

SOCIAL-INFORMATION USE IN HETEROGENEOUS LANDSCAPES: A PROSPECTUS

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Abstract. The use of social information has recently been documented in a wide variety of animals, with potentially diverse consequences for those living in heterogeneous landscapes. Here we review and synthesize investigations on the use of social information in heterogeneous landscapes and provide a conceptual framework for interpreting the role social information plays for birds living in human-modified landscapes. Our framework emphasizes the spatial components of the availability and value of social information and how landscape change can alter the availability and perceived value of social information to individuals. As an example of the utility of an information-based perspective, we discuss investigations of habitat use by the Bobolink (*Dolichonyx oryzivorus*) in agricultural landscapes. Overall, work to date provides unique insight into the importance of social-information use at large scales but also underscores that much uncertainty remains regarding the role of social information in driving distributions and dynamics across landscapes.

Key words: connectivity, conspecific attraction, habitat loss, habitat fragmentation, inadvertent social information, landscape ecology, patch size, public information

Uso de Información Social en Paisajes Heterogéneos: Un Prospecto

Resumen. El uso de información social ha sido documentado recientemente en una amplia variedad de animales, con diversas consecuencias potenciales para aquellos que habitan paisajes heterogéneos. Aquí revisamos y sintetizamos investigaciones sobre el uso de información social en paisajes heterogéneos y brindamos un marco conceptual para interpretar el rol que juega la información social para las aves que viven en ambientes modificados por el hombre. Nuestro marco enfatiza los componentes espaciales de la disponibilidad y valor de la información social y como los cambios en el paisaje pueden alterar la disponibilidad y el valor percibido de la información social por los individuos. Como ejemplo de la utilidad de una perspectiva basada en la información, comentamos investigaciones de uso de hábitat por parte de *Dolichonyx oryzivorus* en paisajes agrícolas. De modo general, el trabajo disponible al momento brinda claves únicas sobre la importancia del uso social de la información a grandes escalas, pero también subestima la gran incertidumbre que aún existe acerca del rol de la información social en las distribuciones y las dinámicas que se observan a través de los paisajes.

INTRODUCTION

To understand and predict the distribution and abundance of organisms, ecologists and conservation biologists rely increasingly upon landscape perspectives. This focus is illustrated with a wealth of avian research that has played a central role in our knowledge of how landscape heterogeneity influences animal distributions, population dynamics, and community structure (e.g., Gates and Gysel 1978, Robbins et al. 1989, Robinson et al. 1995, Rodewald and Yahner 2001, Ferraz et al. 2007). Most of this research has emphasized variation in structural measures of landscapes (i.e., physical attributes reflecting the amount and configuration of habitats) and how such variation can influence avian distributions and dynamics.

A behavioral perspective can provide novel insights for interpreting large-scale patterns of avian distribution and abundance. Indeed, much of the focus of avian landscape ecology centers either implicitly or explicitly on habitat selection, a spatially oriented decision-making process based in behavior. Other concepts, such as variation in species interactions, distribution patterns like “edge avoidance” and “area sensitivity,” and movement through corridors, can emerge from individuals’ decision-making. As a consequence, a behavioral perspective for landscape ecology could provide a rich view into the effects of continuing landscape change, as well as a more refined perspective on large-scale modeling (Lima and Zollner 1996, Bélisle 2005). For instance, many large-scale models contain little to no information on the behavioral process of dispersal (Lima and Zollner 1996), even though how animals make decisions

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regarding movement and dispersal can have major implications for population dynamics (Wiegand et al. 1999, Revilla et al. 2004, Armsworth and Roughgarden 2005).

Decision-making by individuals can benefit from the acquisition and use of information (Danchin et al. 2008). Information is often valuable to guide decision-making because information may reduce uncertainty in potential outcomes, thereby potentially allowing a more adaptive response (Dall 2005, Danchin et al. 2005). Animals use a variety of sources of information in decision-making, including both personal and social information (Danchin et al. 2004, Dall et al. 2005). Personal information is typically defined as information acquired through direct interactions with the environment, whereas social information is any information acquired by observing the behavior of other individuals, including signals and inadvertent cues regarding the location or performance of other individuals of the same or different species. For example, when birds use a win-stay lose-switch rule for nest-site selection (Schmidt 2001), this rule is based on personal information acquired through previous breeding efforts. In contrast, when birds use conspecific attraction (Ward and Schlossberg 2004), this behavior is driven by the presence of conspecifics, or conspecific social information.

Here, we aim to connect the seemingly disparate topics of avian landscape ecology and information-based perspectives from behavioral ecology to provide insights into the developing field of behavioral landscape ecology. To do so, we provide a general framework for interpreting information use in heterogeneous landscapes by identifying the spatio-temporal nature of information availability and value, and how landscape structure can alter these characteristics. Throughout, we draw from relevant theoretical and empirical work on birds in both information ecology and landscape ecology to develop this framework. Because the interplay of social-information use and landscape ecology is just beginning to receive treatment from ecologists and conservation biologists, we emphasize that much of our discussion should be treated as working hypotheses. As a case study, we review investigations of habitat use by the Bobolink (*Dolichonyx oryzivorus*) in agricultural landscapes and how an information perspective provides new insight on the Bobolink's distribution.

A FRAMEWORK FOR SOCIAL-INFORMATION USE IN LANDSCAPES

Our framework rests on the idea that the use of social information is mediated through both the availability of information and its perceived value. We define *information availability* as the accessibility of information to an individual (cf. Johnson 1980). Importantly, information is acquired through cues in the environment; such cues must be available for information to be obtainable. Cues become information only if an animal can recognize and interpret some facts regarding the cue(s) that are relevant to decision-making (Danchin et al. 2008). Interpretation of facts may be as simple as recognizing that a conspecific is

present, affecting the decision to settle (e.g., as in habitat copying), or more complex, such as assessing the relative quality of a habitat via cues regarding offspring quality (Doligez et al. 2002). Following Gould (1974) and Stephens (1989), we define *information value* as an animal's gain in fitness from using information over its fitness if it does not use the information (i.e., changes in a so-called "pay-off" function). We emphasize that in our framework for information use, we focus on the perceived value, rather than the actual value, of information (Sieving et al. 2010). Such a distinction will be necessary for interpreting the likelihood of information use in human-modified landscapes (see Landscape Effects on Information Value). Taken together, our framework emphasizes that *the likelihood of information being used is a function of its perceived value, conditional on the availability of information to an individual*.

In developing a framework for social-information use in landscapes, acknowledging that the source, or type (sensu Fletcher and Miller 2008), of information can vary both in value and availability will be critical. Social information can be gleaned from numerous sources, such as from conspecific or heterospecific social cues reflecting the location of resources, cues reflecting the quality of the resource(s) (e.g., conspecific reproductive success), or from signals reflecting intentional communication between a sender and receiver (Danchin et al. 2004). Some forms of social information, such as performance-based cues, may have great value in reducing uncertainty but might be used infrequently because of limited availability in space and time (Doligez et al. 2002). Other information, such as the mere presence of conspecifics or heterospecifics, may have less value in indicating resource quality but might be used more often because of the easy access to such information (Doligez et al. 2004, Nocera et al. 2006, Fletcher and Miller 2008).

To link information use to heterogeneous landscapes, we (1) identify the spatial nature of information and (2) identify how landscape heterogeneity (hereafter, landscape effects) likely mediates the availability and value of information. Furthermore, we highlight how spatial aspects of information vary with the type of information, which may alter the likelihood of a bird using one information source over another. These issues can operate at different scales commonly addressed in studies of landscape ecology, including within a patch, between patches, and still larger landscape scales. While temporal aspects of information availability and value are also crucial for interpreting information use (Doligez et al. 2003, Seppänen et al. 2007, Fletcher and Miller 2008), here we focus primarily on spatial issues.

INFORMATION IN SPACE

Availability. Even in entirely homogeneous environments, the availability of social information relative to other information depends on how the *perceptual range* of different cues varies. Perceptual range has been defined as "the distance from which a particular landscape element can be perceived as such (or detected) by a given animal. An animal's perceptual range

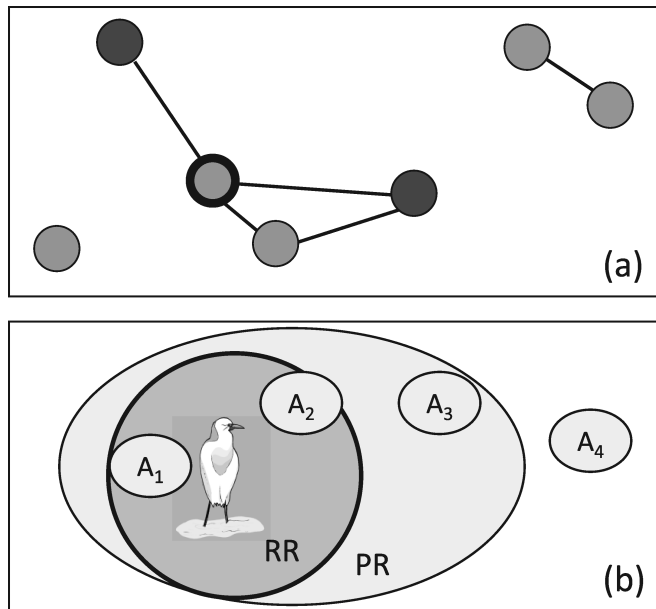


FIGURE 1. (a) If social cues (e.g., song) are available at spatial scales different from those of vegetation cues, through variation in the perceptual range of different cues, the functional connectivity of landscapes will change. In this example, a graph-theoretic diagram depicting connectivity, the focal node in bold is equidistant from the two left nodes, yet it is connected only to the node containing social cues (black node), which might increase the threshold distance via an increase in the spatial range of response. (b) In practice, estimating the perceptual range of a cue is limited by the response range. In this example, the egret can detect the presence of three conspecifics foraging (A_{1-3}) within its perceptual range (PR). But today, the egret is likely to hunt for prey only on the basis of cues given by A_1 and A_2 from within its foraging patch. This defines a response range (RR) smaller than the perceptual range. In the future, the egret may hunt in the location of A_3 , on the basis of this current detection only (filing the information in memory; i.e., using prior information).

represents its *informational window* onto the greater landscape” (Lima and Zollner 1996; the italics are ours). We extend this definition to include any source of information. For example, in many instances, the perceptual range of auditory cues likely differs from that of visual cues. Such variation in the spatial extent of perception of cues will undoubtedly play an important role in a number of landscape issues, such as estimating functional connectivity for organisms (Fig. 1a). If social information attained through conspecific or heterospecific song is available at spatial scales different from those of visual cues, estimates of functional connectivity that rely entirely on structural features might be biased. While this is certainly possible, to date there have been no tests with birds to address this question. Swanson et al. (2007) reported an experiment that tested the range at which of American toads (*Bufo americanus*) and Cope’s gray treefrogs (*Hyla chrysoscelis*) perceive conspecific calls but did not contrast these estimates with the distance at which the animals perceive other cues.

In practice, estimating the true perceptual range of information cues can be difficult to ascertain relative to what we term an individual’s *response range* (Fig. 1b). Response ranges are effectively what is often measured in studies of perceptual range (e.g., Zollner 2000); the response range is the distance from which an organism alters its behavior in response to a cue. In many situations, an organism may perceive a cue from a greater distance but chooses not to respond to the cue, because of other conflicting demands or because other, closer cues have a greater probability of being used (because they have greater value; see below). Playback experiments, for example, often reveal response ranges smaller than perceptual ranges when stimuli are played to test subjects known to be within hearing range (e.g., Sieving et al. 2000, 2004).

When social information is used in decision-making, its availability in space can have novel effects because social cues will invariably become aggregated. When animals use social cues as a positive proximate stimulus in decisions to move, forage, or settle, individuals will aggregate (Turchin 1989, Beauchamp et al. 1997, Doligez et al. 2003). These aggregations will subsequently alter the availability of social cues in space. This dynamic aggregation of information availability can have major consequences on a species’ distribution when resource distribution varies across a heterogeneous landscape (see Landscape Effects on Information Availability).

Finally, the spatial distribution of social information can be driven by variation in community structure when individuals use heterospecific social information in decision-making. For example, Pied Flycatchers (*Ficedula hypoleuca*) use heterospecific social information from resident titmice (*Parus* spp.) as a positive proximate stimulus in habitat selection (Forsman et al. 1998, 2002). Similar patterns of titmice being used as positive cues for settlement have been documented with other migratory birds in North America and northern Europe (Mönkkönen et al. 1990, 1997). As a consequence, any spatial variation in the distribution of titmice will alter the spatial availability of these cues to other community members. Thus, when heterospecific social information is used, variation in one species’ distribution can alter the decisions of other species, including small-scale movements (Sieving et al. 2004), responses to predators (Langham et al. 2006), or larger-scale habitat selection (Forsman et al. 2002, Fletcher 2008).

Value. The value of information is also thought to change over space, such that even if information is available at great distances, that information may have lower value, and lose value faster, than nearby signals or cues (Seppänen et al. 2007). For example, Fernández-Juricic and Kacelnik (2004) found that European Starlings (*Sturnus vulgaris*) are more likely to use social information in foraging decisions when conspecifics are nearby than farther (3 m) away.

The potential spatial degradation of information value is based, in part, on the assumption that resources are spatially autocorrelated (Fig. 2). By analogy, we can draw from

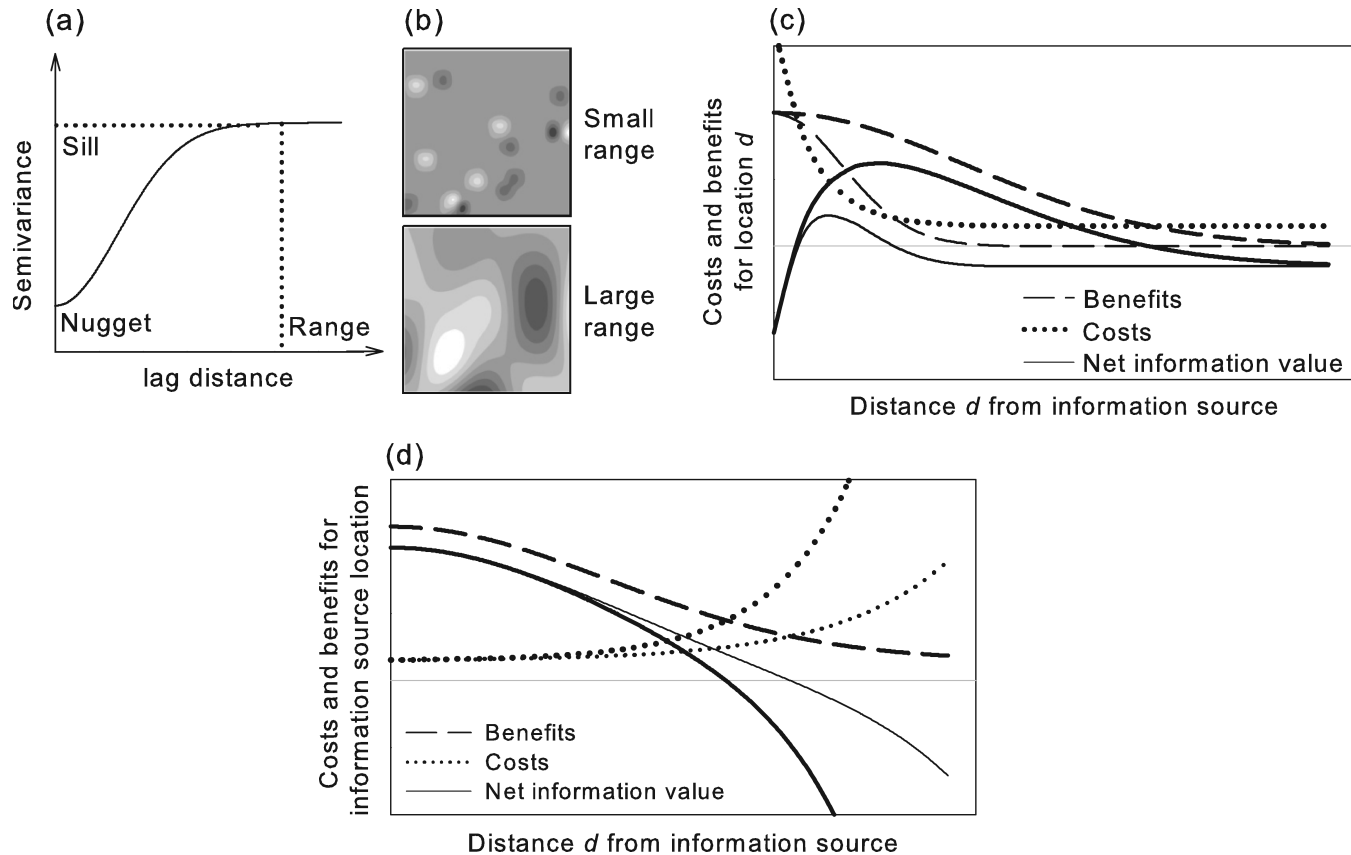


FIGURE 2. Spatial autocorrelation in resources can influence information value. (a) A Gaussian model semivariogram and its parameters, highlighting how the semivariance increases as a function of lag distance. Semivariograms provide information on the spatial extent of autocorrelation (the range) as well as the relative magnitude of autocorrelation (sill – nugget/sill; Li and Reynolds 1995), as shown with (b) kriged maps of two landscapes that differ only in the assumed range of spatial autocorrelation (50 m vs. 300 m for a 1- × 1-km map). (c) The degree of spatial autocorrelation in resources is predicted to alter the value of information to individuals making decisions regarding the quality of their current location (e.g., for foraging or settlement) as a function of the distance from the information source (modified from Seppänen et al. 2007). Thick lines denote high autocorrelation, whereas thin lines represent low autocorrelation for a given cost function. Benefits of information use come from autocorrelation in resources, whereas costs can arise at close distances, such as from exploitative competition. When spatial autocorrelation is low, the information is valuable only at short distances from its source. (d) The value of information for decisions to move may be driven by different costs and benefits because individuals do not use information to assess their current location but rather the location of the information source. With respect to the benefits of information use, spatial autocorrelation in resources should be less influential although benefits may still attenuate with distance with the decrease in the signal-to-noise ratio (i.e., less certainty in distinguishing information; single dashed line). Instead, the cost of movement to the information source's location may be more important for net information value (thick lines represent high cumulative movement costs and thin lines represent low cumulative movement costs). In both (c) and (d), the gray reference line indicates zero costs or benefits.

discussions of information use and temporal autocorrelation in resources to interpret how spatial autocorrelation of resources influences information value in space. A game-theoretic model developed by Doligez et al. (2003) using demographic data from Barn Swallows (*Hirundo rustica*) and Black-legged Kittiwakes (*Rissa tridactyla*) suggests that when resources are temporally correlated over time, social information, particularly performance-based cues, can be a reliable source of information for decision-making. As temporal autocorrelation declines, social information loses value because the world is less predictable in time. Similarly, as temporal autocorrelation approaches unity, fixed strategies (e.g., philopatry; Doligez

et al. 2003) provide the most parsimonious evolutionarily stable strategy because resource quality is constant over time. By extending these arguments over space, we might expect social information to be most valuable where resources are moderately aggregated spatially.

Fletcher (2006) considered this issue theoretically in the context of individuals using conspecific attraction to guide movement and settlement decisions under various scenarios of habitat fragmentation, where fragmentation was generated through fractal algorithms that altered the relative degree of spatial aggregation of resources. Using individual-based simulations of different movement and settlement strategies, the

model indeed suggested that when resources are not spatially aggregated or very strongly aggregated (the simple random landscapes and $H = 1$ landscapes of Fletcher 2006, respectively), using conspecifics as settlement cues was not superior to a random strategy. Only at moderate levels of spatial aggregation was using conspecific cues for settlement an improvement over a random strategy (see fig. 5d of Fletcher 2006).

Further understanding of the role that spatial autocorrelation of resources plays in information value would shed light on the likelihood of information use. For instance, spatial autocorrelation in resources can be described on the basis of three parameters of model-based semivariograms: the range, the sill, and the nugget (Fig. 2a). These parameters help describe both the spatial extent and relative magnitude of autocorrelation (Li and Reynolds 1995). The potential for information value to vary in space can thus arise through either variation in the spatial extent of autocorrelation of resources, the magnitude of autocorrelation, or both.

Information value can also degrade over space from a decrease in the signal-to-noise ratio of cues, independent of the spatial autocorrelation of resources. In this context, signal-detection theory has been applied to a variety of behavioral decisions that birds make to interpret the likelihood of a decision being made as a function of the signal-to-noise ratio (Wiley 1994, Getty 1995). Applications of signal-detection theory to interpret decision-making in space could help explain variation in information use, even when information is within an individual's response range.

In regards to interpreting information value, we note that the effective content of information may also vary over space. Consider the use of conspecific cues, such as bird song, in settlement decisions. Well-known examples of conspecific attraction show that individuals use song cues as a positive proximate stimulus in settlement decisions, or choice of site for breeding (Ward and Schlossberg 2004, Hahn and Silverman 2006). Yet the cue—song—often functions as a negative stimulus at very local scales (choice of breeding territory) because of the potential for interference competition (Krebs 1976). Therefore, the use of the same cue, as a positive or negative stimulus in habitat selection, varies with scale. The cue has not changed, and the value of the cue might be large at both scales, but the content of the information in the cue (potential competition versus habitat quality) has changed. Such a role of information as a negative stimulus in decision-making is only starting to be considered in the growing literature of information use (Thomson et al. 2003, Fletcher 2007, 2008, Forsman et al. 2008).

LANDSCAPE EFFECTS ON INFORMATION

Availability. In heterogeneous landscapes, the availability of information can be greatly altered through anthropogenic changes. As the amount of edge increases and the size of habitat patches declines with continuing habitat loss and

fragmentation, the availability of social-information cues can diminish. When animals use social cues for settlement, this reduction could decrease the probability of small patches being occupied. Over 15 years ago, conservation biologists first suggested this possibility with songbirds (Verner 1992, Reed and Dobson 1993), although tests of it are still few. More recently, Fletcher (2006) showed through simulation modeling that distributions of individuals using conspecific attraction should emerge as patterns of putative sensitivity to patch size and edge-avoidance behaviors. These patterns were driven by the potential for social information cues being diminished in small patches and near edges, not from individuals responding to area or edge per se. These patterns are concordant with other recent investigations finding that species of forest birds sensitive to patch size also have aggregated patterns of distribution (Bourque and Desrochers 2006).

A recent field experiment highlights the possibility that patterns of area sensitivity can indeed be driven by the use of social information. Fletcher (2009) broadcast the song of the Least Flycatcher (*Empidonax minimus*) across a gradient of sizes of patches of riparian forest in Montana. The Least Flycatcher has been previously shown to be attracted to conspecifics (Fletcher 2007) and sensitive to patch size (Fletcher and Hutto 2008), as it avoids small patches of riparian forest in Montana. Vegetation structure, nest-predation rates, and nest-parasitism rates were not sufficient to explain patterns of distribution as a function of patch size. However, when Fletcher (2009) simulated conspecific cues across a gradient of patch sizes, flycatchers settled in all patches—and their sensitivity to patch size vanished—providing strong support for the conspecific-attraction hypothesis (Fletcher 2009).

Similarly, Fernández-Juricic (2002) investigated the distributions of species and occurrence of flocks as a function of habitat fragmentation in Madrid, Spain. He found that the presence of conspecifics and heterospecifics increased the occurrence of flocks, but that species' distributions followed a nested pattern, many species being less likely to occur in small, isolated patches, after he accounted for variation in habitat structure. Fernández-Juricic hypothesized that the reduced occurrence of flocks in small, isolated patches was driven by a decrease in the social information available in those patches.

The structural or physical connectivity of habitats can also alter the availability of social cues, as suggested by Fernández-Juricic (2002). As connectivity declines, search costs will increase via a decline in information availability, potentially favoring the use of social information that allows for more rapid assessments (Mönkkönen et al. 1999). Structural connectivity also undoubtedly interacts with variation in the perceptual range of different information sources to influence functional connectivity. Furthermore, as structural connectivity and patch size decrease, and time since isolation of patches increases, for many species sensitive to habitat loss

the proportion of patches occupied will likely decrease. In these situations, the proportion of patches occupied by conspecifics that could provide navigational cues to influence functional connectivity will decrease (Castellón and Sieving 2006, 2007). Such possibilities could help explain why structural measures of isolation and/or connectivity tend to perform poorly in explaining species' distributions (Winfree et al. 2005). Assessing the role of social information relative to structural measures in explaining functional connectivity could shed new light on connectivity across heterogeneous landscapes.

Value. As landscapes continue to change through natural or human perturbations, the value of information sources may also change. Changes in information value can occur through at least two different routes: (1) changes in the costs or benefits of using information because changes in the landscape context alter the utility of the information (i.e., the costs/benefits of information use), and (2) a decoupling of cues used and their information content because of landscape change.

As landscapes become more fragmented, the costs and benefits of using information may change, even when the information is available to organisms. For instance, Fletcher (2006) showed that as the amount of habitat declines, the fitness benefits of using conspecifics as social cues increases, relative to a random strategy. This pattern arose by directing movement and reducing costly forays into inhospitable matrix, and its effects were more pronounced as mortality risk increased (cf. Haydon et al. 2008). In an intriguing example, Sieving et al. (2004) found that some forest birds were more likely to cross forest boundaries into open habitats in the presence of Tufted Titmice (*Baeolophus bicolor*), presumably because titmice provide valuable information on predation risk (Sieving et al. 2010). Consequently, as landscapes become more fragmented, the value of information gleaned from titmice may increase and could be important for movement of individuals across risky landscapes. In a source-sink model of interspecific interactions between resident and migrant birds, Mönkkönen et al. (1999) showed that using resident social cues by migrants to guide settlement is an effective strategy because doing so reduces the costs of sampling. This benefit is contingent, however, on the proportion of the landscape that contains high-quality (source) habitat and the likelihood that source habitat provides heterospecific social cues. This result was driven by the assumption that residents provide accurate information on habitat quality.

The decoupling of cues used and their information content falls under the concept of the evolutionary trap. An evolutionary trap is a potentially important problem that arises when formerly adaptive behaviors become maladaptive because the cues animals use in decision-making no longer provide reliable information (Schlaepfer et al. 2002). In an information context, either (1) the cues are the same, but the information value declines because the information is either less reliable

or becomes entirely false (Koops 2004), or (2) novel cues are added to the landscape that are similar in structure to historic cues but have different effects on fitness (e.g., polarized light from roads). One important type of evolutionary trap that has received considerable theoretical and empirical attention is the ecological trap, which occurs when individuals prefer to settle in poor-quality habitats over better alternatives. In this situation, there is a spatio-temporal decoupling of information's actual value and the value an individual perceives.

For social-information use, a decoupling of information cues and their value can be particularly problematic because of the potential for informational cascades (Giraldeau et al. 2002). Informational cascades can result in maladaptive decision-making that arises from individuals copying the decisions of conspecifics or heterospecifics that arose from poor choices. Maladaptive decisions can thereby cascade through a population or community quickly through space and/or time. Thus, the potential for evolutionary traps could be great for individuals using social information in decision-making. For instance, Betts et al. (2008) showed that Black-throated Blue Warblers (*Dendroica caerulescens*) could be attracted to clear-cut habitat of very low quality with the addition of conspecific cues, highlighting the potential for informational cascades in selection of breeding habitat (see also Nocera et al. 2006).

VARIATION IN SOCIAL-INFORMATION SOURCES AND DECISIONS

Finally, we emphasize that spatial aspects of different sources of social information could also influence both the availability and value of information across landscapes. For instance, the perceptual range of location cues that arise from song is likely greater than that of performance-based cues arising from parents feeding offspring. We might also expect that the value of different types of social information varies spatially. Information sources that reflect issues occurring at a broader spatial scale or coarser grain (e.g., greater spatial autocorrelation as reflected in a larger range in semivariogram analyses; Fig. 2b) may degrade more slowly over space (termed "functional grain"; Baguette and Van Dyck 2007), and thus be more valuable at greater distances, than other information cues reflecting resources operating at smaller spatial scales of heterogeneity.

Information value will likely vary for different kinds of decisions that animals make. Seppänen et al. (2007) hypothesized that when resources are autocorrelated spatially, information value will decline with distance as a function of the degree of autocorrelation because as distance from the information source increases, the benefits from autocorrelated resources decline (Fig. 2c). Note here that the value of information pertains to decisions made at specific distances away from the information source in reference to the animal's current location, as when information cues from adjacent

patches guide an animal's decision to settle or forage in its current patch. For movement or searching behaviors, information value as a function of distance depends less on spatial autocorrelation of resources because an individual is using the information for interpreting the location of the information source rather than interpreting its current location. Benefits of information may still decline with distance because of decreasing signal-to-noise ratios (see above), but its value will also be heavily contingent on the costs of movement as a function of distance from the information source (Fig. 2d). For instance, Fletcher (2006) simulated social-information use across a wide range of population, landscape, and behavioral conditions. Simulations suggested that using social information in decisions to move consistently improves fitness across landscapes in which resources vary in degree of spatial autocorrelation, whereas using social information in decisions to settle has more variable effects on fitness, depending on spatial autocorrelation.

AN APPLICATION TO BOBOLINKS BREEDING IN AGRICULTURAL LANDSCAPES

To illustrate the potential utility of an information-based perspective for avian ecology, we draw from investigations of Bobolinks breeding in the fragmented grasslands of North America. Because grasslands have been lost at devastating rates throughout the United States and much of Canada, biologists have been concerned about the potential effects of habitat loss and fragmentation on grassland birds, including the Bobolink. Numerous studies have concluded that Bobolinks often avoid small patches and habitat edges (e.g., Herkert 1994, Johnson and Igl 2001, Fletcher and Koford 2003). Outside the context of social-information use, several hypotheses have been considered to explain these patterns of distribution. These include variation in vegetation structure (Herkert 1994, Fletcher and Koford 2003) and rates of nest predation and parasitism increasing with fragmentation (Renfrew et al. 2005), yet there has been relatively little evidence for these hypotheses.

More recently, Nocera et al. (2006) used an information-based perspective to experimentally test for social-information use in the Bobolink's habitat selection by adding song cues either just prior to breeding or just after breeding and documenting subsequent settlement decisions. This experiment showed that Bobolinks (primarily second-year birds) use conspecific cues to guide habitat selection, suggesting that the value of this information to younger birds was greater than to older birds (see also Ward and Schlossberg 2004). However, the Bobolinks studied used only post-breeding social cues, not pre-breeding cues, to guide settlement decisions. Because of the Bobolink's highly synchronous breeding behavior, pre-breeding cues might be less available when the birds are settling. Betts et al. (2008) also hypothesized that the information value of post-breeding cues could be greater than that

of pre-breeding cues because such cues may provide more information regarding the performance of conspecifics. In any case, this result is somewhat similar to that of Bollinger and Gavin (1989), who found stronger correlations between the Bobolink's site fidelity and overall site quality, measured by the combined reproductive success of all Bobolinks at the site, than with the reproductive success of the individual.

Nocera et al. (2006) also found that not only did Bobolinks use social cues in settlement decisions but that some birds responding to the experimental cue attempted to settle in shrubby habitats in which Bobolinks normally do not breed. These results suggest an informational cascade and highlight the potential for an ecological trap arising from social-information use. Indeed, in hayfields Bobolinks often reach densities as high or higher than in other, more suitable habitats (Bollinger et al. 1990)—a pattern often considered as prime example of an ecological trap (but see Robertson and Hutto 2006). Social-information use could be one means by which this potential ecological trap persists, if, during the post-breeding period, individuals moving across landscapes provide inadvertent cues to other individuals that use those cues in the subsequent breeding season for settlement decisions.

It is still unclear, however, whether this use of social information by the Bobolink explains its consistent patterns of distribution in fragmented landscapes or the apparent ecological trap of hayfields. Nocera et al. (2009) have further demonstrated the Bobolink's pattern of aggregated settlement, which, coupled with its consistent area sensitivity, is consistent with conspecific attraction as a potential mechanism for its sensitivity to fragmentation (cf. Fletcher 2009). From these results it is clear that an information-based perspective on these issues has shed new light on our understanding of the Bobolink's distribution, and it raises new hypotheses for explaining the species' area and edge sensitivity, as well as vulnerability to ecological traps.

CONCLUSIONS: OPPORTUNITIES FOR LANDSCAPE ECOLOGY

Much of avian landscape ecology focuses on interpreting, either implicitly or explicitly, the behaviors of birds in heterogeneous landscapes. Information-based perspectives provide a guiding framework for behavioral ecology (Danchin et al. 2008) and should be helpful for interpreting the effects of landscape change. Stamps (1988, 1991) has argued that migratory songbirds are good candidates for the study of conspecific attraction because of their seasonal breeding distributions, mobility, and the potential for singing males to be detected from afar. Migratory birds might also be likely to use social information in breeding settlement because, when returning to the breeding grounds, they are more time-limited than residents (Mönkkönen et al. 1990, Thomson et al. 2003). We further extend these arguments to other forms of information use.

Our framework emphasizes that addressing factors influencing information availability will be useful for interpreting when and where birds are likely to use social information. Furthermore, because different types of information likely vary in their availability, accurately assessing information availability might help us better explain variation in social-information use, particularly in situations where some information sources may have more information value but are not used by individuals. Estimating the perceived value of information, given its availability, and how information value changes under different ecological contexts will also help us better predict the likelihood of social-information use.

Most of our discussion of social-information use in heterogeneous landscapes should be treated as working hypotheses, amenable to future testing, rather than facts about the importance of such behaviors. Indeed, although recent theory has suggested the potential importance of this interface of animal behavior and landscape ecology (Mönkkönen et al. 1999, Fletcher 2006), empirical evidence still remains scarce. Yet because social-information use may be widespread in birds (Dolby and Grubb 1998, Forsman et al. 2002, Hahn and Silverman 2006, Parker et al. 2007, Betts et al. 2008), and birds are strongly influenced by spatial structure (Robbins et al. 1989, Bélisle et al. 2001, Rodewald and Yahner 2001), we expect that information-based perspectives will shed new light on avian ecology in heterogeneous landscapes.

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LITERATURE CITED

- ARMSWORTH, P. R., AND J. E. ROUGHGARDEN. 2005. The impact of directed versus random movement on population dynamics and biodiversity patterns. *American Naturalist* 165:449–465.
- BAGUETTE, M., AND H. VAN DYCK. 2007. Landscape connectivity and animal behavior: functional grain as a key determinant for dispersal. *Landscape Ecology* 22:1117–1129.
- BEAUCHAMP, G., M. BELISLE, AND L.-A. GIRALDEAU. 1997. Influence of conspecific attraction on the spatial distribution of learning foragers in a patchy habitat. *Journal of Animal Ecology* 66:671–682.
- BÉLISLE, M. 2005. Measuring landscape connectivity: the challenge of behavioral landscape ecology. *Ecology* 86:1988–1995.
- BÉLISLE, M., A. DESROCHERS, AND M. J. FORTIN. 2001. Influence of forest cover on the movements of forest birds: a homing experiment. *Ecology* 82:1893–1904.
- BETTS, M. G., A. S. HADLEY, N. RODENHOUSE, AND J. J. NOCERA. 2008. Social information trumps vegetation structure in breeding-site selection by a migrant songbird. *Proceedings of the Royal Society B* 275:2257–2263.
- BOLLINGER, E. K., AND T. A. GAVIN. 1989. The effects of site quality on breeding-site fidelity in Bobolinks. *Auk* 106:584–594.
- BOLLINGER, E. K., P. B. BOLLINGER, AND T. A. GAVIN. 1990. Effects of hay-cropping on eastern populations of the Bobolink. *Wildlife Society Bulletin* 18:142–150.
- BOURQUE, J., AND A. DESROCHERS. 2006. Spatial aggregation of forest songbird territories and possible implications for area sensitivity. *Avian Conservation and Ecology* 1:3.
- CASTELLÓN, T. D., AND K. E. SIEVING. 2006. An experimental test of matrix permeability and corridor use by an endemic understory bird. *Conservation Biology* 20:135–145.
- CASTELLÓN, T. D., AND K. E. SIEVING. 2007. Patch network criteria for dispersal-limited endemic birds of South American temperate rain forest. *Ecological Applications* 17:2152–2163.
- DALL, S. R. X. 2005. Defining the concept of public information. *Science* 308:353–354.
- DALL, S. R. X., L.-A. GIRALDEAU, O. OLSSON, J. M. MCNAMARA, AND D. W. STEPHENS. 2005. Information and its use by animals in evolutionary ecology. *Trends in Ecology and Evolution* 20:187–193.
- DANCHIN, E., L. A. GIRALDEAU, AND F. CEZILLY. 2008. *Behavioural ecology*. Oxford University Press, Oxford, England.
- DANCHIN, E., L.-A. GIRALDEAU, T. J. VALONE, AND R. H. WAGNER. 2004. Public information: from nosy neighbors to cultural evolution. *Science* 305:487–491.
- DANCHIN, E., L.-A. GIRALDEAU, T. J. VALONE, AND R. H. WAGNER. 2005. Defining the concept of public information—response. *Science* 308:355–356.
- DOLBY, A. S., AND T. C. GRUBB. 1998. Benefits to satellite members in mixed-species foraging groups: an experimental analysis. *Animal Behaviour* 56:501–509.
- DOLIGEZ, B., E. DANCHIN, AND J. CLOBERT. 2002. Public information and breeding habitat selection in a wild bird population. *Science* 297:1168–1170.
- DOLIGEZ, B., C. CADET, E. DANCHIN, AND T. BOULINIER. 2003. When to use public information for breeding habitat selection? The role of environmental predictability and density dependence. *Animal Behaviour* 66:973–988.
- DOLIGEZ, B., T. PART, E. DANCHIN, J. CLOBERT, AND L. GUSTAFSSON. 2004. Availability and use of public information and conspecific density for settlement decisions in the Collared Flycatcher. *Journal of Animal Ecology* 73:75–87.
- FERNÁNDEZ-JURICIC, E. 2002. Nested patterns of species distribution and winter flock occurrence of insectivorous birds in a fragmented landscape. *Ecoscience* 9:450–458.
- FERNÁNDEZ-JURICIC, E., AND A. KACELNIK. 2004. Information transfer and gain in flocks: the effects of quality and quantity of social information at different neighbour distances. *Behavioral Ecology and Sociobiology* 55:502–511.
- FERRAZ, G., J. D. NICHOLS, J. E. HINES, P. C. STOUFFER, R. O. BIERREGAARD, AND T. E. LOVEJOY. 2007. A large-scale deforestation experiment: effects of patch area and isolation on Amazon birds. *Science* 315:238–241.
- FLETCHER, R. J. JR. 2006. Emergent properties of conspecific attraction in fragmented landscapes. *American Naturalist* 168:207–219.
- FLETCHER, R. J. JR. 2007. Species interactions and population density mediate the use of social cues for habitat selection. *Journal of Animal Ecology* 76:598–606.
- FLETCHER, R. J. JR. 2008. Social information and community dynamics: nontarget effects from simulating social cues for management. *Ecological Applications* 18:1764–1773.
- FLETCHER, R. J. JR. 2009. Does attraction to conspecifics explain the patch-size effect? An experimental test. *Oikos* 118:1139–1147.
- FLETCHER, R. J. JR., AND R. R. KOFORD. 2003. Spatial responses of Bobolinks (*Dolichonyx oryzivorus*) near different types of edges in northern Iowa. *Auk* 120:799–810.
- FLETCHER, R. J. JR., AND R. L. HUTTO. 2008. Partitioning the multi-scale effects of human activity on the occurrence of riparian forest birds. *Landscape Ecology* 23:727–739.

- FLETCHER, R. J. JR., AND C. W. MILLER. 2008. The type and timing of social information alters offspring production. *Biology Letters* 4:482–485.
- FORSMAN, J. T., J. T. SEPPÄNEN, AND M. MÖNKKÖNEN. 2002. Positive fitness consequences of interspecific interaction with a potential competitor. *Proceedings of the Royal Society of London B* 269:1619–1623.
- FORSMAN, J. T., M. MÖNKKÖNEN, P. HELLE, AND J. INKEROINEN. 1998. Heterospecific attraction and food resources in migrants' breeding patch selection in northern boreal forest. *Oecologia* 115:278–286.
- FORSMAN, J. T., M. B. HJERNQUIST, J. TAIPALE, AND L. GUSTAFSSON. 2008. Competitor density cues for habitat quality facilitating habitat selection and investment decisions. *Behavioral Ecology* 19:539–545.
- GATES, J. E., AND L. W. GYSEL. 1978. Avian nest dispersion and fledging success in field–forest ecotones. *Ecology* 59:871–883.
- GETTY, T. 1995. Search, discrimination, and selection: mate choice by Pied Flycatchers. *American Naturalist* 145:146–154.
- GIRALDEAU, L.-A., T. J. VALONE, AND J. J. TEMPLETON. 2002. Potential disadvantages of using socially acquired information. *Philosophical Transactions of the Royal Society of London B* 357:1559–1566.
- GOULD, J. P. 1974. Risk, stochastic preference, and the value of information. *Journal of Economic Theory* 8:64–84.
- HAHN, B. A., AND E. D. SILVERMAN. 2006. Social cues facilitate habitat selection: American Redstarts establish breeding territories in response to song. *Biology Letters* 2:337–340.
- HAYDON, D. T., J. M. MORALES, A. YOTT, D. A. JENKINS, R. ROSATTE, AND J. M. FRYXELL. 2008. Socially informed random walks: incorporating group dynamics into models of population spread and growth. *Proceedings of the Royal Society B* 275:1101–1109.
- HERKERT, J. R. 1994. The effects of habitat fragmentation on midwestern grassland bird communities. *Ecological Applications* 4:461–471.
- JOHNSON, D. H. 1980. The comparison of usage and availability measurements for evaluating resource preference. *Ecology* 61:65–71.
- JOHNSON, D. H., AND L. D. IGL. 2001. Area requirements of grassland birds: a regional perspective. *Auk* 118:24–34.
- KOOPS, M. A. 2004. Reliability and the value of information. *Animal Behaviour* 67:103–111.
- KREBS, J. R. 1976. Bird song and territory defence. *New Scientist* 70:534–536.
- LANGHAM, G. M., T. A. CONTRERAS, AND K. E. SIEVING. 2006. Why pishing works: titmouse (*Paridae*) scolds elicit a generalized response in bird communities. *Ecoscience* 13:485–496.
- LI, H., AND J. F. REYNOLDS. 1995. On definition and quantification of heterogeneity. *Oikos* 73:280–284.
- LIMA, S. L., AND P. A. ZOLLNER. 1996. Towards a behavioral ecology of ecological landscapes. *Trends in Ecology and Evolution* 11:131–135.
- MÖNKKÖNEN, M., P. HELLE, AND K. SOPPELA. 1990. Numerical and behavioural responses of migrant passerines to experimental manipulation of resident tits (*Parus* spp.): heterospecific attraction in northern breeding bird communities? *Oecologia* 85:218–225.
- MÖNKKÖNEN, M., P. HELLE, G. J. NIEMI, AND K. MONTGOMERY. 1997. Heterospecific attraction affects community structure and migrant abundances in northern breeding bird communities. *Canadian Journal of Zoology* 75:2077–2083.
- MÖNKKÖNEN, M., R. HARDLING, J. T. FORSMAN, AND J. TUOMI. 1999. Evolution of heterospecific attraction: using other species as cues in habitat selection. *Evolutionary Ecology* 13:91–104.
- NOCERA, J. J., G. J. FORBES, AND L.-A. GIRALDEAU. 2006. Inadvertent social information in breeding site selection of natal dispersing birds. *Proceedings of the Royal Society of London B* 273:349–355.
- NOCERA, J. J., G. J. FORBES, AND L.-A. GIRALDEAU. 2009. Aggregations from using inadvertent social information: a form of ideal habitat selection. *Ecography* 32:143–152.
- PARKER, M. W., S. W. KRESS, R. T. GOLIGHTLY, H. R. CARTER, E. B. PARSONS, S. E. SCHUBEL, J. A. BOYCE, G. J. MCCHESENEY, AND S. M. WISELY. 2007. Assessment of social attraction techniques used to restore a Common Murre colony in central California. *Waterbirds* 30:17–28.
- REED, J. M., AND A. P. DOBSON. 1993. Behavioral constraints and conservation biology: conspecific attraction and recruitment. *Trends in Ecology and Evolution* 8:253–256.
- RENFREW, R. B., C. A. RIBIC, AND J. L. NACK. 2005. Edge avoidance by nesting grassland birds: a futile strategy in a fragmented landscape. *Auk* 122:618–636.
- REVILLA, E., T. WIEGAND, F. PALOMARES, P. FERRERAS, AND M. DELIBES. 2004. Effects of matrix heterogeneity on animal dispersal: from individual behavior to metapopulation-level parameters. *American Naturalist* 164:E130–E153.
- ROBBINS, C. S., D. K. DAWSON, AND B. A. DOWELL. 1989. Habitat area requirements of breeding forest birds of the middle Atlantic states. *Wildlife Monographs*:1–34.
- ROBERTSON, B. A., AND R. L. HUTTO. 2006. A framework for understanding ecological traps and an evaluation of existing evidence. *Ecology* 87:1075–1085.
- ROBINSON, S. K., F. R. THOMPSON, T. M. DONOVAN, D. R. WHITEHEAD, AND J. FAABORG. 1995. Regional forest fragmentation and the nesting success of migratory birds. *Science* 267:1987–1990.
- RODEWALD, A. D., AND R. H. YAHNER. 2001. Influence of landscape composition on avian community structure and associated mechanisms. *Ecology* 82:3493–3504.
- SCHLAEFFER, M. A., M. C. RUNGE, AND P. W. SHERMAN. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* 17:474–480.
- SCHMIDT, K. A. 2001. Site fidelity in habitats with contrasting levels of nest predation and brood parasitism. *Evolutionary Ecology Research* 3:633–648.
- SEPPÄNEN, J. T., J. T. FORSMAN, M. MÖNKKÖNEN, AND R. L. THOMSON. 2007. Social information use is a process across time, space, and ecology, reaching heterospecifics. *Ecology* 88:1622–1633.
- SIEVING, K. E., M. F. WILLSON, AND T. L. DE SANTO. 2000. Defining corridor functions for endemic birds in fragmented south-temperate rainforest. *Conservation Biology* 14:1120–1132.
- SIEVING, K. E., T. A. CONTRERAS, AND K. L. MAUTE. 2004. Heterospecific facilitation of forest-boundary crossing by mobbing understory birds in north-central Florida. *Auk* 121:738–751.
- SIEVING, K. E., S. A. HETRICK, AND M. L. AVERY. 2010. The versatility of graded acoustic measures in classification of predation threats by the Tufted Titmouse *Baeolophus bicolor*: exploring a mixed framework for threat communication. *Oikos* 119:264–276.
- STAMPS, J. A. 1988. Conspecific attraction and aggregation in territorial species. *American Naturalist* 131:329–347.
- STAMPS, J. A. 1991. The effect of conspecifics on habitat selection in territorial species. *Behavioral Ecology and Sociobiology* 28:29–36.
- STEPHENS, D. W. 1989. Variance and the value of information. *American Naturalist* 134:128–140.
- SWANSON, E. M., S. M. TEKMEEN, AND M. A. BEE. 2007. Do female frogs exploit inadvertent social information to locate breeding aggregations? *Canadian Journal of Zoology* 85:921–932.
- THOMPSON, R. L., J. T. FORSMAN, AND M. MÖNKKÖNEN. 2003. Positive interactions between migrant and resident birds: testing the heterospecific attraction hypothesis. *Oecologia* 134:431–438.
- TURCHIN, P. 1989. Population consequences of aggregative movement. *Journal of Animal Ecology* 58:75–100.

- VERNER, J. 1992. Data needs for conservation biology: have we avoided critical research? *Condor* 94:301–303.
- WARD, M. P., AND S. SCHLOSSBERG. 2004. Conspecific attraction and the conservation of territorial songbirds. *Conservation Biology* 18:519–525.
- WIEGAND, T., K. A. MOLONEY, J. NAVES, AND F. KNAUER. 1999. Finding the missing link between landscape structure and population dynamics: a spatially explicit perspective. *American Naturalist* 154:605–627.
- WILEY, R. H. 1994. Errors, exaggeration, and deception in animal communication, p. 157–189. *In* L. Real [ED.], *Behavioral mechanisms in ecology*. University of Chicago Press, Chicago.
- WINFREE, R., J. DUSHOFF, E. E. CRONE, C. B. SCHULTZ, R. V. BUDNY, N. M. WILLIAMS, AND C. KREMEN. 2005. Testing simple indices of habitat proximity. *American Naturalist* 165:707–717.
- ZOLLNER, P. A. 2000. Comparing the landscape level perceptual abilities of forest sciurids in fragmented agricultural landscapes. *Landscape Ecology* 15:523–533.