson 1985).

Our examination of potential negative consequences of socially acquired information suggests new lines of empirical inquiry. We hope this paper serves to stimulate both research on incompatibilities between different types of information acquisition and investigations into the conditions under which individuals in groups should use social information from cues or decisions. In cases where decisions are used, informational cascades may occur and the likelihood and consequences of erroneous cascades may influence an individual's propensity to use social cues or decisions. Identification of a true informational cascade is still forthcoming. However, the possibility exists that phenomena for which adaptive explanations have been sought for some time without much success, as for example the formation of night roosts and many forms of

behaviour copying can simply be interpreted as informational cascades. We conclude that socially acquired information is not always a benefit and call for more extensive empirical evaluations of the conditions under which social information can be profitable.

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GLOSSARY

ESS: Author to supply definition●●4●●