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# Information-Mediated Allee Effects in Breeding Habitat Selection

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**ABSTRACT:** Social information is used widely in breeding habitat selection and provides an efficient means for individuals to select habitat, but the population-level consequences of this process are not well explored. At low population densities, efficiencies may be reduced because there are insufficient information providers to cue high-quality habitat. This constitutes what we call an information-mediated Allee effect. We present the first general model for an information-mediated Allee effect applied to breeding habitat selection and unify personal and social information, Allee effects, and ecological traps into a common framework. In a second model, we consider an explicit mechanism of social information gathering through prospecting on conspecific breeding performance. In each model, we independently vary personal and social information use to demonstrate how dependency on social information may result in either weak or strong Allee effects that, in turn, affect population extinction risk. Abrupt transitions between outcomes can occur through reduced information transfer or small changes in habitat composition. Overall, information-mediated Allee effects may produce positive feedbacks that amplify population declines in species that are already experiencing environmentally driven stressors, such as habitat loss and degradation. Alternatively, social information has the capacity to rescue populations from ecological traps.

**Keywords:** Allee effect, Allee threshold, ecological trap, habitat selection, social information.

## Introduction

By sampling their environments (e.g., patches, mates, habitats) and subsequent links to performance (prey harvest rates, offspring production), organisms often both use and produce information about their environment, which in many cases is publicly available (Danchin et al. 2004). Social information use is likely a pervasive and important process in ecology and evolution that affects species' population growth and persistence (e.g., Doligez et al. 2003;

Schmidt et al. 2015*b*). However, the degree to which feedbacks occur between population growth and social information are not well explored. For instance, at low population density, one would expect lower potential for information collection at the individual level because there are fewer information providers. Consequently, per capita population growth should be reduced at low density through the effects of reduced information availability. This may, in turn, produce an information-driven Allee effect. In this article, we present a general model for such an information-mediated Allee effect.

Allee effects may be caused by numerous, nonmutually exclusive mechanisms affecting one or more fitness components (e.g., reproduction and survival), or what Stephens et al. (1999) refer to as a component Allee effect. In turn, these may produce a demographic Allee effect, characterized by the presence of positive density-dependent per capita population growth (Stephens et al. 1999; Allee 1941). Demographic Allee effects are important in conservation because they may increase the extinction vulnerability of small populations (Courchamp et al. 2009). Demographic Allee effects may be categorized as strong or weak. In a weak Allee effect, per capita population growth is reduced at low density but remains positive. In a strong Allee effect, per capita population growth is negative at low density, which can threaten population extinction. Thus, strong Allee effects produce two population equilibrium points (excluding population size  $N = 0$ ). The larger equilibrium,  $N_s^* = K$  (or carrying capacity), is stable. The smaller, unstable equilibrium occurs in the region of positive density dependence ( $0 < N_v^* < K$ ). This point is called an Allee threshold (Boukal and Berec 2002), because below  $N_v^*$ , the population will decline toward extinction in the absence of external influence.

Explicit recognition that social information may contribute to Allee effects has received limited attention, although several common mechanisms often implicitly invoke social information, such as finding mates, food, and safety in numbers (Courchamp et al. 2009). The many-eyes

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hypothesis is partially the cogent realization that more eyes scanning for predators reduce the uncertainty in an individual's estimate of the instantaneous risk of predation. Dilution effects also contribute to safety in numbers, hence information- and noninformation-based mechanisms may operate in tandem.

Social information can influence numerous behavioral and life-history strategies of organisms (Dall 2005; Danchin et al. 2004). We focus on information use as it applies to breeding habitat selection in spatially heterogeneous landscapes where variation in the quality of breeding sites is manifested as differences in breeding success (e.g., variation in the risk of nest mortality; Schmidt et al. 2006; Schmitt and Holbrook 2007). By sampling prospective territories, organisms can collect direct or indirect information about current or future quality based on current territory occupation or past reproductive performance of conspecifics (Boulinier and Danchin 1997; Doligez et al. 2002; Forsman et al. 2012). The latter can lead to simple habitat copying or settlement at sites where conspecifics were successful (i.e., performance-based cues; Reed et al. 1999).

#### A Phenomenological Model of an Information-Mediated Allee Effect

We start with a phenomenological model that incorporates density-dependent information use into the process of breeding habitat selection. We use this model to explore the population-level phenomenon of habitat selection that is influenced by both personal information and social information. The model is heuristic and analytically tractable, making it broadly applicable across taxa and tactics of information use. Information requires spatial heterogeneity in site quality and a positive temporal correlation between mean reproductive outcomes in any given site (Boulinier and Danchin 1997). For simplicity, we assume that habitat consists of good and bad sites and that site quality is fixed in time (we relax this assumption in a subsequent model; see "Adding Mechanisms of Information Use"). We calculate expected per capita population growth rates (see below) based on the expected number of future adults produced within good and bad sites (i.e., the population is geographically closed). The probability that an individual settles at a site of specific quality is determined by the relative availability of sites at the time of settlement, which changes under nonrandom habitat selection with the number of individuals that have settled previously. Nonrandom habitat selection, in turn, is determined by information available to individuals. For this process of settlement, we make the following simplifying assumptions: (1) individuals sequentially settle within a single vacant breeding site, (2) individual settlement is biased with respect to both personal ( $w_0$ ; i.e., nonsocially acquired) and social ( $a$ ) information regard-

ing site quality, (3) social information saturates with the number of conspecifics, and (4) the two types of information are additive in their effect on settlement. These assumptions yield the following relationship for total information ( $w$ ):  $w = w_0 + aN/(1 + aN)$ , where  $w_0$  is a measure of information available independent of the density of conspecifics and  $a$  determines the rate of increase in social information with density. Note that our use of the terms "personal" and "social" does not refer to the source of information but specifically to whether the information depends on the number of conspecifics (i.e., social information) or not (personal information). When placed in the context of density-dependent population growth, there is an important functional difference between these terms. Our use of these terms, therefore, differs from that of previous authors (e.g., Wagner and Danchin 2010).

Personal information may include experience, such as prior reproductive success, natal habitat imprinting (Davis and Stamps 2004), active sampling for predators (e.g., Morton 2005; Schmitt and Holbrook 2007) or parasites (Forsman and Martin 2009), and innate preferences for habitat features (Arlt and Pärt 2007). Likewise, several mechanisms may be used to acquire social information. One mechanism with broad empirical support is social information acquired through eavesdropping on the reproductive performance of conspecifics—for example, the number and/or quality of fledged young or litter size (Danchin et al. 1998; Doligez et al. 2002; Betts et al. 2008).

Based on the above assumptions, we conceptualize a population of individuals that settle sites sequentially based on the availability of options and information available. The Wallenius hypergeometric distribution (henceforth, WHGD; Fog 2008; Schmidt et al. 2015b) provides an analytically tractable approach to determine per capita population growth rates based on informed habitat selection. The WHGD is similar to the more familiar hypergeometric distribution, however, the former takes into account unique biases assigned to the different objects that are sampled. Breeding sites may be good (G) or bad (B), and the number of sites of each quality is denoted, respectively,  $T_G$  and  $T_B$  ( $T$  = total number of sites). Heuristically, sites are picked like colored balls sampled from an urn. However, information biases the sampling and, hence, choice. Specifically, good and bad sites have weights associated with their probability of being chosen and thus occupied, and together these weights determine the odds ratio:  $w$ . We assume the odds ratio is a function of personal and social information, which saturates with population density according to equation (1). For a population size  $N$ , the WHGD distribution gives the probability distribution for the number of good sites selected, with bias  $w$ , after  $N$  trials. The WHGD distribution is difficult to compute, in general, but the expected number of good draws can be implicitly determined following the ap-

proximation derived by Fog (2008). To adopt Fog's approximation in the context of our model assumptions: If the population density is  $N$ , and provided  $N < T$ , then the population picks  $N$  number of sites. We thus obtain the expected number of good sites occupied,  $E_G$ , as the solution to

$$E_G/T_G + (1 - E_B/T_B)^w = 1, \quad (1)$$

where  $E_B$  is simply  $N - E_G$ . We thus can derive the expected future population size ( $N_{t+1}$ ) as

$$N_{t+1} = S_A N_t + S_J (R_G E_G + R_B E_B), \quad (2)$$

where  $S_A$  and  $S_J$  are adult and juvenile survivorship, respectively, and  $R_G$  and  $R_B$  are expected reproductive success in good and bad sites, respectively. In all cases, we evaluated the model using Matlab to find numerical solutions to equation (1) that were applied to equation (2) and evaluated across a population density gradient of  $N = 1-100$ .

We define  $K$ , or carrying capacity, as the stable equilibrium population density such that the per capita population growth rate ( $\lambda$ ) equals 0, where  $\lambda$  is calculated as  $\lambda = (N_{t+1} - N_t)/N_t$ . Consider first the case without social information ( $a = 0$ ). Assuming individuals are informed ( $w_0 > 1$ ), good sites are filled faster than poor sites as the population increases (i.e.,  $\lambda > 0$ ), in turn producing negative density dependence (McPeck et al. 2001). Therefore, to ensure some  $K < T$  exists, we choose parameter values for  $R_G$ ,  $R_B$ ,  $S_A$ , and  $S_J$  such that the population cannot sat-

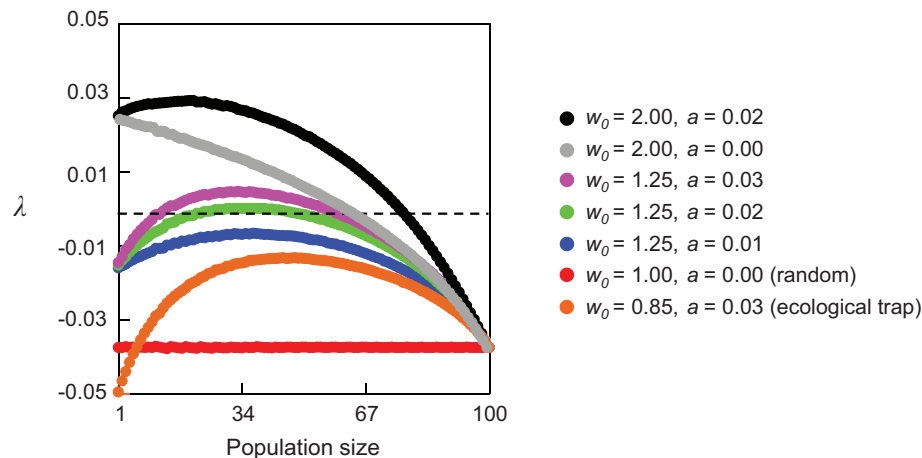
urate the habitat; that is,  $\lambda < 0$  as  $N \rightarrow T$  (fig. 1, gray curve). If individuals are uninformed ( $w_0 = 1$ ), they fill sites randomly and the population has density-independent dynamics. Since, in the first scenario,  $\lambda < 0$  as  $N \rightarrow T$ , uninformed individuals in the second scenario, which differ only by the absence of information, cannot persist; that is,  $\lambda < 0$  for all  $N \in [0, K]$  (fig. 1, red curve). Last, consider the addition of social information that saturates with population density. Social information will produce a hump-shaped relationship (positive density dependence at low  $N$ ) between per capita population growth ( $\lambda$ ) and population density (fig. 1). Either weak or strong Allee effects may be present. (Note that assuming  $\lambda < 0$  for an uninformed population restricts the model's outcomes to strong Allee effects when  $a > 0$ . Relaxing this assumption can produce weak Allee effects but requires adding an additional mechanism of density dependence. We illustrate this in app. A; apps. A and B available online.)

There are nine unique qualitative combinations of  $w_0$  and  $a$  (fig. 2). However, we consider only the following subset:

*Combination 1.*  $w_0 = 1$  and  $a = 0$  (fig. 2, center). This produces random habitat selection and density-independent population growth.

*Combination 2.*  $w_0 > 1$  and  $a = 0$  (fig. 2, bottom center). There is a preexisting bias toward choosing good sites but no social information.

*Combination 3.*  $w_0 > 1$  and  $a > 0$  (fig. 2, bottom right). There is a preexisting bias toward choosing good sites, and



**Figure 1:** Allee effects produced by varying the strength of personal ( $w_0$ ) and social ( $a$ ) information. Random habitat selection is shown in red and negative-density dependent growth in gray. All other simulations show an Allee effect. A weak Allee effect is present when  $w_0$  is large (black). Strong Allee effects (e.g., violet, green) are present when  $w_0$  is reduced, but social information is strong. When both  $w_0$  and  $a$  are weak, a population may not be sustainable at any density ( $\lambda < 0$ ) and will go extinct (blue). An ecological trap is present when  $w_0 < 1$  (orange), which increases extinction risk. Parameter values are as follows:  $T_G = 50$ ,  $T_B = 50$ ,  $R_G = 1.5$ ,  $R_B = 0.25$ ,  $S_A = 0.70$ ,  $S_J = 0.3$ ,  $T = 100$ . See text for definition of terms. Data underlying figure 1 were produced using Matlab scripts and are deposited in the Dryad Digital Repository: <http://dx.doi.org/10.5061/dryad.k4c21.2> (Schmidt et al. 2015a).

	$a < 0$	$a = 0$	$a > 0$
$w_0 < 1$	Ecological trap and social reinforcement	Prior Information only Ecological trap	Ecological trap and social amelioration
$w_0 = 1$	No prior information -DD social Information	No prior or social information (random habitat selection)	No prior information +DD social Information
$w_0 > 1$	Prior information and conflicting social information	Prior information only	Prior information and social reinforcement

**Figure 2:** Nine unique combinations of personal information bias ( $w_0$ ) and density dependence in social information ( $a$ ) based on our modeling approach. Our framework integrates the concept of ecological traps ( $w_0 < 1$ ; *top row*) with information use and illustrates how traps may be reinforced (*top left*) or ameliorated (*top right*) through social information. We also recognize a new type of ecological trap (social information trap) that emerges from the consideration of social information ( $a < 0$ ; *left column*). It may reinforce the traditional ecological trap (*top left*), act independently (*left center*), or conflict with personal information (*bottom left*; see fig. 1 for an example).

conspecifics (social information) reinforce personal biases in a density-dependent manner.

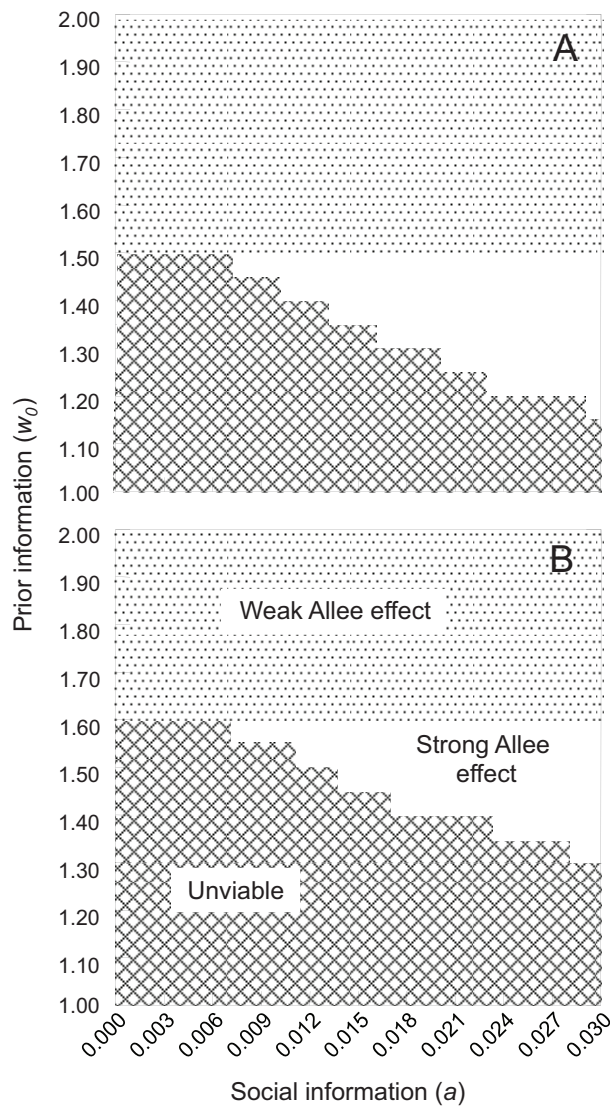
*Combination 4.*  $w_0 < 1$  and  $a > 0$ . Here  $w_0 < 1$  implies there is a preexisting bias toward choosing bad sites in the absence of social information. This is an ecological trap following Robertson et al.'s (2013) broad definition. However, since  $a > 0$ , social information can ameliorate and potentially reverse the bias toward bad sites in a density-dependent manner (e.g., Kokko and Sutherland 2001).

### Results of the Phenomenological Model

Personal and social information have unique influences on the per capita population growth rate. Personal information determines the per capita population growth rate in the absence of conspecifics (i.e., the growth rate intercept in fig. 1), whereas social information influences the rate of change in  $\lambda$  with population size (fig. 1). The presence of social information produces a hump-shaped relationship between  $\lambda$  and the number (or density) of conspecifics (fig. 1), which reflects the existence of a weak or strong Allee effect. All else equal, increasing  $w_0$  promotes a weak Allee effect, provided social information is present (e.g., green to black in fig. 1). In turn, decreasing  $w_0$  promotes a strong Allee effect or population extinction. Increasing social information shifts the Allee threshold, when pres-

ent, to the left, resulting in a smaller minimum viable population size (fig. 1, green to violet). Concomitantly, the stable equilibrium shifts to the right, resulting in a greater equilibrium population size. Decreasing social information reverses these effects and flattens the per capita population growth rate curve, potentially eliminating all nonzero equilibrium points and resulting in extinction (fig. 1, blue). Ecological traps ( $w_0 < 1$ ) decrease  $\lambda$  at low population density. If the trap is severe, the population will decline regardless of population size and commensurate social information. For example, compare the scenario with a bias for good sites ( $w_0 = 1.25$ ; fig. 1, violet curve) to a severe ecological trap ( $w_0 = 0.85$ ; orange) under equivalent per capita levels of social information. In this scenario, if the trap were weaker ( $w_0 \sim 0.95$ ), there would be a strong Allee effect that included a stable equilibrium. We call this social amelioration of an ecological trap (fig. 2).

The qualitatively unique outcomes in figure 1 can be generalized based on a population's location in the information state space ( $w_0$ - $a$  plane; fig. 3). Weak Allee effects are produced under sufficiently high personal information,  $w_0$ . Below this, the population will be unviable or may exhibit a strong Allee effect if social information is high. Transitions between qualitatively unique outcomes can be abrupt if changes to  $w_0$  or  $a$  occur. Likewise, a population near the boundary between regions may be extinction prone under



**Figure 3:** Variation in qualitative outcomes as a function of the parameter values for personal information (varied at 0.05 increments) and social information (varied at 0.003 increments) for two different habitat compositions:  $T_G = 50$ ,  $T_B = 50$ ,  $R_B = 0.25$  (A);  $T_G = 40$ ,  $T_B = 60$ ,  $R_B = 0.46$  (B). Fixed parameter values are as follows:  $S_A = 0.70$ ,  $S_I = 0.3$ ,  $R_G = 1.5$ . See text for definition of terms.

temporal fluctuations in density. We note that these qualitative outcomes depend not only on a population’s capacity for information (i.e.,  $w_0$ - $a$  plane; fig. 3) but also the value of information (Koops 2004), which is predicated, in part, on habitat composition. In other words, changing the relative proportion (i.e., variance) of options, even if mean quality remains unchanged, influences per capita population growth rates when individuals are informed (cf. figs. 3A and 3B). See Donaldson-Matasci et al. (2010) and appendix B for further elaboration.

### Adding Mechanisms of Information Use

Although our model is general, the absence of mechanism limits its application. For instance, we would like to understand whether explicit mechanisms of information use could produce a level of selection bias necessary to produce the noted outcomes. Second, information based on prior experience will decline over time. In this section, we build on Schmidt et al.’s (2015b) use of the WHGD approach for examining informed habitat selection in the context of breeding passerines. Individuals may use multiple sources of information (Doligez et al. 2003), however, for simplicity, we consider a scenario of assessing habitat quality using offspring activity (e.g., fledgling vocalizations; Betts et al. 2008) as a performance-based cue.

Consider again a habitat with  $T_G$  good and  $T_B$  bad breeding sites. We assume individuals prospect for cues of offspring activity, which bias habitat selection in the following breeding season. We denote fledgling vocalization rates as  $\Phi_G$  and  $\Phi_B$  for good and bad sites, respectively. Good sites have higher success/productivity than bad sites, therefore,  $\Phi_G > \Phi_B$ . For the moment, we assume site quality is constant through time. We let  $\Pr_{(G)}$  and  $\Pr_{(B)}$  be the probabilities of detecting fledgling activity in a given site. Assuming the probability of no detection over a prospecting time,  $X_{obs}$ , is Poisson distributed, the expected probability of detecting fledglings in good and bad habitat is, respectively,

$$\Pr_{(G)} = f_G(1 - (\exp(-\Phi_G X_{obs}))), \quad (3a)$$

$$\Pr_{(B)} = f_B(1 - (\exp(-\Phi_B X_{obs}))), \quad (3b)$$

which yields the social odds ratio ( $S_{odds}$ ):

$$S_{odds} = \frac{\Pr_{(G)}((1 - \Pr_{(B)}))}{(1 - \Pr_{(G)})(\Pr_{(B)})}, \quad (4)$$

where  $f_G$  and  $f_B$  are fledgling rates in good and bad sites, respectively. Assuming  $X_{obs}$  is independent of habitat type, the odds ratio is determined by fledgling rates, detection rates, or both. Competition over sites could negatively affect  $X_{obs}$  through frequency-dependent selection, and this model is amenable to a game theoretical approach (Schmidt et al. 2015b). However, at the end of the breeding, there is little competition for breeding sites. Thus,  $X_{obs}$  could be large, and the likelihood of not detecting fledglings, if present, may be small. In this case, detection of fledglings is driven mainly by the ratio  $f_G/f_B$ , the number of individuals producing information, and the number of sites sampled by prospectors. Assuming each individual randomly samples  $m$  unique sites from a total of  $T$  sites available, the proportion of  $T$  sites that have been sampled at least once is given by  $1 - (1 - m/T)^N$ , which reaches an asymptote of one as  $N$

increases. For a large population size, all sites will have been sampled at least once, so social information is maximized for a given  $m$  and  $T$ . As  $N$  converges to zero, there is no social information collected through prospecting, and individuals must use personal information only. This produces a formulation for social information ( $S$ ):

$$S = S_{\text{odds}} \left[ 1 - \left( \frac{1-m}{T} \right)^N \right]. \quad (5)$$

We assume that individuals randomly prospect sites independently of each other and that sampled sites are representative of the habitat composition at large (i.e., we take a mean value approximation as opposed to tracking individuals or sites). Likewise, we do not track settlement to individual sites that a prospector visited. Instead, we assume prospecting time,  $X_{\text{obs}}$ , is spread over many sites that form a representative sample of the environment from which an individual chooses a site to occupy based on the WHGD.

Finally, we can examine the effects of temporal variability in site quality following the approach of McNamara and Dall (2011). A site that is good in one year is bad in the next year with probability  $Q_{GB}$  ( $Q_{BG}$  denotes the reverse) and remains bad (or good) for  $1/Q_{GB}$  (or  $1/Q_{BG}$ ) years, on average. We assume all sites change independently of each other, and therefore, the proportion of sites of quality  $i$  are  $P_i = Q_i / (Q_{GB} + Q_{BG})$ . We assume  $Q_{GB} = Q_{BG} = Q$ , such that  $P_G = P_B = 0.50$ , the point at which information cues have their maximum value (Donaldson-Matasci et al. 2010;

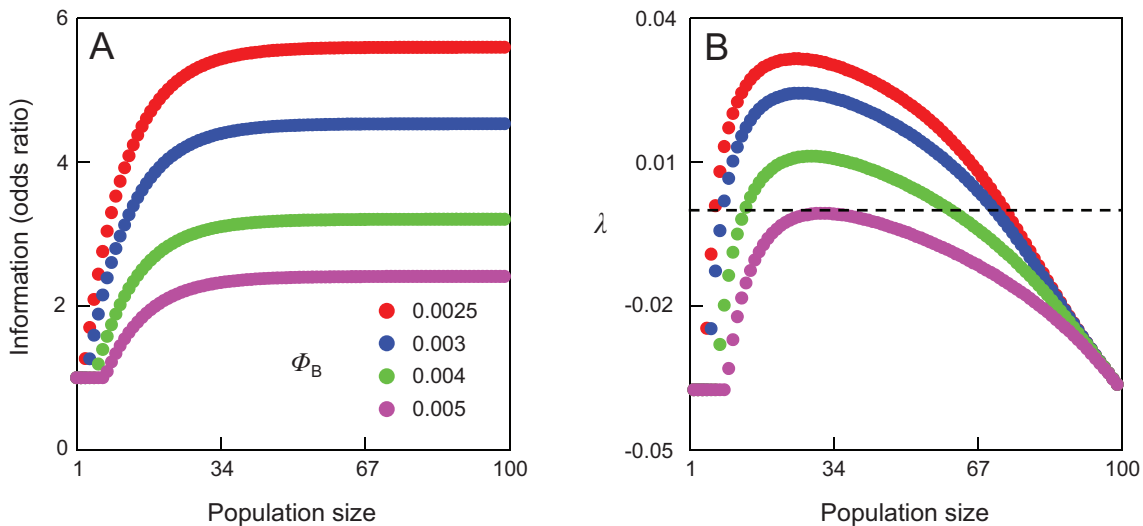
app. B). The final formulation of the odds ratio combines prior odds and social odds additively, minus one to prevent double counting (i.e., since  $w = 1$  represents no bias):

$$w = w_0 + S(1 - Q) - 1. \quad (6)$$

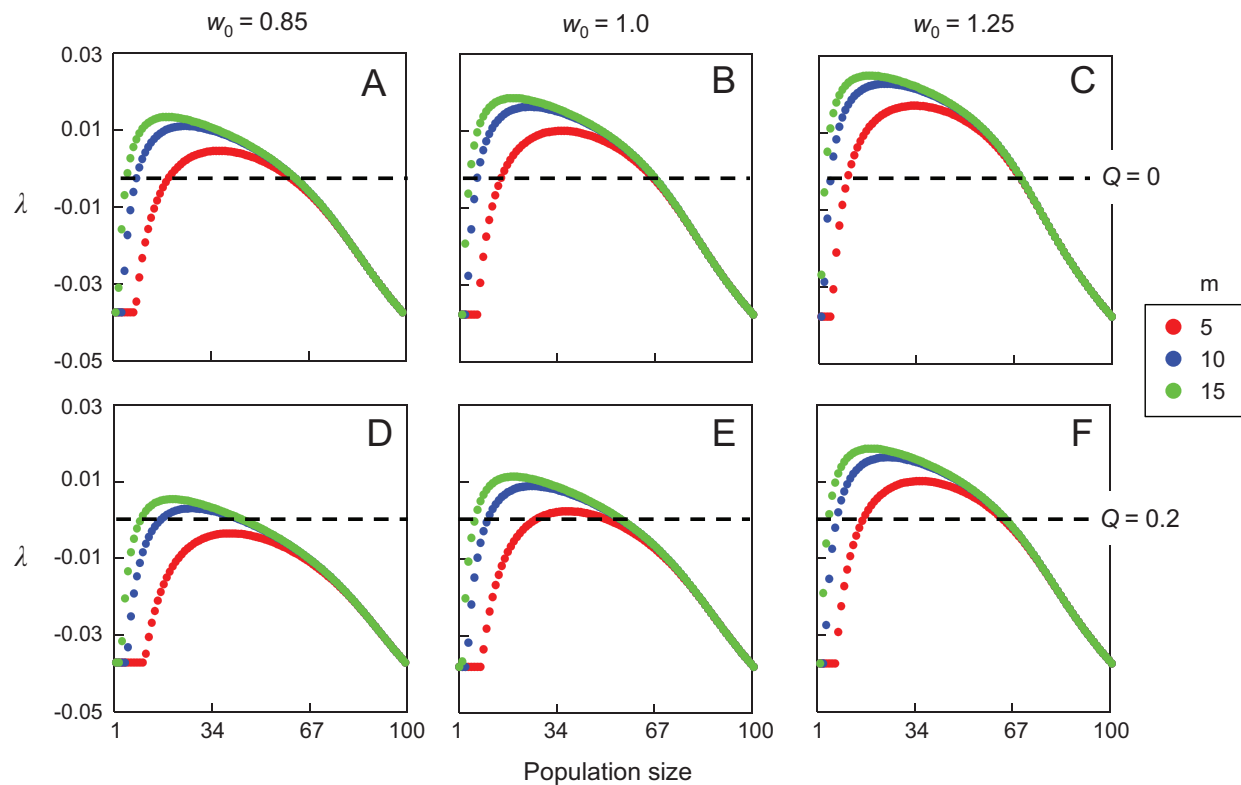
*Results of the Prospecting Model*

A full analysis of the mechanistic model is not our goal. Rather we limit our analyses to (1) whether the social prospecting mechanism produces the phenomena we observed in the general model, (2) how individual sampling effort in time ( $X_{\text{obs}}$ ) and space ( $m$ ) influence the odds ratio and  $\lambda$ , and (3) how temporal variability influences the odds ratio and  $\lambda$ .

The qualitative relationship between the  $\lambda$  and  $N$  of the prospecting model retains key features of the phenomenological model (fig. 4). Reducing the social odds through cue detection (eq. [3]; fig. 4A) lowers  $\lambda$  (fig. 4B). However, social information is also present through differences in fledging rates ( $f_G, f_B$ ), which produces the unimodal growth curve. Information increases with greater heterogeneity in habitat-specific detection of conspecific success and can rise rapidly with the number of conspecifics and saturate at low population size (fig. 4A). A social trap (fig. 2, lower, left-hand box) may be present if, for example, hungrier fledglings in bad habitats beg more frequently or habitat structure facilitates cue detection in bad habitat (fig. 4B, purple curve:  $\Phi_B > \Phi_G$ ).



**Figure 4:** Information-mediated Allee effects under the social prospecting model with variation in social cues in the bad habitat,  $\Phi_B$ , as the good habitat,  $\Phi_G$ , is held constant ( $\Phi_G = 0.004$ ). Increasing the variation in social cues, that is,  $\Phi_G - \Phi_B$ , increases the odds ratio (A) and per capita population growth rate (B). An ecological trap may exist when  $\Phi_B > \Phi_G$ ; that is, fledglings are more likely to be detected in bad habitat (e.g., undernourished birds beg more frequently; purple). Parameter values are as follows:  $w_0 = 1$ ,  $T_G = 50$ ,  $T_B = 50$ ,  $R_G = 2.5$ ,  $R_B = 2$ ,  $S_A = 0.70$ ,  $S_I = 0.3$ ,  $X_{\text{obs}} = 100$ ,  $\Phi_G = 0.004$ ,  $m = 10$ ,  $f_G = 0.5$ ,  $f_B = 0.25$ ,  $Q = 0$ . See text for definition of terms.



**Figure 5:** Qualitative and quantitative difference per capita population growth and Allee effects due to differences in sampling effort (number of sites sampled,  $m$ ) and temporal variation ( $Q$ ). Increasing either  $m$  or  $Q$  shifts the Allee threshold (when present) to the left and decreases the per capita population growth rate. Fixed parameter values are as follows:  $T_G = 50$ ,  $T_B = 50$ ,  $R_G = 2$ ,  $R_B = 2$ ,  $S_A = 0.70$ ,  $S_I = 0.3$ ,  $X_{\text{obs}} = 50$ ,  $\Phi_B = 0.004$ ,  $\Phi_G = 0.0025$ ,  $f_G = 0.5$ ,  $f_B = 0.25$ . See text for definition of terms.

Sampling effort for social information also varies with the number of sites each individual prospects,  $m$ . When individuals sample few sites ( $m = 5$ ), the population is limited by both the number of information providers and poor sampling (fig. 5, red growth curves); therefore, per capita population growth is unaffected by an initial small increase in  $N$ . Increasing sampling effort accelerates the increase  $\lambda$  with population density. In turn, the maximum achievable per capita population growth rate increases, which buffers the population against temporal variation (fig. 5, cf. top and bottom rows) and shifts the Allee threshold to the left (smaller minimum viable population size) but has little effect on  $K$ . Temporal variability (fig. 5, bottom row), in general, produces a decline in social information and per capita population growth.

### Discussion

When spatial heterogeneity in habitat quality exists, per capita population growth is influenced by biases in habitat selection. Indeed, a sufficient amount of bias may be necessary for population persistence. That is not to say that

uniformed or poorly informed populations are vulnerable to extinction, since biases will evolve through selective pressures (McNamara et al. 2006; McNamara and Dall 2011). However, there is a growing consensus that information is an important driver of population dynamics (Schmidt 2004; Armsworth and Roughgarden 2005; Lister 2014). When information is partially socially derived (Boulinier and Danchin 1997; Danchin et al. 1998; Jaakkonen et al. 2013), weak or strong Allee effects will be present. Under these circumstances, small population size will reduce the quantity and/or quality of information available to individuals. Hence, even though personal information may be available ( $w_0 > 1$ ), per capita population growth may be negative below a minimum viable density, that is, the Allee threshold. If the population size drops below the Allee threshold, it is vulnerable to extinction in the absence of ameliorating influences, such as improved environmental conditions. Moreover, a lower Allee threshold, as occurs with higher  $S_{\text{odds}}$  (or  $a$ ), can buffer populations against other environmental influences that may occasionally result in small population sizes.

We examined these possible scenarios using both a phenomenological and mechanistic model, focusing on strong



Allee effects for their greater conservation implications. Phenomenologically, we unify personal and social information, Allee effects, and ecological traps into a common framework in terms of the direction of personal bias and the mediating influence of social information (fig. 2). Second, we note that small changes to personal information and the per capita increase in social information ( $a$ ) can lead to abrupt transitions between qualitatively different outcomes, including extinction (figs. 1, 3). Third, we observed that per capita population growth of informed habitat selectors is both quantitatively and qualitatively influenced by the level of environmental uncertainty and the fitness value of information (fig. 3; app. B). This suggests a richer connection to information theory (e.g., see Donaldson-Matasci et al. 2010) and unforeseen opportunities to manage information for conservation value (see app. B).

Our mechanistic model, derived from prospecting on conspecific success, demonstrates that the qualitative results from the phenomenological model are robust to a more realistic derivation of social information and moderate levels of temporal variability. We also show that information increases with greater heterogeneity in detection rates from prospecting (fig. 4) and can rise rapidly with the number of conspecifics, shifting the Allee threshold further to the left than the general model. The resulting strong positive density dependence at low  $N$  facilitates a rapid return time to  $K$ .

Finer variation in the relationship between per capita population growth and population density, including the presence or location of an Allee threshold and the strength of density dependence, will be largely predicated on the details of personal and social information acquisition, the structure of spatiotemporal variation, and coexistence of multiple tactics of information use. For instance, personal information could be based on an individual's own past performance (Switzer 1997) or natal experience (Davis and Stamps 2004), or currently assessed via prospecting on reproductive risk (Emmering and Schmidt 2011). If variation in site quality is strongly spatially autocorrelated (e.g., colonial breeders), social information use based on assessing patch reproductive success, as opposed to individual reproductive success, may emerge (Boulinier and Danchin 1997). Even focusing on a single informed tactic is likely to be too simplistic, as shown in Doligez et al.'s (2003) game theoretical analysis of multiple competing tactics. So while the capacity for Allee effects exists when social information is available to habitat selectors, there is a risk of overgeneralizing from any given model.

Although our emphasis has been on information that produces biases in breeding habitat selection, it is important to investigate additional ecological contexts. Prominent among these may be information used in assessing spatial and temporal variability in resources (Jackson et al. 2008)

or predation risk. The latter includes alarm networks, which may produce group mobbing (Krams et al. 2006) or anticipatory antipredatory behavior (Lima 2009). In addition, multiple Allee effects are known to operate within individual systems and are beginning to receive greater attention (Berec et al. 2006). Cues used by individuals to select breeding sites within a spatially heterogeneous environment may interact with other density-dependent processes that may modify coexisting component or demographic Allee effects produced through other mechanisms. This includes anthropogenic Allee effects (Courchamp et al. 2006; Hall et al. 2008), which result from, for example, increasing exploitation pressure of rare species as their real or perceived economic value increases.

Allee effects may also combine with ecological traps illustrating how social information and individual biases (innate or driven by environmental cues) may operate together (Kokko and Sutherland 2001). Traps that bias habitat selection toward bad sites depress population growth. At higher population densities, social information may ameliorate the ecological trap, but at low densities, Allee effects may be particularly strong. If traps are severe and information from conspecifics does not compensate local population, extinction may ensue. Alternatively, if social information is not based on reproductive performance (e.g., myopic habitat copying or conspecific attraction), it could reinforce other individuals' initial use of improper cues (social information traps; fig. 2; e.g., Rodewald et al. 2011) or override innate habitat preferences (Nocera et al. 2006; Betts et al. 2008).

An alternative to widespread information use was recently proposed by McNamara and Dall (2011) as the multiplier effect, in which unconditional strategies (e.g., natal philopatry), which ignore all but the most reliable environmental cues, may evolve whenever genotypes accumulate in habitats in which they do well. Under this effect, social information should be ignored, and socially mediated Allee effects would not be present. Likewise, the evolution of social versus individual learning may be contingent on the spectral properties of temporal variation (Whitehead 2007), with implications for information-mediated Allee effects. Despite these caveats on theoretical grounds, it would be rash to ignore the ubiquitous empirical support for widespread use of personal and social cues in breeding habitat selection (see reviews in Danchin et al. 2004; Valone 2007; Blanchet et al. 2010; Chalfoun and Schmidt 2012; Szymkowiak 2013).

Few empirical studies have examined the population-level consequences of information use (but see Ponchon et al. 2015) or how individuals weigh personal and social information (Fletcher 2006; Fletcher and Sieving 2010). Current case studies include conspecific attraction based on location and population density as cues for habitat quality

(e.g., Forbes and Kaiser 1994; Sarrazin et al. 1996; Huijbers et al. 2012). For example, Fletcher (2009) suggested that infrequent occupancy of small habitat fragments in least flycatchers (*Empidonax minimus*), a common pattern in birds, may be due to reduced conspecific cues ultimately resulting in habitat underutilization.

In conclusion, our analytical models demonstrate how social information, a widely used phenomenon in habitat selection and other contexts, may generate positive density dependence at low population size resulting in information-mediated Allee effects. This tendency has the potential to produce positive feedbacks in declining populations: an environmentally driven stressor (e.g., fragmentation reduces dispersal to small patches, a toxin reduces adult survival) causes an initial population decline, and a subsequent reduction in information providers amplifies the initial population decline. The population may go extinct in a deterministic fashion or be subject to a greater risk of extinction through stochastic events that tip it below an Allee threshold. In this way, information-mediated Allee effects may contribute to the extinction debt incurred from habitat loss and other anthropogenic stressors (Tilman et al 1994).

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