



REVIEW

Expanding the scope for social information use

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Our understanding of how, why, and the circumstances under which animals use social information has been facilitated by three principal areas of research, social learning, public information use and social eavesdropping. With few exceptions, these related concepts have remained remarkably distinct within the literature, with little discussion or integration among them. Are these distinctions warranted? We tackle the issue by exploring similarities and differences between the concepts with respect to how animals gather and use social information, the type of information gathered, how information is packaged, and the relative payoffs to individuals involved. We contend that none of the currently dominant paradigms, social learning, public information use, or social eavesdropping, provide a unifying theme for studying social information use. Instead, we favour the central characteristic of the three concepts, social information use, as the overarching umbrella, and advocate a broader conceptual framework for understanding more comprehensively how animals behave with their social environments. Our intention is not to revolutionize the fields of social learning, public information use or social eavesdropping, but rather to stimulate discussion among researchers investigating the abilities of animals to extract information from the social environment.

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The ongoing fragmentation of knowledge and resulting chaos in philosophy are not reflections of the real world but artifacts of scholarship.
(Wilson 1998, page 8)

The social environment provides individuals with an opportunity to gather and use information resulting from the behaviour of others (Brown & Laland 2003). Our current understanding of whether, how, and by what mechanisms animals use social information is largely a result of a long history of experimental and theoretical research within the field of social learning. Investigations into social eavesdropping and public information use, however, have been similarly effective at elucidating the importance

of social context in the transfer of information among individuals. Despite striking conceptual similarities, these lines of research have remained remarkably distinct in the literature, with limited attempts to establish ties among them or to consider a more comprehensive framework encompassing all aspects of social information use (Nordell & Valone 1998; Brown & Laland 2003; Danchin et al. 2004; Miklósi 2005). Perhaps the failure to unify these concepts stems from the fact that they emerged from different fields, including comparative psychology and behavioural ecology, and at different times during the ontogenetic trajectory of ideas relevant to learning in a social context. Empirical work on social eavesdropping, for instance, has proliferated over the past decade, but this short history is but a small fraction of a rich timeline of studies on social learning. It also is possible that the apparent fragmentation of these concepts arose because each attempts to resolve different aspects of social information use. Whereas social learning addresses a wide variety of issues, the empirical focus of public information use and social eavesdropping rests primarily on resource quality, and aggression and mating strategies, respectively.

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Given the rapid expansion of studies on social eavesdropping and the steady flow of theoretical and empirical work on public information use and social learning, we felt that it would be valuable to ascertain whether strict distinctions between these concepts are warranted or, as succinctly stated by Wilson (1998), reflect an artefact of scholarship. We begin with brief outlines of social learning, public information use and social eavesdropping using widely accepted definitions and some classic examples. We then explore notable similarities and differences and attempt to highlight significant conceptual intersections among them. Finally, we argue that no one concept can effectively unify our understanding of social information use, despite previous attempts to do so (e.g. Danchin et al. 2004). Our focus is on conceptual and functional aspects of social learning, eavesdropping and public information use. A critical comparison of neural and other biological substrates underlying these three phenomena will provide interesting insights into the finer details of these modes of social information use. This type of comparison, however, is outside the scope of this review owing to limited studies of this sort in the areas of eavesdropping and public information use (Oliveira et al. 2001; Kavaliers et al. 2006), targeted studies in only certain areas of social learning (e.g. imitation, recognition: Heinrichs 2003; Iacoboni 2005), and the possible relevance of a vast literature on the neuroendocrine mechanisms of learning and social behaviour (e.g. Insel & Young 2000; Dohanich 2002; Ferguson et al. 2002; Kim & Jung 2006).

Our primary aim is not to reconstruct the fields of social learning, public information use and social eavesdropping, but rather to provide some fodder for stimulating intellectual exchange and debate among researchers studying these important issues related to the acquisition of information in a social milieu. Ultimately, we promote a broadened perspective, whereby social learning, public information use, social eavesdropping, and other related phenomena all are subsumed under a conceptually integrative framework of social information use.

Information

Because information, taken alone, is notoriously difficult to define operationally (Dall 2005), it often is described on the basis of how one might detect that information is available (Jablonka 2002; Dall 2005). We view social information as a subcategory of Jablonka's (2002) biological information, which she defines as a property of some source, such as the behaviour of an animal or interactions between two or more individuals that 'elicits a change in the state of the receiver in a (usually) functional manner'.

Social Learning

Much of what is known about how animals, from invertebrates to primates, gather and use the information provided by the behaviour of others can be found within the literature on social learning. Throughout its rich history, dating back to at least the late 19th century (e.g. Romanes 1884), the study of social learning among

animals has been approached from and motivated by diverse perspectives including the evolution and continuity of cognitive capacities, the processes through which behaviour is learned, the development of adaptive behaviour, and more recently, behavioural traditions (Galef 1988). The field was born out of, and has been driven largely by, comparative psychology, but has benefited from complementary interests within behavioural ecology, developmental psychology, mathematical modelling, and to some extent, anthropology. The result is a rich, multifaceted field, which to review comprehensively is not feasible here. We instead direct readers to theoretical and empirical works on social learning (e.g. Zentall & Galef 1988; Heyes & Galef 1996; Galef & Heyes 2004; Galef & Laland 2005), which provide thorough analyses of the literature.

Although numerous definitions of social learning exist, we adhere to a broad definition that classifies social learning as learning that is influenced by the observation of, or interaction with another animal (typically a conspecific) or its products (Heyes 1994). Encompassed within this definition is a range of 'mechanisms', including local and stimulus enhancement, emulation and imitation (see Heyes 1994; Whiten et al. 2004). The result of social learning includes observable changes in an animal's attention towards some aspect of the environment, and/or the acquisition of knowledge about physical properties of the environment, consequences of certain behavioural acts, or the motor skills required to achieve a particular behaviour. Consequently, social learning can bring about a wide range of behaviours, including solutions to novel problems, tool use, foraging skills and strategies, predator avoidance and cultural repertoires (Zentall & Galef 1988; Heyes & Galef 1996; Galef & Giraldeau 2001; Brown & Laland 2003; Frigaszy & Perry 2003; Galef & Heyes 2004).

The broad definition of social learning cited above could lead to some confusion about what might constitute learning from the social environment. For example, an aggressive encounter between two individuals certainly exemplifies an 'interaction with another animal' and there is potentially a significant learned component to the outcome of the contest (i.e. A may have learnt that B is physically stronger; Hollis et al. 1995; Miklósi et al. 1997). The learning that occurs during such an interaction, however, is typically thought to be individual learning rather than social learning. The interaction component of social learning normally refers to indirect interactions between an observer and a demonstrator. This is not to say that physical contact between individuals cannot occur, but instead that a visible change in the behaviour of the observer occurs after observation of another individual. Thus, the information extracted by an observer emerges from the demonstrator's behaviour. Moreover, the demonstrator typically is not actively altering its behaviour for the benefit of the observer, as might be the case in teaching (Boesch 1991; Caro & Hauser 1992; Rendell & Whitehead 2001; Franks & Richardson 2006).

For the most part, social learning has been addressed using two approaches, one functional and the other mechanistic (Shettleworth 1998). These approaches need not be mutually exclusive, and more recent investigations

of social learning have been successful at wedding the two approaches (Miklósi 2005). The functional perspective ascertains the adaptive nature of social learning (i.e. how learning from others affects individual fitness). For example, learning to avoid a predator or learning what foods are safe to eat have unambiguous benefits, even if not all instances of social learning have the same positive results (Laland 1996; Laland & Williams 1998; Giraldeau et al. 2002). In contrast, the mechanistic perspective attempts to identify the particular means by which social information is converted into changes in individual behaviour (e.g. imitation or an assortment of other mechanisms; Whiten & Ham 1992; Zentall 2001; Whiten et al. 2004). Comparative psychology has for over a century favoured this approach, with much emphasis being placed on providing evidence that individuals will imitate the actions of another.

Across a range of taxa, social learning plays a prominent role in the acquisition and processing of food, and as a result, nearly all experimental investigations into social learning involve food rewards (Caldwell & Whiten 2002). Popular topics include food preferences and the manufacture and use of tools and other techniques needed to bypass the natural defences of edible foods, such as the hard casing of a nut. Social learning also has been implicated in avoidance learning (Mineka & Cook 1988) and mate choice (e.g. Dugatkin 1992; Galef & White 1998), and plays an important role in the proliferation and maintenance of behavioural traditions among different populations within a species (Whiten et al. 1999; Rendell & Whitehead 2001; Fragasz & Perry 2003; van Schaik et al. 2003).

In an experimental setting, social learning typically is identified by the fidelity with which observers reproduce a modelled behaviour and/or by a decrease in latency of behavioural acquisition, relative to the acquisition or performance of the same behaviour in the absence of a demonstrator (i.e. when only individual learning is available). As such, traditional experimental paradigms in social learning involved two groups of subjects, an experimental group that has one or more opportunities to observe a proficient model, and a control group that is denied opportunity for observation. With the exception of social context, the experience of individuals in these two groups is the same. If social learning has occurred, similarity in the behaviour of subjects in the experimental group and the model should be apparent. More recently, two-action paradigms, in which subjects observe one of two alternative actions involving the same apparatus, have gained popularity. Because the two actions are always available and are enacted on the same apparatus, social learning, and more specifically imitation, is inferred if observers perform the behaviour demonstrated to them more frequently than the alternative (e.g. Galef et al. 1986; Bugnyar & Huber 1997; Heyes & Saggerson 2002). In addition, reports citing behavioural variation among populations within a species have led to experimental approaches to confirm the role for social learning in the transmission of traditions in captive groups (Galef & Allen 1995; Galef 2004; Whiten et al. 2005; Bonnie & de Waal 2006; Bonnie et al. 2007).

Public Information Use

In comparison to the long history of social learning, public information use is a concept that has emerged relatively recently. Grounded principally within behavioural ecology, public information use was initially formulated to characterize how individuals acquire information about the quality of an environmental resource (e.g. food patches and breeding habitats) by attending to the relative success of others within the same environment (Valone 1989; Valone & Templeton 2002; Danchin et al. 2004). For example, when required to sample several patches to assess food distribution, European starlings, *Sturnus vulgaris*, and red crossbills, *Loxia curvirostra*, sampled fewer patches in the presence of a social partner than they did in a solitary condition (Templeton & Giraldeau 1995, 1996; Smith et al. 1999). These findings show that when accompanied by one or more social partners, individuals spend less time searching for food in an unprofitable patch, compared to circumstances in which individuals must independently evaluate the environment. Individuals then can use the information provided by the performance of social partners to make decisions about the relative quality of the patch, and adjust their foraging behaviour accordingly. More recently, public information has been construed broadly to encompass nearly all information that is potentially available to a wide audience (Danchin et al. 2004). Throughout this review, however, we adhere to the traditional use of the term which focuses on information about environmental quality.

Although similar in many regards, public information use and social learning are unique concepts (Valone & Templeton 2002). Public information use provides information about the quality of a location in the environment and of the resources within it. Social learning, it has been argued, provides information regarding only the location of a resource or how to obtain it, but not about its quality (Valone & Templeton 2002). While, in principle, some researchers studying social learning may also be interested in questions relating to resource quality, in practice they have concentrated on cases concerned with the location of a resource and how to obtain it. The resulting conclusion that can be drawn from the current literature is that while individuals may become aware of or drawn to a particular resource through social learning, public information typically is obtained only after entering a resource patch and may influence an individual's decision of whether to stay or leave (see also Coolen et al. 2003).

Public information use extends beyond a foraging context and into assessments of habitats (Doligez et al. 2002; Part & Doligez 2003; Ward 2005) and potential mates (Nordell & Valone 1998). More recently, differences between species in the use of public information provided by conspecifics and heterospecifics (Coolen et al. 2003), and the responses of animals when public information and personal experience conflict (van Bergen et al. 2004) also have been addressed. In addition, public information use might provide a mechanism to explain nonrandom settlement, movement patterns and aggregative tendencies of individuals of the same or different species, phenomena that have been dubbed conspecific or

heterospecific cueing, or habitat copying (Pruett-Jones 1992; Persaud & Galef 2003; Parejo et al. 2005). Two recent papers (Valone & Templeton 2002; Danchin et al. 2004) provide excellent reviews of these developments.

Investigations of public information use typically are designed to determine whether animals are sensitive to social information about the quality of a resource. Thus, like social learning, studies of public information use compare behaviour of solitary animals with behaviour of individuals exposed to one or more social partners. Measures of public information use vary with the context in which it is investigated. For instance, in the context of foraging, one might evaluate patterns of patch sampling in terms of number of patches visited, samples made in each patch and/or time spent in a patch. In the context of habitat selection, one might evaluate site visits and colonization in future breeding seasons (Doligez et al. 2002; Part & Doligez 2003).

Social Eavesdropping

Social eavesdropping is defined as the act of extracting information from signalling interactions between conspecifics (McGregor & Dabelsteen 1996; McGregor 2005). By witnessing such interactions, a bystander might obtain accurate information about the relative or absolute quality of the signallers (e.g. mating success, fighting ability), and can then use the information in future encounters with the signallers (Peake 2005). Thus, like public information use, social eavesdropping provides individuals with information about quality. Information gleaned from social eavesdropping, however, is a result of signalling interactions between two or more individuals, rather than individual behaviour, as is the case in public information use. Moreover, social eavesdropping should not be confused with interceptive eavesdropping (Shier 2002), a tactic commonly used by predators to detect and capture prey (Balcombe & Fenton 1988; Clark 2004), by competitors to oust interspecific rivals from a food resource (Nieh et al. 2004), or by neighbours to interfere with courtship bouts between adjacent male–female pairs (Balsby & Dabelsteen 2005). Interceptively eavesdroppers usually gather information about the location or proximity rather than the quality of a signaller, hone in on broadcast signals (or cues) rather than directed signalling interactions, and often, but not always, target heterospecifics rather than conspecifics (Peake 2005). Much of the work on social eavesdropping has focused on the behavioural response of a bystander to witnessing either male–male aggressive interactions or male–female courtship interactions. We discuss examples of each of these below.

Social eavesdropping is identified when an individual changes its response towards an observed interactant, but not towards a novel individual, after witnessing a signalling interaction between two or more animals. That is, individuals that gather information from the signalling interactions of others should react in a predictable manner (whether choosing a mate, or initiating an aggressive encounter) when encountering in the future a previously witnessed interactant. To conclude that eavesdropping

has occurred, alternatives for the change in bystander behaviour, such as priming or cueing on physical traits (e.g. size or coloration) or signal properties also must be ruled out (Clotfelter & Paolino 2003; Earley & Dugatkin 2005; Earley et al. 2005).

Although the term eavesdropping appears in animal behaviour literature somewhat earlier (Wiley 1983), social eavesdropping is a young concept, emerging only in the last decade of the 20th century. Explicitly defined as a phenomenon categorically distinct from interceptive eavesdropping by McGregor & Dabelsteen (1996), social eavesdropping has in recent years increasingly attracted the attention of researchers interested in territorial aggression and mate choice, as well those interested in communication networks (McGregor 2005). Most contemporary studies on social eavesdropping have focused on whether male or female bystanders can obtain information about the relative quality of two, usually male competitors, and use this information to guide future agonistic or mate choice decisions, respectively. A number of controlled investigations in birds and teleost fish have demonstrated that male bystanders modulate their agonistic decisions based on information obtained from watching aggressive signalling interactions between unfamiliar males (Naguib & Todt 1997; Oliveira et al. 1998; Peake et al. 2001; Earley & Dugatkin 2002; Paz-y-Miño et al. 2004; Magnhagen 2006). Males of territorial species tend to respond more aggressively to perceived winners (Naguib & Todt 1997; Oliveira et al. 1998; Peake et al. 2001; Mennill & Ratcliffe 2004a; see Mennill & Ratcliffe 2004b for rank-dependent strategy), a strategy that would allow territory holders to identify and expel formidable intruders. In predominantly social species such as swordtail fish, *Xiphophorus helleri*, males avoid observed winners, a strategy that would allow the bystander to avoid the potential costs (e.g. change in dominance status) of engaging in and losing an aggressive contest (Earley & Dugatkin 2002).

Females also use information available in male–male aggressive contests to assess the suitability of future mates. In many species, females choose to associate or mate with the winner of an observed contest (Doutrelant & McGregor 2000; Mennill et al. 2003; Leboucher & Pallot 2004) presumably because winners are more likely to be successful at accessing or defending limited resources, which might have direct or indirect benefits for the female (Ryan 1997). Interestingly, studies on Japanese quail, *Coturnix japonica*, have demonstrated that females assess not only status but also mate compatibility (Ophir & Galef 2003). Male quail that show high levels of contest aggression also are prone to engage in aggressive, possibly injurious courtship behaviour. Females thus tend to choose the losers of male–male contests (Ophir & Galef 2003), and this effect appears to be experience dependent (Ophir & Galef 2004). Eavesdropping is not, however, restricted to females that have not yet found a mate. Recent studies on great tits, *Parus major* (Otter et al. 1999), black-capped chickadees, *Poecile atricapillus* (Mennill et al. 2002), and cichlid fish, *Archocentrus nigrofasciatus* (van Breukelen & Draud 2005) reveal that paired females eavesdrop on aggressive contests involving their mate to gauge his quality and to assess the prospectus for extrapair mating. Males

also will strategize for extrapair matings. Territorial male European robins, *Erithacus rubecula*, tune in to interactions between a neighbouring male and his female (i.e. 'seep' call rate) to determine the male's provisioning rate and the probability of female defection (Tobias & Seddon 2002).

Females also might gauge the quality of a male by witnessing courtship interactions. Females that observe a male successfully court or mate with a 'model' female tend to copy the mate choice decision of the model, a phenomenon dubbed mate choice copying (see Dugatkin 1996; Galef & White 2000; White 2004 for reviews; see below for more thorough treatment). Although there are exceptions to the general rule 'choose a male that has been chosen' (e.g. age- or experience-dependent effects; Dugatkin & Godin 1993), intrasexual mate choice copying appears to be widespread among birds and fish. Gonçalves et al. (2003) also demonstrated in a fish with alternative reproductive tactics that this phenomenon might extend to intersexual copying (e.g. sneaker males choose on the basis of female affiliations with parental males). As such, this form of nonindependent mate choice has received extensive empirical, conceptual and theoretical attention (Servedio & Kirkpatrick 1996; Westneat et al. 2000; Uehara et al. 2005).

Many of the aforementioned experimental studies of eavesdropping have not demonstrated unequivocally whether the information used by bystanders is embedded in signals or based on individual cues. Studies on acoustic eavesdropping in songbirds, which use playback to present signals (and signalling interactions) to a bystander in the absence of other possibly salient cues, provide the most compelling evidence for the significance of signals in modifying bystander behaviour (Naguib et al. 1999; Peake et al. 2001, 2002). A pair of studies on *Betta splendens* used a clever experimental design to elucidate the roles of signals versus cues in guiding bystander behaviour (McGregor et al. 2001; Peake et al. 2006). In both cases, cues presented by the observed individuals were not sufficient to explain changes in bystander behaviour, while components of the interaction itself (whether real or 'apparent') appeared to play a considerable role in modifying the agonistic response of the bystander. Nevertheless, it is of great importance for the field of social eavesdropping to further illustrate that signals conveyed during social interactions are the predominant trigger for changes in bystander behaviour.

Mate Choice Copying: an Example of Missing Integration

Remarkably, mate choice copying is the only behavioural strategy associated with social information use that has been couched in terms of public information (Nordell & Valone 1998; Galef & White 2000), social eavesdropping (Earley & Dugatkin 2005) and social learning (Dugatkin 1996; White 2004). What is it about mate choice copying that makes it amenable to each of these interpretations? The fact that observer females tend to reproduce the choice of model females immediately establishes ties with some

corners of social learning, particularly 'copying'. Public information often refers to cues provided by the behaviour of others about the profitability of limited resources, usually food. Males are valuable commodities, and information about male quality, via association with and successful courtship of other females, is available to a broad audience. Thus, mate choice copying can be considered a response to public information. Similarly, because females might capture additional information about male quality from a male's success in peripheral signalling interactions, mate choice copying fulfils the definition for social eavesdropping. With all of this said, mate choice copying appears to be one example of a behavioural phenomenon that falls at the intersection of the three major concepts of social information use. Indeed, mate choice copying embodies the notion that information use in a social context cannot productively be distilled to one or many isolated phenomena. This is not to say that public information, social eavesdropping and social learning should be merged because, as we discuss below, there are important similarities and differences that warrant attention. Identifying points of intersection and divergence among these phenomena, however, should allow us to alleviate some conceptual impermeability and promote a broader view of social information use.

Similarities and Differences

The source of information, namely the behaviour of a conspecific or many conspecifics, is the common thread that binds social learning, public information use, social eavesdropping and other related phenomena. Information in these cases is available to all group members within detection range. The fact that information is accessible to a broad audience distinguishes social information concepts from 'private' or 'personal' information (Templeton & Giraldeau 1996; Koops & Abrahams 1999; Kendal et al. 2004; Dabelsteen 2005) in which information is acquired through individual experience in the absence of social partners. All types of social information are not the same, and we feel that appreciating differences between them is as important as understanding similarities among them. As such, we have identified important similarities and differences including the type of information gathered, how information is packaged, and the relative costs and benefits to the individuals involved.

Information content

Regardless of the mode of social information use (social learning, social eavesdropping, or public information use), the probability that one individual opts to gather information from another can depend on a host of characteristics of the demonstrator(s) including relative status, size, sex, age, affiliation, and so forth (e.g. Dugatkin & Godin 1993; Coussi-Korbel & Fragazy 1995; Laland 2004; Mennill & Ratcliffe 2004b). Laland's (2004) description of 'who' strategies embodies this potential for observation decisions to be context dependent. Once the decision to observe has been made, however, the types of information gained through social learning, social

eavesdropping and public information belong to three basic categories.

By extracting information from the social environment, individuals can learn about properties of their physical environment ('about what'), how to manage the environment or about the interactions of others with the environment ('about how'), or about the characteristics and/or quality of one or more individuals in the social environment ('about whom'). Social learning has primarily been concerned with 'what' and 'how' types of information. For example, through local and stimulus enhancement, attention of observers is drawn towards locations or features of the environment, and information 'about what' can be obtained. Likewise, imitation, and indirectly emulation, provide information 'about how' an action may be performed or a goal is achieved. Social learning about predators also fits within the category of 'about what', as observers gather information about the potential dangers lurking within the environment (e.g. Mineka & Cook 1988; Brosnan et al. 2003; Griffin 2004; Ellard & Byers 2005; Wong et al. 2005).

Like social learning, public information contributes information 'about what', but in a slightly different way. Whereas social learning provides discrete information (e.g. presence or absence of feature), public information contributes information about relative quality of a particular resource. Information about 'whom' is almost entirely restricted to social eavesdropping. Because nearly all social information is gathered from conspecifics (but see Coolen et al. 2003), we limit our treatment of 'about whom' to conspecifics only.

Information packaging

Social information is packaged in one of two modes: (1) as signals, traits that have been selected for communicative purposes (Wisenden & Stacey 2005), or (2) as cues (cf. 'inadvertent social information'; Danchin et al. 2004), behaviours or characteristics not specialized for communication, but which contain pertinent information (Otte 1974).

Whereas both cues and signals provide information for all individuals in range to attend to them, cues are not produced with the intent of communication. While signals are selected for their efficacy in communication, individuals providing cues are selected to perform as well as possible, rather than to inform others (Danchin et al. 2004). That is, cues are by-products of form, physiology and behaviour (Sorensen & Scott 1994; Wisenden & Stacey 2005). Cues are given in the absence of receivers but become potentially relevant in their presence. In contrast, signals carry an inherent social relevance in that their production typically is contingent upon the presence (or presumed presence) of a receiver, and this social relevance is magnified in the presence of individuals for which the signal was not intended. If cues or signals are divorced from a social context and the process of social information, their significance, in both cases, is lost.

In instances of both social learning and public information use, observers use cues almost exclusively, the one exception being reports of teaching among nonhuman animals (Boesch 1991; Rendell & Whitehead 2001; Franks & Richardson 2006). In contrast, eavesdroppers attend to

signals exchanged between two or more individuals. In the case of eavesdropping, signals directed from one individual specifically towards another are exploited by attentive bystanders, for which signals were unintended.

The type of information required for eavesdropping (or available for bystanders to use through eavesdropping) provides an additional level of information not accessible in other contexts. Signals or cues alone provide certain types of important, but static information. The information available in a signalling interaction, however, is arguably greater than the sum of its parts (i.e. isolated signals or cues) because interactions make available to bystanders information on the relative quality of the signaller (e.g. aggressive interactions) or information on the absolute quality of a signaller that could not be realized in the absence of interaction (e.g. efficacy of courtship displays and mating success) (McGregor & Dabelsteen 1996; McGregor et al. 2001).

Payoffs to bystanders, demonstrators and signallers

The literature on social information use provides many examples of the benefits that naïve individuals might obtain by attending to the behaviour of others (see previous sections for relevant literature). For instance, inexperienced animals might learn about productive foraging locations, quality breeding sites, predator location and behaviour, or the competitive prowess of other individuals in the group. Obtaining this same information on one's own can be costly, in the form of energy depletion during aggressive contests, time lost assessing habitat quality, time spent sampling a patch, or death or injury due to predation events. Provided that there is little cost associated with acquiring social information relative to individual trial and error, and provided that the benefits of doing so are significant, it pays an animal to attend to the behaviour of others.

Recently, a strong case has been made for exploring more systematically the assumption that social information use is inherently beneficial, particularly because there are some circumstances in which socially acquired information appears to be disadvantageous (Giraldeau et al. 2002; Laland 2004). Regardless of whether bystanders attend to cues or signals and irrespective of the type of information available (about what, how, or whom), the basis for understanding the potential payoffs of social information to the bystander is the same. The benefits of attending to the behaviour of others should increase as a function of the reliability and/or relevance of available information, and should be inversely related to the costs associated with acquiring or utilizing the information. Such costs can include susceptibility to predation or lost opportunity arising from limited attention (Dukas 2002), time and energy deficits emerging from active pursuit of social information, or imperfect information processing due to the cognitive load associated with complex social and physical environments (Barrouillet 1996; Ayres 2001).

Environmental stability and the relative frequency of asocial versus social learners (e.g. producers versus

scroungers) in the population could influence the reliability of social information and, in turn, the benefits accrued by bystanders. When the environment is unpredictable, it might pay to sample the environment individually rather than rely on possibly outdated cues provided by conspecifics or heterospecifics about, for instance, patch profitability (Boyd & Richerson 1988; Giraldeau et al. 2002). Similarly, as the frequency of individuals utilizing asocial learning strategies decreases, the probability that bystanders will obtain up-to-date information about a fluctuating environment necessarily decreases, rendering social information less useful (Laland et al. 1996; Kameda & Nakanishi 2002; but see Vilhunen et al. 2005). The complexity of the attended cue or signal and the ability of bystanders to accurately process the information (i.e. error rates) also might affect information reliability and the benefits to using socially acquired information. Experience could also mediate the ability of animals to parse out the relative importance of personally versus socially acquired information (Valone & Giraldeau 1993; Templeton & Giraldeau 1996; Ophir & Galef 2004) and the minimization of assessment or processing errors. Thus, we might also expect the benefits of obtaining social information to depend on social context (i.e. experience of, or relationships between, demonstrator(s)/signaller(s) and the bystander).

From the perspective of information producers, the benefits and costs to behaving in a public domain are a bit more opaque. There are some clear instances where behaving in the presence of others could impose substantial costs. The ability of observant western scrub-jays, *Aphelocoma californica*, (and other corvids) to identify and pilfer the food caches of others represents one such obvious cost (Bugnyar & Kotschal 2002; Emery et al. 2004). Other classic events of social information use, however, are not easily labelled as costly or beneficial to the demonstrator/signaller. Cueing patch profitability could be costly if the inadvertent recruitment of additional competitors reduces food availability, but it could be beneficial if additional eyes increase predator vigilance (Lima 1995). Engaging in aggressive interactions in the presence of an audience could be beneficial for the winner (e.g. deter future opponents or attract mates) but not the loser, or vice versa (see *Social Eavesdropping*). Indeed, several studies have demonstrated that contestants alter their conduct during aggressive interactions when being watched, suggesting that the social environment might exert selection pressure on signal design and performance (Zajonc 1965; Grinnell & McKomb 2001; Matos & McGregor 2002; Dziewczynski et al. 2005; but see Dziewczynski et al. 2006). There presumably also are cases where demonstrating has neutral consequences, such as might be the case in skill acquisition, however, to our knowledge this aspect of social learning has not yet been explored explicitly.

Establishing a Broader Framework

Evaluating the content (e.g. about what) and packaging (e.g. signal versus cue) of social information allows us to distinguish among the three concepts, with social eavesdropping showing the most pronounced divergence.

Differences at the level of information type raise the question of whether any of the three concepts can be hoisted as a unifying paradigm for studying social information use. Danchin et al. (2004) advanced the concept of inadvertent social information, which contributed insights into how social information could mediate the development of, among other things, cultural and communication systems. The authors proposed that many of the behavioural phenomena associated with social learning and eavesdropping can be subsumed under the auspices of public information (the same term as described above but, applied in a much broader way), often neglecting important differences between the information streams. Rather than elevating one or the other concept as distinctly coalescent, we favour the central, shared characteristic of the three concepts, social information use, as the unifying umbrella. Of course, it is rather obvious that social learning, social eavesdropping and public information hinge on the use of social information. Our broader framework is more a plea to dissolve some of the boundaries that apparently have prevented these fields from interacting productively in the past. By adopting a more expansive view, social information use writ large, perhaps we gain new insights into how and in what capacity the various information streams targeted by each of the three concepts (e.g. about what, how, or whom) could affect the behaviour of an observer.

Implications of a Broader Framework

There are at least two marked advantages to softening the divides among social learning, public information and social eavesdropping, and thus broadening the scope through which we tackle questions regarding social information use. In doing so, we first acknowledge that social animals are exposed to a barrage of information types that may be packaged in different ways. Individuals might engage in social learning, access public information about resource quality, or eavesdrop on signalling interactions, each serving to reduce uncertainties about their social and/or physical environments (Dall 2005). Second, we recognize the possibility that individuals might further clarify their surroundings by using different acquisition strategies or by attending to different information streams either simultaneously or sequentially. Van Bergen et al. (2004) demonstrated that nine-spined sticklebacks, *Pungitius pungitius*, effectively integrate public and private information, favouring public information to guide decisions on habitat choice. There are no studies that we know of that evaluate the relative contribution of different types of social information (and the strategies that accompany the acquisition of such information) to individual decision making.

For instance, an individual might be drawn to a resource patch because other animals are present (i.e. through social facilitation or conspecifics cueing) but its decision to stay at the patch may be driven by cues available in the behaviour of others that are indicative of patch quality (i.e. public or inadvertent social information), by its response to watching social interactions between others

(i.e. social eavesdropping), or both. A reductionist view of social information use does not effectively allow one to partition the different forms of social information that might be available to and used by a bystander. Our broader framework enriches the social environment by appreciating that animal social behaviour is not simply the product of processing a single information stream but rather emerges from integrating sometimes overlapping information streams. In turn, we are left with an abundance of important questions to pursue. Do animals assimilate these different types of social information? Under what circumstances, if ever, do animals favour one type of social information over another? Do closely related species with different social systems rely heavily on the same or different types of social information?

Empirical studies investigating the independent or interactive contributions of multiple, distinguishable social information streams to changes in bystander behaviour will require integrating the rich literatures on social learning, public information and social eavesdropping. With few exceptions, conceptual developments within these areas of social information use have followed independent trajectories without much in the way of cross-referencing of important findings except in passing. The goal of this review was to challenge researchers to think more broadly about social information and to resist elevating any one concept as uniquely encompassing. Furthermore, although current terminological distinctions (e.g. public information versus social eavesdropping) are warranted for reasons outlined above (*Similarities and Differences*), the expanded view that we propose should discourage additional semantic deconstructions of these types of behavioural phenomena unless absolutely necessary. To this end, we hope to initiate more fruitful and fluid intermingling of existing ideas and historical and contemporary discoveries from all corners of social information research. As this field advances, we also anticipate that the study of proximate mechanisms underlying the processing of and subsequent behavioural changes that accompany the extraction of social information will be pursued in greater detail. Merging mechanistic and functional aspects of social information use will provide another benchmark for evaluating whether, how and to what extent different information streams are managed by similar or disparate neural and endocrine substrates.

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