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The role of public information in ecology and conservation: an emphasis on inadvertent social information

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Public information is an emerging major topic in ecology and evolution. We review the literature about the role of public information in ecology and conservation while mainly focusing on inadvertent social information (ISI), which constitutes a major form of public information. We first define the terms of biological information that we use. We then review the accruing evidence for ISI use in many fitness-affecting decisions in plants and animals. We generalize concepts of information to encompass interspecific interactions. We then develop how intra- and interspecific information flows actually shape ecological and evolutionary dynamics. We then discuss some of the application of adopting an information-driven approach to ecology and evolution in conservation biology. Our hope is to favor the transfer of knowledge from ecology and evolution to conservation biology. We claim that this is the only way to design efficient conservation actions and illustrate how ignoring concepts of information may lead us to design conservation actions that drive endangered populations toward rather than away from extinction.

Keywords: ecology; evolution; public information; inadvertent social information; conservation biology

Introduction: toward a unified framework of biological information

Life is essentially a matter of information flow across generations and space. Evolutionary biologists often stress the importance of genetic information flow. However, evidence is accruing that inheritance is not limited to the sole genetic information (reviews for instance in Refs. 1–14). More generally, many forms of information flow are likely to greatly affect ecological and evolutionary dynamics.[14] From an ecological perspective, population and community dynamics can be viewed as essentially resulting from the dynamics of information flows across time and space.

Although population geneticists strive to study "gene flow" within a metapopulation, evolutionary ecologists need to adopt a broader approach and consider the impact of all "information flows," be it genetic or nongenetic, within metapopulations, metacommunities, and meta-ecosystems. To do this,

we first define the main terms of information that we will use in this review. The terminology of information has been discussed at length in a series of papers particularly in recent years.[15–22] A brief review of these papers highlights the absence of a consensus about terms of information. The terms used in this review are extracted from Ref. 22, who proposed an extended glossary of concepts of information with the hope to help building a consensus about terms of information in biology.

Definitions

Most of the debates about biological information results from the ignorance that, such as energy, information can be either potential or realized.[22] Potential information only becomes realized information when it is detected by an organism. However, the same potential information may be processed and used (i.e., realized) very differently by various organisms. For instance, a given event, such as male A, but not male B, found food may be interpreted and
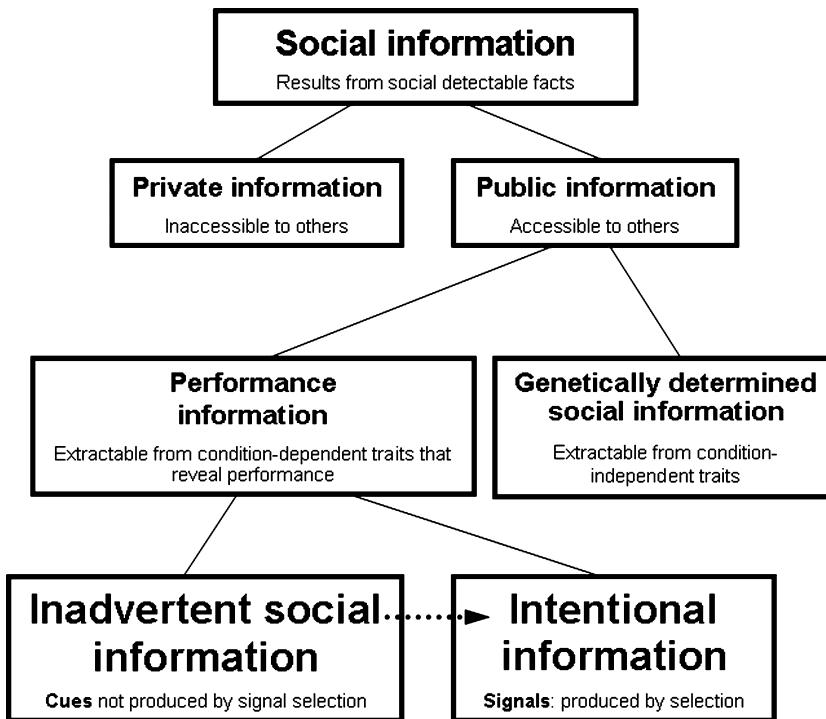
Figure 1. Categories of social information. When social information is inaccessible to others it constitutes private information, and when it is accessible it is public information. Public information encompasses both performance information, which is provided by condition-dependent traits that reveal performance, and genetically determined social information, which may be extracted from condition-independent traits. Performance information may result from the detection of facts that produce information intentionally or unintentionally. It thus encompasses both inadvertent social information and signals. The black dotted arrow linking inadvertent social information to intentional information indicates that the former may lead to the evolution of signals. Extracted from Ref. 22.

used differently by different phenotypes. Females looking for a mate may increase their willingness to mate with A, whereas a hungry male or female may decide to follow male A at its next foraging trip.

These considerations show that classifications of the various forms of information should be based on potential (i.e., detectable facts about the environment before being detected) rather than realized information (i.e., detected and used) because the former is much more objective.[22] In this context, potential *biological information* can be defined as factors that may affect the phenotype in ways that may influence fitness. These factors bring some "knowledge" that can be used for optimizing individual development or decision. Here knowledge is used in its broadest sense that includes all the information possessed by an individual, including genetic information.[22] Biological information can be either genetic or nongenetic. The information

encoded in DNA sequences is *genetic information.* *Nongenetic information* encompasses factors that may affect the phenotype but that are not encoded in DNA.

There are many forms of nongenetic information (for a more exhaustive review, see Ref. 22). Nongenetic information may be either social or nonsocial. *Nonsocial information* can be acquired from physical detectable facts in the environment. *Social information* can be extracted from interactions with, or observations of, the phenotype of other organisms (Fig. 1). Once realized, that is, once detected, processed, and used, all these forms of information contribute to the phenotype of an individual organism and constitute the knowledge of that individual. Only part of the information possessed by an individual organism may be accessible to other individuals. That part of the knowledge constitutes *public information* (Fig. 1), which is potential social

information to others. *Public information* is opposed to *private information*, which is the information possessed by an organism that is inaccessible to others.

Public information encompasses *performance information*, which is extracted from condition-dependent traits that reveal the performance of other individuals. Performance information can be either inadvertent or intentional. *Intentional information* is synonymous with *Signal*, which qualifies traits or behaviors produced by selection to intentionally transmit information, the adaptive function of which is to alter the behavior of receivers to the benefit of the sender. An example is that of alarm signals of birds that inform others about danger to the benefit of the alarm producer. Inadvertent social information (ISI) results from facts that are unintentionally (and often unavoidably) produced by organisms and may be detected by other organisms.[22] An example is that of local average reproductive success that unintentionally reveal breeding habitat quality to prospecting conspecifics.

Outline

In this review we focus on the role of public information in ecology and conservation. More specifically, we focus on the unintentional component of public information that is on ISI (Fig. 1). The reasons of this choice are that although intentional information has been the focus of many studies and reviews (e.g., Ref. 23), unintentional information only became an important topic relatively recently.[24] This is all the more surprising because information flows at the scale of metapopulations, metacommunities, and meta-ecosystems are likely to mainly involve many forms of unintentional information, with intentional information remaining quantitatively relatively rare. We also emphasize ISI because it likely provides the platform from which intentional communication may evolve[17], implying that it constitutes a primary form of information for ecological and evolutionary studies.

We first review some of the evidence for ISI use in many fitness-affecting decisions. These decisions concern foraging, predation avoidance, habitat choice, choice of host nest by brood parasites, dispersal, and mate choice. We do not intend to be exhaustive but rather try to illustrate the various facets of information use, whether intra- or interspecific. This first section is thus individually centered. In section "ISI: implications for ecological interactions," we discuss how individually acquired information can affect higher biological levels of organization such as population dynamics, community structure, and ecosystem functioning. In section "ISI: applications in conservation biology," we tackle more applied aspects by illustrating how the ISI framework can help us designing efficient conservation actions.

One of our main goals in this review is to show how every ecological and evolutionary approach as well as conservation biology can benefit from adopting an information-driven approach.[25] We believe that the study of ecological and evolutionary processes would greatly benefit from the reformulation of our questionings in terms of information flows. In other words, we advocate that concepts of information are central to ecology and evolution.

ISI: the evidence

ISI may affect an organism's accuracy in appraising the environment in most ecological contexts.[22] Since Valone's seminal paper in 1989,[26] the study of social information use by individuals of a wide range of taxa (including plants) increases rapidly in terms of number of publications (Fig. 2) and several examples deserve consideration.

Most studies focused on ISI use intraspecifically (i.e., by gathering information from conspecifics). However, other studies, e.g., Refs. 15, 20, and 27–33 have demonstrated and formalized the idea that individuals may also be able to gather information from the performance of heterospecifics (i.e., members of different species). This can be called "interspecific ISI use" as opposed to "intraspecific ISI use." In both cases, ISI is informative because it is extracted from individuals sharing the same ecological requirements, which includes conspecifics as well as heterospecifics exploiting the same resources (i.e., competitors). Thus, by gathering information from competitors, individuals may increase their own fitness if this information provides valuable information about the environment. Hence, contrary to the conventional beliefs, members of competing species can inadvertently be a valuable source of information for each other.[34] This expansion of social information use greatly expands the scope of ISI because it broadens concepts of information from the individual to the population, community, and ecosystem levels.
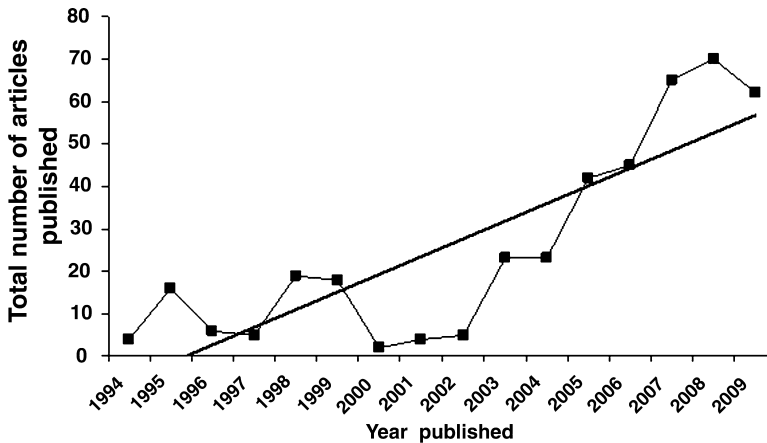
Figure 2. Total number of articles published per year (from 1994 to 2009) that were found using the keywords "social information" in the ISI Web of Science engine search (accessed October 2, 2009). The search was done for the following journals: *Animal Behaviour*, *Behavioral Ecology*, *Behavioral Ecology and Sociobiology*, *Behaviour*, *Ecology*, *Ethology*, *Journal of Animal Ecology*, *Oikos*, and *Proceedings of the Royal Society B*.

We now provide a series of recent examples illustrating the idea that ISI use (both at the intra- and at the interspecific levels) is pervasive for most fitness-affecting activities such as foraging, breeding site selection, brood parasitism, predator and parasite avoidance, dispersal, and mate choice.

ISI use in a foraging context

One of the most popular and prolific area of research on ISI use concerns foraging (reviewed in Ref. 21). In this context, food patch quality is defined as the quantity and quality of resources that are available in a patch (irrespectively of the presence or absence of predators) that lead to a given rate of food intake expected in the patch. The main assumption is that foraging conspecifics should spend more time and/or have a higher consumption rate in "rich" than in "poor" patches. Hence, by observing the foraging performance and success of conspecifics, individuals using ISI should estimate resources faster and better than uninformed individuals[26,35] (review in Ref. 21). Many examples involving fish, birds, or insects have confirmed these two predictions.[29,36,37]

Typically, experiments involve an observer individual that is given the opportunity to watch two groups of demonstrators simultaneously, one foraging on a "rich" and the other on a "poor" patch. Then, after removing the groups of "demonstrator" foragers, the observer is offered the choice to forage in the two patches system. The observer is expected to choose the "rich" patch more often than by chance. This classical design can then be expended to study the role of various effects such as personal information or the effect of demonstrators' group size. For instance, in nine-spined sticklebacks (*Pungitius pungitius*), Coolen *et al.*[38] manipulated both the number of demonstrators in each patch (two or six individuals) and food patch quality in two experiments. In the first experiment, the two groups of demonstrators were of different sizes. In the second experiment, both group size and patch quality differed. A two-fish group of demonstrators were feeding on a rich patch whereas a six-fish group was feeding on a poor patch simultaneously. In the first experiment, they found that observers spent significantly more time in the patch were six foraging fish were visible during the demonstration. In the second experiment, observers preferred the rich patch despite the fact that only two fishes were foraging there during the demonstration.[38] This elegant design allowed these authors to conclude that nine-spined sticklebacks preferably use the foraging success over group size when choosing a foraging patch.

Other experiments used a different approach by manipulating the accessibility of ISI. For instance, by hiding food at the bottom of a flat or a deep opaque cup, Templeton and Giraldeau made ISI available or not and showed that the socially foraging starlings

(*Sturnus vulgaris*) use public information only when it is easily available.[39]

Similar test have been performed at the interspecific level. For instance, Coolen *et al.*[29] investigated whether fish can exploit heterospecific ISI in a system of sister species with similar ecological requirements. They used the nine-spined sticklebacks and three-spined sticklebacks (*Gasterosteus aculeatus*). As in previous experiments, the experimental design involved a three compartments tank. All the borders of the compartments, but the middle one, were transparent. An observer fish from one species was placed in the central compartment from where it could observe two groups of three demonstrator heterospecific foraging fish in the other compartments. A feeder in each compartment provided bloodworms at different rates. One feeder ("the rich patch") provided three times more bloodworms per unit time than the other ("the poor patch"). Feeders were designed so that the observer fish could not see the food but only the feeding demonstrators. Therefore, the only clue to the observer was the foraging success. After 10 min of demonstration, demonstrators were removed and the observer was realized in the tank. Records included the proportion of observer fish first entering the rich patch and the proportion of time they spent in front of the feeders of the two patches over a 5 min period. They found that nine-spined stickleback, but not three-spined sticklebacks, entered the rich patch more often and spent more time in it. Altogether, these results show that individuals of some species can monitor the foraging behavior of heterospecifics and make decisions according to their performance. However, this study also shows that not all species (even closely related ones) use heterospecific ISI. Understanding how evolution has shaped such interspecific differences remains one of the main challenges of future studies on interspecific ISI use.

ISI and predation avoidance

Being eaten is one of the most common tragedies in nature. To avoid and limit predation risks, preys have evolved the ability to recognize cues of predators as well as to produce and recognize alarm signals. In general, preys reply to these signals by displaying clear antipredator behavior, such as hiding, decreasing feeding rate, flight, or increased vigilance (e.g., Refs. 40–43). By themselves, such unavoidable reactions constitute a valuable source of ISI about the current level of danger. Relying on such cues rather than on direct evaluation such as actual encounters with the predator may be particularly adaptive in preys with low escapement capacity. Although the role of ISI has been less studied in the context of the detection of danger than that of foraging, evidence exists in fish, birds, mammals, noncolonial insect (reviewed in Ref. 44) and even plants.[45] We detail a few exemplary studies, in fish, noncolonial insects, and birds.

Fish can learn danger from the reaction of others
In fish, prey can directly assess predation risks by detecting the chemical cues released from the skin cells of predators or by damaged preys.[46] Another strategy is to learn to recognize the predator by observing the response of others to the detection of danger. For instance, Ferrari *et al.*[47] investigated the ability of predator–naïve fathead minnows (*Pimephales promelas*) to learn to recognize an unknown predator, the brook charr (*Salvelinus fontinalis*). They first conditioned minnows to recognize the odor of brook charr and to associate this odor to danger. This was done by exposing minnows directly to various combinations of chemical cues. Then, using these conditioned individuals as demonstrators, they tested whether naïve minnows could be conditioned to recognize brook charr by watching the behavior of experienced conspecifics. To do so, they set pairs of tanks side by side, one with a naïve minnow (the observers) and the other with three tutors fishes (the previously conditioned demonstrators). Then the observer fish received charr odor whereas demonstrators received simultaneously skin extracts of conspecifics (a signal of danger) and charr odor. Observers were therefore watching a group of fish behaviorally responding to signal of dangers while they were receiving charr odor. After this conditioning protocol, they transferred the observer fish into a new tank in which they injected charr odor, and measured the behavioral response of the observer fish to the stimulus. They found that observers that had previously watched tutors responding to minnow skin extracts spent significantly less time moving and more time hiding under a shelter when exposed again to charr odor than nonconditioned naïve minnows,[47] so that the foraging success of the former fish was halved.[48] Minnows therefore socially learned about predation risks by associating the fright reactions of

conspecifics with a given cue (the smell of brook charr). As all studies of social learning, this constitutes a typical case of ISI use.

Social cues of danger in insects

Insect do also use ISI in various contexts. For example, in an elegant experiment, Isabelle Coolen *et al.*[49] tested whether uninformed wood crickets (*Nemobius sylvestris*) would detect and react to the behavior of other wood crickets that had detected the presence of spiders. Juvenile wood crickets tended to be less visible to a human observer at the surface of the forest floor's leaf litter when in the presence of predatory spiders. These authors found that these antipredatory behavioral changes were used by naïve crickets, which then remained hidden as if they had themselves encountered predatory spiders. In other words, wood crickets use ISI to learn about danger in the environment. A surprising result is that plants also use ISI in a very similar context. This will be developed in the eavesdropping section later.

Social detection of danger among passerine communities

A recent study showed that alarm calls are used interspecifically in an Australian community of passerines in which species practice a form of interspecific eavesdropping.[50] Experiments used playback and observations of natural alarm calling to study the interspecific use of aerial "hawk" alarms among three species of passerine, superb fairy-wrens (*Malurus cyaneus*), white-browed scrubwrens (*Sericornis frontalis*) as well as New Holland honeyeaters (*Phylidonyris novaehollandiae*). Superb fairy-wrens and white-browed scrubwrens are ecologically similar and can share mixed-species flocks, whereas New Holland honeyeaters are ecologically distinct and do not flock with the other species. They found that fairy-wrens and scrubwrens fled to cover to each other's alarm calls, but they also both fled to honeyeater alarms. Honeyeaters fled to scrubwren but usually not to fairy-wren alarms. These variations in interspecific eavesdropping on alarm calls directly depended on the reliability of the call for the eavesdropping species. The frequencies of natural alarm calls showed that New Holland honeyeaters called only to predators of all three species and so provided reliable information to all. From a honeyeater's perspective, superb fairy-wrens were

least reliable, as they gave 52% of their calls to nonpredators, whereas white-browed scrubwrens gave only 18% to nonpredators. However, from a scrubwren's perspective, fairy-wrens were largely reliable because most calls to nonpredators were to red wattlebirds (*Anthochaera carunculata*), which pose a physical threat to fairy-wrens and scrubwrens but not honeyeaters.[50] This study thus not only demonstrates interspecific eavesdropping on alarm calls in species that do not form multi species flocks, but also suggests an explanation to the observed variations in this behavior among species.

Understanding the role of social learning in predator avoidance has both evolutionary and applied implications.[44,51] For instance, socially acquired predator avoidance can help designing the prerelease antipredator training in programs of reintroduction of endangered species.[51] More generally, the many studies of contextual fear conditioning, which analyzes how animals learn to form conspecifics to avoid specific types of dangers,[52] have long demonstrated the generality of ISI use in the context of the detection of danger. However, despite the fact that these studies manipulate the fear reaction of conspecifics to a given (often benign) cue to study how this affects the behavior of naïve individuals, they are not usually placed in the context of ISI use.

ISI and habitat choice

For a long time, the study of habitat selection has been dominated by correlational approaches, with studies interpreting the distribution of individuals in the environment as evidence for habitat preferences. However, as often in science it is difficult to infer processes from the sole study of patterns. A given distribution may result from various mechanisms each with very different implications in terms of habitat choice.[53] Distributions result from habitat preferences, but also from the selection resulting from habitat suitability. For instance, imagine a plant spraying seeds randomly over the environment. Some will fall in favorable habitats, other in poor habitats. After a while, only those plants in good habitat will survive. Thus, although the distribution of plants certainly indicates habitat suitability, in the case of plants nobody would argue that plant distribution is evidence for habitat choices by seeds. More generally, the study of habitat choice cannot simply be based on the study

of patterns. Habitat selection usually comprises a decision-making process that necessarily involves information gathering and processing. Concepts of information are thus central to the study of habitat selection.

Correlational evidence

The idea that ISI may be an important source of information in breeding habitat selection was introduced in the context of habitat selection by several authors well before the term ISI was invented. Judith Stamps, for instance, suggested that the presence of conspecifics may reveal habitat quality and constitute a valuable source of information in breeding habitat choice.[54,55] All studies about conspecific attraction also implied ISI use (e.g., Meadows, 1972, 1156; Veen, 1977, 341; Kiester, 1979, 1503; Burger, 1988, 430; Shields, 1988, 1092; Stamps, 1988, 1109; Podolsky, 1989, 552; Gröndahl, 1989, 1504; Smith, 1990, 1111; Danchin, 1991, 994). Alternatively, animals may cue on the breeding success of conspecifics to select a breeding habitat.[56–61] In a cliff-nesting seabird for instance, the kittiwake (*Rissa tridactyla*), colonies that were less than 2 km apart showed contrasted demographic and behavioral patterns. On breeding cliffs where most pairs were successful, failed breeders showed high rates of attendance for the rest of the breeding season, long after they had lost their progeny. In contrast, on cliffs where most pairs were unsuccessful, failed breeders disappeared immediately from their nests and were often observed visiting other, more successful colonies where they eventually recruited in the following breeding season. A more in depth analysis[59] revealed that dispersal and settlement decisions were strongly related to the focal individual's own reproductive success, as well as to the average reproductive success of conspecifics on the focal individual's cliff. In other words, the mean breeding performance of other kittiwakes on a cliff significantly predicted dispersal and local recruitment of new breeders in the next breeding season. This was true even after controlling for the effect of individual reproductive success and other potentially confounding effects such as sex or year. Despite the fact they did not use the expression ISI, which was only coined several years later,[17] these authors proposed that the patch reproductive success (PRS) revealed local habitat quality and could thus be used by prospectors as a cue from which ISI could be extracted.

This interpretation was supported by the fact that juvenile kittiwakes and nonbreeders also prospect breeding colonies,[62] a behavior that allows them to gather ISI in order to choose their future breeding location.[63–65] This mechanism has later been called "Habitat Copying" because it leads prospectors to copy the habitat choice of successful conspecifics.[66] Both simple optimality,[67] and ESS models[68] confirmed that habitat copying is evolutionarily expected under most natural conditions at least in birds.

Experimental evidence

These studies, however, were purely correlational and it was necessary to perform experiments to demonstrate that prospecting animals do estimate patch habitat quality through the average PRS of conspecifics and use this information to choose their subsequent breeding site. The first experimental support for habitat copying was provided in a migratory passerine, the collared flycatcher (*Ficedula albicollis*) on Götland Island, Sweden, by manipulating the average reproductive success of entire woodlands.[69] To reduce the PRS of three plots and increase that of three others plots, chicks were transferred from nests of the reduced plots to those of the increased plots. Results clearly confirmed the hypothesis. For instance, more birds recruited in the woodlands where the PRS had been increased in the previous year than in controls, and more in controls that in plots where the PRS had been decreased. This demonstrated that individual flycatchers use the PRS of their conspecifics as a source of ISI for their dispersal and settlement decisions. Similar results were later obtained in the blue tit (*Cyanistes caeruleus*), a nonmigratory passerine.[70]

These results were extended to synchronously breeding birds that cannot obtain information about the number of young produced by neighbors but only the location of their nests. Nocera *et al.*, for instance, experimentally deployed decoys and song playbacks of breeding males to provide ISI in either suitable or suboptimal habitats during both pre- and postbreeding periods.[71] They monitored territory establishment during the subsequent breeding season for a social bird, the bobolink (*Dolichonyx oryzivorus*), and a more solitary species, Nelson's sharp-tailed sparrow (*Ammodramus nelsoni*). The more solitary sparrows did not use ISI but the more social bobolinks responded strongly to postbreeding

ISI irrespective of habitat quality. The following year, 17/20 suboptimal plots to which bobolink males recruited using the manipulated source of ISI were defended for at least two weeks. Interestingly, 16 recruited males were natal dispersers, as expected if ISI is used by individuals with little opportunity to sample their natal habitat quality directly.

The "habitat copying" hypothesis has been generalized to interspecific.[31] The "heterospecific habitat copying" hypothesis states that individuals of one species may use the performance of members of other species as a source of ISI to select a breeding site. This hypothesis has been tested in birds[34,72]. Particularly, early breeding resident species may constitute a valuable source of information for migratory bird species. For instance, Seppanen and Forsman[34] recently showed with a field experiment that two migrant flycatcher species (*Ficedula albicollis* and *F. hypoleuca*) use information from two resident tits species (*Parus major* and *C. caeruleus*) and can thus acquire an arbitrary preference for new breeding sites. They used pairs of nest boxes of which only one could be occupied by the territorial resident tits. They then painted a circle or a triangle at the entrance of the boxes, attributing always the same symbol to the occupied box. They then provided pairs of empty nest boxes with the two symbols to migratory flycatchers and found that they had developed a preference for the boxes with the symbol associated with tit occupation. Furthermore, they found that the preference for boxes of the right symbol increased from early-to-late arriving pairs. This trend may reveal the well known fact that early females are often older and less subject to social information than later and younger individuals.[34] Alternatively it may be because the proportion of occupied nest boxes with of the right symbol increased with time. This result constitutes one of the first experimental evidence that interspecific ISI use can be effective in the wild. Experiments are needed to test whether species can use heterospecific fitness components rather than the mere presence of heterospecifics to select breeding habitat. Although it is still early to set clear-cut conclusions, recent evidences suggest that this may well be the case.[31,72]

ISI use in brood parasites

A more recent development highlighting the importance of ISI use in fitness-affecting decisions was proposed in a study of the common goldeneye (*Bucephala clangula*), a cavity-nesting duck that has a significant level of intraspecific brood parasitism.[32] In that species, some females follow a mixed strategy that consists of laying eggs in their own nest while also laying supplementary eggs in neighboring nests of conspecifics. In previous experiments, Pöysä showed that parasitic females preferentially lay eggs in safe nest sites, implying that nest predation was an important ecological determinant of conspecific nest parasitism. In a subsequent experiment, he focused on the nature of the information used by parasitic females to decide where to lay their parasitic eggs. He found that female goldeneyes prospected active nest-sites at the end of the nesting season more frequently than nest-sites that did not have a nest in the current season. It further appeared that nest-sites that had been prospected more frequently by females in one year had a higher probability of being parasitized in the following breeding season. This suggests that parasitic females prospect active nests at the end of a breeding season and return to lay parasitic eggs in the formerly most successful ones. This enables brood parasites to target safe nests. These findings may create a new perspective for the study of the evolution and occurrence of conspecific brood parasitism. Such a mechanism has later been extended to obligate brood parasites such as cuckoos.[33]

ISI and dispersal

Dispersal (individual movement resulting in a change of social unit or habitat between the natal and the first breeding site or between two successive breeding sites) has often been thought as a way of achieving an Ideal Free Distribution (IFD).[73–75] One assumptions of the IFD is that individuals have a perfect knowledge of the position and quality of all the available patches. This implies that only species with the highest mobility or with no prospecting costs could possibly achieve it. Accordingly, predictions from IFD models were thus matched in many organisms from different taxa with a high mobility.[76,77] Species with a restricted mobility or with a restricted perceptual range were not expected to reach an IFD through dispersal. Although this might be true, species can expand their perceptual range by other ways than exploration. For instance, the phenotype of immigrants into a population may provide a source of information to resident

individuals about the quality and possibly the position and distance of their patch of origin.

This hypothesis was tested in the common lizard (*Lacerta vivipara*) where Cote and Clobert manipulated the density of the patch of origin of immigrants to a recipient population and measured the emigration from the recipient population resulting from the arrival of these immigrants.[78] Results demonstrated that the presence of immigrants increased emigration from the recipient population and that the density of the patch of origin of these immigrants also influenced the emigration from the recipient population. Interestingly, they further demonstrated that the information brought by the immigrant (through their phenotype[79,80]) was not used by all individuals of the recipient population in the same way as they found a significant interaction between resident phenotype and the density of the immigrants' patch of origin. A similar phenomenon has been recently found also in a ciliate (*Tetrahymena thermophila*, A. S. Chaine personal communication) and in a mite species (*Sancassania berlesei*, T. G. Benton personal communication). This illustrates that ISI can take multiple forms, and suggests how elaborate active information delivery about food patch location and distance such as in bees may have evolved from the use of phenotypic characteristics of conspecifics (here spatial components of individual history) as a source of ISI.

ISI and mate choice

Mate choice is a crucial decision for all sexually reproducing organisms. The literature on mate choice mainly focuses on intentional information carried by secondary sexual signals. However, several approaches focusing on the nature of the information that is used in mate choice have underlined that ISI may also play prominent roles in mate choice. Two complementary approaches have been proposed, mate choice copying and eavesdropping. They both raise interesting questions about the very nature of ISI that we will tackle at the end of this section.

Mate choice copying

Mate choice copying is hypothesized to provide time constrained or inexperienced individuals with a mean to increase the efficiency of their mate choices by copying the mate choices of more experienced or less time constrained conspecifics. This idea emerged in the late 1980s to explain the strong

skew in male mating success in avian lekking species. Convincing experiments were later developed in the 1990s and produced support in favor of this mechanism in several animal taxa.

Mate copying experiments in fish usually use compartmented tanks. These experiments are conducted in three sequential steps. In the pretest, the natural preference of an observer female relative to the two male phenotypes is measured. In the demonstration, the same observer female is placed in a transparent glass tub in the center of the tank that prevents her from interacting with the males. Two demonstrator females are placed in compartments adjacent to each male but opaque partitions allow the observing female to see both males but only one of the demonstrator females. Seeing a female with a male is supposed to provide the observer female with the information that it is more attractive to other females than the other male. This is because another female apparently chose him. In the posttest, the demonstrator females are removed, and the observer female is released so that her preference can be tested again in the same situation as in the pretest.

Such an experiment in the sailfin molly (*Poecilia latipinna*) clearly showed that providing ISI to females strongly influences their future mate preferences.[81] Similar results were found in the Japanese quail (*Coturnix coturnix japonica*) by Galef and colleagues. They showed that one could use such a design to create female preference for artificially produced traits, such as a red or blue patch on the male's body.[82] This was rather unexpected because models of the evolution of male traits and female preference often assume that variation in mating preferences is mainly due to variation in genes that emerged either in the context of mate choice or that was previously selected in another context such as foraging.[83]

A recent experiment showed that even the fruit fly *Drosophila melanogaster* can perform mate copying.[84] In a first step, when offered the choice between males dusted with green or pink powder, observer females did not show any copulation preference for one of the two male types. However, preferences emerged after observing demonstrations of a green (or pink) male being accepted by a virgin demonstrator female followed by a pink (or green) male being rejected by another recently mated (and thus reluctant) demonstrator female. Then, when offered the choice between a green and a pink male, observer

females copulated preferentially with the male type they had seen being accepted. That result is particularly surprising because it reveals that female *Drosophila* can extract from the demonstration the general rule of "prefer green (or pink) over pink (or green) males." This is what is usually called stimulus generalization, which constitutes a relatively complex task for an animal with such a small brain.

By focusing on the information used by females in building their mating preferences, mate choice copying shows that contrary to what is usually assumed, variation in sexual preferences is not under the sole control of genes. It is however likely that the capacity to copy other females is at least partly under genetic control. This discovery is likely to drastically change our perception of sexual selection and in particular the evolution of mating preferences, secondary sexual characters and sexual selection-based speciation.

Eavesdropping

Eavesdropping is the other form of ISI use in a mate choice context. The experiments on mate copying show that females use ISI produced by other females to choose mates. Several studies revealed that females also observe male–male interactions to obtain information about their relative qualities. This has been termed eavesdropping by Peter McGregor[85] because eavesdroppers extract information from observing interacting individuals without being involved in the interaction themselves. By eavesdropping on the interactions of others, animals can thus gather valuable information about interacting conspecifics. Females, for instance, may learn that one male is a winner whereas the other is a looser. Evidence for eavesdropping mainly comes from a few situations involving birds, lizard,[86] and fish but also plants in the context of detection of danger.[45]

For instance, female birds eavesdrop on song competitions between neighboring males[85] and obtain extra-pair fertilizations from the winning singer.[87–89] Interactive song broadcasting (i.e., song playback) to engage territorial male black-capped chickadees (*Podecile atricapilla*) in countersinging interactions showed that high-ranking males that lost song contests with a simulated intruder lost paternity more often than those that received a playback simulating a submissive intruder. In other words, females paired with high-ranking males that lost the simulated playback intrusions somehow

were informed that their male lost and hence behaved as if they were paired with a low-ranking male. Only two short playback sessions were sufficient to alter females' perceptions of their mates' status in high-ranking, but not low-ranking males. Information available through eavesdropping therefore may play an important role in female assessment of male quality.

Eavesdropping is also suggested by the behavior of female fighting fish (*Betta splendens*) that prefer to mate with winners after witnessing the outcome of a male–male contest.[90–92] Females that had observed fights between two males preferred the winner whereas females that had not seen the fights showed no preference.[93]

The notion of eavesdropping has been applied to two interesting situations. The first one concerns detection of danger in plants. When hurt by herbivores, plant release airborne molecules that can be sensed by untouched neighboring wild tobacco (*Nicotiana attenuate*) plants that react by strongly increasing the number of seeds they produce.[45] This behavior may be adaptive because strong predation in the environment may mean diminished competition, hence the interest in producing many offspring. Alternatively, this reproductive strategy may be adaptive because high predation diminishes the chances of surviving until reproduction. However, Karban *et al.*[45] only document changes in the intensity of reproduction, suggesting that there may not be any detectable acceleration of reproduction.

The second application of eavesdropping is in the context of obligate brood parasites (which always lay their eggs in nests of other species). Obligate brood parasites may also eavesdrop on the within pair interactions of their potential hosts to detect individual host pairs that are likely to be the best parents for their parasitic offspring. In many species where males participate in raising the brood, male sexual signaling is likely to reveal paternal quality. Thus, in these species, sexual signals probably broadcast paternal ability to feed the offspring, which attracts females. This information may thus be parasitized by brood parasites, which are essentially parasitizing parental care. Thus, a brood parasite able to eavesdrop on the sexual signaling of host pairs to choose hosts with the highest parental ability would be favored by natural selection. The consequence is that the selective pressure resulting from brood parasites may change the balance of cost and benefits

of sexual signaling in host populations. Parejo and Avilés reviewed evidence for this hypothesis[33] and found evidence for benefits linked to host selection by avian brood parasites. One of the reviewed studies reported on the attenuation of a sexual ornament in host populations under strong pressure by brood parasites. Such attenuation would be expected if brood parasites eavesdrop on sexual signals. It is interesting to see how adopting an information centered approach, Parejo and Avilés reinterpreted previous findings in a way that changes the functioning of host–parasite interaction. In fact, brood parasites not only tend to parasite species with flashy sexual ornaments as previously suggested, but within such species they tend to parasitize those pairs with the flashiest ornaments or behavior because they are likely to be the best parents for their offspring. To our knowledge this hypothesis has not been tested experimentally yet.

Inadvertent versus intentional information
The study of the role of ISI in mate choice raises interesting questions about the limit between inadvertent and intentional information. In eavesdropping for instance, while fighting males are intentionally producing signals to their opponent, females have evolved the capacity to exploit these signals as a source of information for their own benefit. The signals emitted by the fighting males are public and thus are a form of public information. However, from the eavesdropper's point of view, these signals can be considered as a source of ISI as fighting signals have not evolved primarily to inform eavesdroppers (the same reasoning holds for the brood parasites example). Two kinds of information therefore coexist in eavesdropping: (1) signals to competitors or potential mates and (2) these same signals are exploited by unintended females as ISI.

However, the situation may be more complex than that because it has been shown that the detected presence of a female audience, but not that of a male audience, increases the fighting rates of males.[94] This audience effect suggests that eavesdropping may entail a transition from ISI to signals because ordinary behaviors that did not evolve as signals may subsequently be modified by the audience effect.[24] Thus, ISI may be viewed in some contexts as the platform from which signals evolve, and the eavedropping situation may reveal a transition between these two types of information use.

This shows that the limits between inadvertent and intentional information are note necessarily clear (as indicated by the dotted arrow linking these two boxes in Fig. 1).

ISI: implications for ecological interaction

In natural settings, information use can generate specific dynamics. For instance, genes and gene expression modify phenotypes in long- or short-lasting ways.[95] Several recent studies have shown that, even if subtle, phenotypic changes can have strong effects on community and ecosystem properties.[96,97] This means that genetic or genomic information can flow across components of an ecosystem through indirect interactions (or cascading effects) and affect the dynamics of these systems. We can expect similar information dynamics when phenotypic changes result from ISI use. The goal of this section is to build on the previous sections to discuss how ISI can affect the ecological dynamics of populations, communities, and ecosystems. In other words, to what extent ISI use can be important for ecological theories.

Consequences of ISI use at the population level
At the population level, the concept of informed dispersal into landscape ecology is likely to change our view about the functioning of metapopulations and fragmented populations.[65,98] Up to recently, dispersal had mainly been seen as a fixed trait and individuals as molecules passively distributing themselves into the landscape.[77,99,100] The rapidly accruing evidence for condition-dependent habitat choices[65,101] and dispersal has profoundly changed this view. Individuals were shown to use many types of cues in this context. However, social cues and in particular ISI appear to be of paramount importance. Cues may be about kin, neighbors, or unfamiliar individuals and shape dispersal decision during every stage from early development to adulthood.[98,102]

In this context, it is worth noting that ISI use can stabilize or destabilize the spatial dynamics of a population. For example, basing dispersal solely on the occurrence of immigrants stabilizes exchanges among populations and help reaching the IFD.[103,104] However, it will reduce colonization rates, thereby enhancing risks of extinction of the whole system.

On the other hand, a strategy only based on the presence of kin induces the departure of individuals even at low population density, enhancing the risk of a local extinction.[103,104] However, this strategy increases chances of colonization events[103,104] thus deeply affecting population dynamics and invasive processes.[98,105] ISI coming from other conspecifics can stabilize or destabilize population dynamics according to whether the presence of conspecifics reveals habitat quality or competition.[98,106] Furthermore, the interaction among social sources of information[98,106,107] can generate "information dynamics" driving spatial ecological dynamics. The theoretical unraveling of connections between dispersal, individual personalities and social information are only in their infancy, but they are central to our understanding of the functioning of fragmented populations especially in the context of global change.

Consequences of ISI use at the community level

At the community level, heterospecific ISI use among species sharing ecological requirements could also have unconventional consequences. Interspecific ISI use may for instance facilitate species coexistence thereby affecting the entire community dynamics. An exciting avenue about interspecific ISI use concerns the functional convergence (i.e., the role a species has in an ecosystem) that may arise when social information about the environment propagates among competing species.[20] For instance, the example provided above about tits and flycatchers show that the noninformed flycatcher converges toward the same breeding site preferences as the informant tits.[34] This new form of functional convergence provides a new potential mechanism of species coexistence, which should be considered in future studies.

Consequences of ISI use at the ecosystem level

ISI use can further affect the functioning of ecosystems when at least two species from two different trophic levels are involved. There are to our knowledge no studies that have considered simultaneously the consequences of ISI use on two (or more) trophic levels. However, ISI use has now been demonstrated in plant–pollinators interactions, where the reproductive dynamic of the plant strongly depends upon the feeding habits of the consumer.

An example is that of the social transmission of nectar-robbing behavior.[108] Nectar robbing occurs when insects either bite through the base of a flower to "steal" nectar or use robbing holes made by others.[108] Leadbeater and Chittka[108] demonstrated experimentally that the robbing behavior of bumblebees (*Bombus terrestris*) can be partially transmitted to naïve individuals through ISI. A second example documents ISI use in pollinating bumble-bees exploiting two kinds of artificial flowers (i.e., rewarding flowers with nectar, deceptive flowers providing only water) in a foraging area.[37] Naïve bees were released in the arena with or without a demonstrator conspecific that had been previously trained to forage on the rewarding flowers.[37] Results showed that naïve bees foraged more often on rewarding flowers in the presence of a demonstrator. This result was however only found when flowers were distributed patchily as opposed to randomly. This suggests that bumble-bees use ISI but that this behavior is adaptive only when resources are distributed patchily.[37]

Altogether, these two studies suggest that the reproductive dynamic of one trophic level (the flowers) may depend upon the ability of the next trophic level (the pollinator) to use ISI. Particularly, in the second example, the efficiency of naïve bees in pollinating deceptive flowers was lowered in the patchy flower distribution, a situation when bees rely on ISI.[37] This result may explain why in natural systems deceptive flowers (e.g., Orchidacea) often mimic rewarding flowers and are never found in patches. Hence, by learning to avoid deceptive flowers, pollinators could strikingly affect the biomass and composition of floral communities.

It is clear that we still dramatically lack of data on the consequences of ISI use on multiple trophic systems. The earlier examples suggest that the use of intra- and interspecific ISI in natural systems is likely to be far more common than previously believed. Even host–parasite interactions are likely to be affected by ISI use,[109] suggesting that the ISI framework could improve our understanding of host–parasite interactions. More generally, the major role of parasite in structuring food webs and ecosystems,[110–112] suggests that adopting an information-driven approach to ecology and evolution may profoundly affect our understanding of ecosystem functioning and dynamics.

ISI: applications in conservation biology

We now explore some of the potential applications of an information-driven approach to ecology and evolution. We first want to illustrate how this can help in conserving threatened species, a field sometimes called behavioral conservation. In doing so, we further focus on the importance of ISI for conservation biology.

ISI about potential mates and breeding programs in zoos

Breeding programs in zoos are notorious for their high cost. Zoos are sending males of endangered species across the planet to mate with females with the hope of boosting captive breeding. Too often these costly practices are surprisingly unsuccessful. In this context, it is striking to see that the literature on captive breeding rarely considers the role of choice processes and are never placed within the framework of sexual selection.[113,114] For instance, a rapid check of the Web of Knowledge with the keywords "Captive breeding" and "Zoo*" produced 252 hits. When adding the term "behavio*" this number dropped down to 85 hits. Replacing the word "Behavio*" by "sexual behavio*" produced only 10 hits. Among these 10 hits none actually dealt with theories about mating systems or strategies of mate choice. This underlines the lack of communication between conservation biology and behavioral ecology. The absence of behavioral ecology theory in the framework of captive breeding is particularly striking in view of the fact that several books and papers were published linking behavioral ecology to conservation biology.[113,115] Here we argue that adopting an information-driven approach to behavior may greatly help increasing the efficiency of captive breeding programs.

For practical reasons, captive breeding programs ignore the type of mating system of the species under concern.[116] It is clear that in nature females usually can choose among several, and often many, males and copulate only with one of them. In zoos, females are usually presented one, rarely two males, never more, implying that in fact they have no real choice. This may raise real problems of sexual stimulation in most mating systems, and even more in some species such as lekking species, where females have been selected to visit many males in a short period of time before choosing one. It is

clear that such situations are often impossible to recreate in zoos. However, the literature about mate choice copying has shown that videos of copulating males may be enough to stimulate females.[117] This has been beautifully illustrated by Galef's group in Japanese quails in which video and live demonstrations have similar effects on mating preferences (references in 25 and 118). Mate choice copying is also exemplar as it shows that females of species as varied as birds, fishes, and insects can be manipulated to prefer a given male or a given type of male.

As a consequence, one could imagine a new and much cheaper captive breeding design in which the target female first receives social information about various males from zoos of all over the world in the form of videos in which only one male, the one that we plan to bring to her, successfully manage to copulate with females. This should increase her preference toward that specific male, so that when she is offered that male, she might be more willing to copulate with it (Susana A.M. Varela, personal communication). We may also use eavesdropping to further enhance the target female's preference for that male by showing her videos of that male wining fights with other males. Furthermore, Japanese quail females fertilize a higher proportion of their eggs when randomly assigned to copulate with their preferred male.[119] An amazing result is that this effect on egg fertilization rate is also affected by social information, which not only can inverse the observer female's copulation preference but also the fertilization rate of eggs. For instance, when the observer female naturally prefers male A and fertilizes more eggs after copulating with him, after receiving ISI suggesting that male B is more successful with other females, she changes her preference for male B and fertilizes more of male B's eggs.[119] So the earlier protocol may not only boost copulation but also fertilization. Finally, the literature on mate choice and parental investment shows that females of many species invest much more in their progeny when they are mated with attractive males. For instance, in the highly managed Houbara bustard (*Chlamydotis undulata undulata*), females watching male sexual displays invest more in their progeny, which leads to higher hatching success and improves offspring growth (Adenine Loyau, personal communication). So the transposition of the mate choice copying and eavesdropping designs to captive breeding may not

only boost copulation and fertilization but may also lead females to invest more in their progeny, which should increase the chances of the progeny to survive to adulthood.

We suggest that this kind of protocol may be applied to test whether it boosts captive breeding success. If successful this captive breeding design would probably allow us to save some of the many endangered species for which captive breeding is the only solution because the only remaining populations are in zoos. This would constitute an example of how insights from an information-driven approach to ecology and evolution may help solving the biodiversity crisis.

More generally ignoring natural processes of choice may lead to unsuccessful conservation actions. More and more studies underline the importance of genetic compatibility between mates.[116,120,121] Females may thus refuse to mate with a given male for a number of genetic, physiological, and behavioral reasons. Even if we manage to increase copulation rates in zoos, offspring may still have poor viability due to problems of incompatibility between mates, leading to poor immune defense or differential parental investment. For instance, studies have demonstrated more than 15 years ago how, even in humans, mating preferences may be influenced by subtle and unsuspected parameters such as the genetic compatibility at the Major Histocompatibility Complex loci.[122,123] This may imply that in the earlier suggested captive breeding design we need to first genotype individuals for important loci such as MHC to choose the male that we bring to a female according to its genetic compatibility with that female. Several supplemental breeding programs have used this kind of approach to maximize the general genetic diversity within the managed population.[120] We are not aware, however, of situations when this has been applied to specific loci such as MHC.

ISI and Allee effects

Small-sized populations are not only prone to extinction due to demographic stochasticity in the age and sex structure,[124–127] but because decreasing density also negatively impacts individual fitness for social reasons, which further increases extinction probability, a mechanism known as the Allee effect. The Allee effect might be caused by several

mechanisms, including the difficulty of finding an appropriate mate, the absence of familiar neighbors (thus increasing fights and decreasing benefits from cooperation), and the fact that low density may be used as a cue revealing low habitat quality (review in Refs. 113, 128, and 129).

The absence of social stimulation has often been seen as a major threat for captive populations. In this context, mate and habitat copying demonstrate that social information plays a prominent role as sources of information and stimulation that are necessary for the onset of reproduction in natural populations. Mate and habitat copying are probably the most important forms of ISI use at play in Allee effects when social interactions diminish below a certain threshold. For example, habitat choice may be impacted because individuals perceive low density as revealing habitats of bad quality.[78,106] In the same way, the lack of social interactions decreases the ability of individuals to evaluate other individuals' quality, thereby increasing the risks of choosing an inappropriate mate or engaging into inappropriate fights or cooperation. All these effects of low density might bring the species/population into an extinction vortex by decreasing fitness, thus accelerating the decrease in population size. Manipulating ISI in this context might be an efficient tool to change the fate of these populations. It can also be of interest in reintroduction programs whenever transplanted individuals' settlement and site fidelity affects the reproductive success of the reintroduction. For example, painting rocks with individuals dropping has proved to increase settlement in targeted locations in the griffon vulture.[130,131] In small-sized populations, play back of interacting individuals or decoys have been proved to help changing the view resident individuals have of the quality of their own population (review in Refs. 53 and 132–135). Such actions have been too rarely attempted in conservation.

What does an information-driven approach contribute to conservation biology?

Here, we further discuss the insights that may be obtained from analyzing conservation issues from an information perspective. Complementary considerations can be found in Refs. 113, 115, 129, and 136–145.

The many examples developed in this review show how an information-driven approach to

ecology and evolution naturally brings a perspective centered on the individuals and shows how their selfish interests often clash with those of the population to which they belong. The few studies that have explicitly studied the links between behavior and population dynamics suggest that accounting for variations in different strategies within populations may profoundly change evolutionary dynamics (e.g., Refs. 68, 74, and 146).

Historically, concepts of information and hence behavioral ecology have been almost completely neglected by conservationists that have more easily used contributions from population genetics and demography. These two disciplines are based on means, frequencies, and (at best) population variances rather than on individual characteristics. However, populations are made up of individuals whose varying properties determine the properties of the population.[147] The widespread occurrence of polymorphism essentially results from differences in the information (be it genetic or nongenetic) possessed by individuals. Being defined as the evolutionary approach using individual organisms as units of selection, behavioral ecology naturally studies phenotypic variation and thus contributes an individual-centered approach to conservation. It has sometimes provided counter-intuitive solutions to conservation problems (the best example is that of the kakapo[148–151]).

More generally, we think that conservation biology should assume the existence of polymorphisms in populations and incorporate the possibility of an interaction between ISI use and polymorphism. We think that this information centered approach is the major original contribution of behavioral ecology to conservation biology. Furthermore, the earlier example of mate choice in captive breeding illustrates how accounting for theories of behavioral ecology may help designing solutions to save particularly endangered species, which should help lessening the biodiversity crisis. The conclusion is that many conservation efforts may be at best inefficient if they do not rely on the host of concepts, theories, and mechanisms that have been proposed within the framework of natural and sexual selection. As a matter of fact, adaptations have evolved specifically to ensure the survival of individuals as well as the production of viable offspring. Ignoring the evolutionary origin of these adaptations may put overall conservation efforts at risk.

Conclusion

Our review first highlights the importance of public information and more specifically ISI in many ecologically and evolutionary relevant individual decisions. These include fitness-affecting decisions such as foraging, habitat, and mate choice, predator avoidance, or dispersal. Second, we suggest that, although literature is still scant, such individual decisions have the potential to strongly affect the ecological dynamics of all higher biological levels of organization, from populations to ecosystems. Previous authors have claimed that interindividual variation within populations needs to be taken into account to understand the functioning of ecosystems.[97,152] Along with these authors, we call for more studies about the consequences of ISI use on population and ecosystem dynamics. In particular, we must consider explicitly the various sources of information that make every individual functionally unique within an ecosystem. We believe the concepts of public and ISI should become major themes in ecology in the future (Fig. 2) and applying an information-driven approach from genes to ecosystems will produce unexpected outputs and shed new lights on the major role of information flows in the ecological and evolutionary functioning of natural systems.

Third, we develop how ISI can be applied to the conservation of endangered species, a major challenge of humanity. In this context, our review shows that we cannot necessarily apply the same treatment to all individuals. The conservation implications of ISI remain largely unexplored. We are convinced that new ideas such as those developed here (mate choice copying and captive breeding, ISI, and Allee effects) will soon arise. More generally, we believe that conservation actions must be rooted in the scientific knowledge of ecological and evolutionary processes to save species from certain extinction.[115,116,120] We urge evolutionary ecologists to transfer their discoveries to conservationists. A failure to do so may increase the risks of massive extinctions in spite of considerable efforts from our societies. Conservation measures are often adopted when the crisis is already critical, and conservationists can therefore not afford to commit errors. We therefore call for more integration between theory- and application-driven approaches. We hope that this review will help bridging this gap.

In conclusion, beyond reviewing the evidence for the role and consequences of the inadvertent component of public information, our main goals in this review was to show how every ecological and evolutionary, as well as conservation approach can benefit from adopting an information-driven approach.[25] We believe that the study of ecological and evolutionary processes would greatly benefit from the reformulation of our questionings in terms of information flows. In other words, we advocate that concepts of information are central to ecology and evolution.

Conflicts of interest

The authors declare no conflicts of interest.

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