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PERSPECTIVES IN ORNITHOLOGY

ADAPTIVE BREEDING-HABITAT SELECTION: IS IT FOR THE BIRDS?

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ADAPTIVE HABITAT SELECTION

The question of why animals choose particular habitats has important implications for understanding behavioral evolution and distribution of organisms in the wild and for delineating between habitats of different quality for conservation and management. Habitats chosen by animals can influence fitness outcomes via the costs (e.g., predation risk) and benefits (e.g., food availability) of habitat use. Habitat preferences should therefore be under selection to favor those that confer fitness advantages (Clark and Shutler 1999). Indeed, prevailing theory suggests that the habitat preferences of animals should be adaptive, such that fitness is higher in preferred habitats (Hildén 1965, Southwood 1977, Martin 1998). However, studies have often identified apparent mismatches between observed habitat preferences and fitness outcomes across a wide variety of taxa (Valladares and Lawton 1991, Mayhew 1997, Kolbe and Janzen 2002, Arlt and Pärt 2007, Mägi et al. 2009). Certainly, one limitation of studies may be that assessment of "fitness" is typically constrained to fitness surrogates such as nest success rather than lifetime reproductive success or classic Fisherian fitness (Endler 1986). Nevertheless, important habitat choices such as nest sites influence the probability that temporarily sedentary, dependent young are discovered by enemies such as predators and parasites. We therefore expect, on average, to see congruence between evolved habitat preferences and relevant components of fitness (e.g., nest success). Here, we (1) review the prevalence of apparent mismatches between avian breeding-habitat preferences and fitness outcomes using nest-site selection as a focus; (2) describe several potential mechanisms for such mismatches, including anthropogenic, methodological, and ecological–evolutionary; and (3) suggest a framework for understanding the contexts in which habitat preferences represent adaptive decisions, with a primary focus on ecological information theory. We largely focus on habitat selection as a behavioral process at the scale of individuals (e.g., Robertson and Hutto 2006), rather than at the scale of population-level patterns (Fretwell and Lucas 1970, Morris 2003, Johnson 2007). However, these two scales cannot be wholly divorced from one another, as we will discuss.

REVIEW OF CONGRUENCE BETWEEN NEST-SITE SELECTION AND SUCCESS

We reviewed refereed journal articles published during a 20-year period (1990–2010) using the search engines Biological Abstracts and Web of Science, with no specific journal restrictions except that papers were written in English. Search terms included combinations of "nest-site selection," "nest-site choice," nest-site preference," "nest-patch selection," and "habitat selection" with "fitness," "nest success," "nest predation," "reproductive success," and "breeding productivity." We restricted results to native, noncolonial species, natural nest substrates (i.e., no nest box or artificial nest studies), and observational data (no experiments). Our first-cut inclusion criterion was that authors addressed nest-site choice and resulting nest success with respect to at least some of the same habitat metrics simultaneously during the same study. Authors needed to document differential choice (i.e., not just habitat use) via some sort of use-versus-availability analysis. Fitness responses were restricted to nest success (not clutch size, nestling growth, etc.). Nest success could be evaluated by either binary (i.e., successful versus depredated) or continuous (e.g., daily nest survival probability or number

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of young fledged) metrics. We focused on papers that assessed nest success with respect to nest predation and/or parasitism to limit the confounding influence of factors such as weather and food limitation. We restricted the review to studies with sample sizes of ≥30 nests per species to limit instances of null results because of limited replication and statistical power. Analyses were limited to the nest-substrate or nest-patch scale. For papers that evaluated more than one species, each species was treated as an individual test.

For each included paper, we recorded authors, publication year, focal species, geographic location (by continent), general habitat type (forest, grassland, shrubland, riparian, or mixed), study duration (years), number of nests, and nest type (cavity, ground, and open cup or dome). In addition, we recorded the individual habitat variables assessed with respect to nest-site preferences and nest success, whether preferences were documented, and whether and which habitat attributes differed with respect to nest success. We considered nest-site preferences and success to be congruent when nest-site preferences and resulting success were associated with the same habitat metric(s). Congruence was calculated as a percentage of documented preferences (by metric) that were also positively associated with success. For example, if a species showed a preference for two metrics (e.g., tree height and percent grass cover) but only tree height was associated with success, congruence was recorded as 50%. Percent congruence data were arcsine transformed (though we present actual values) and evaluated by factors of interest using univariate analysis of variance (location, habitat type, nest type, spatial scale) or linear regression (study duration and nest sample sizes). Moreover, we documented whether any assessed preferences were neutral or negatively related to nest success. Finally, we extracted any hypotheses that were posed by authors to explain observed mismatches between nest-site preferences and success in their studies to examine whether any trends emerged in explanations for lack of congruence in preference–performance measures.

Our review yielded a sample of 94 tests from 70 papers focused on 85 species from 36 different avian families (Table S1, an online supplement; see Acknowledgments). Tests were obtained from all continents except Antarctica but were biased toward North America (Table 1). The mean (± SE) number of habitat variables used to assess nest-site selection and success were 10.2 ± 0.83 and 12.1 ± 0.85, respectively. Therefore, the habitat variables used to assess both preference and success did not always overlap completely, with

Table 1. Summary of congruence (percent ± SE) between nest-site preferences and nest success by location. We defined congruence as the percentage of cases in which assessed habitat preferences paralleled nesting success with respect to the same habitat metrics.

Continent	Number of tests	Congruence ± SE
North America	67	23.3 ± 3.8%
Europe	12	23.2 ± 6.9%
South America	7	0 ± 0%
Asia	3	5.7 ± 5.7%
Australia	3	0 ± 0%
Africa	1	20.0 ± 0%

Table 2. Results of tests of congruence (proportion of nest-site preferences positively associated with nest success) with respect to factors of interest. Habitat types were forest, grassland, shrubland, riparian, and mixed; spatial scales were nest substrate, patch, or both; nest types were cavity, ground, and open cup or domed.

Factor	Statistic	df	P
Location (continent)	$F = 1.42$	5 and 93	0.23
Habitat type	$F = 1.88$	4 and 93	0.12
Spatial scale	$F = 2.42$	2 and 93	0.09
Nest type	$F = 0.90$	2 and 93	0.41
Sample size (nests)	$t = 1.74$	—	0.08
Study duration (years)	$t = 0.06$	—	0.96

an overall overlap across studies of 80.0 ± 2.87%. Complete congruence (i.e., all habitat preferences were positively related to success) was observed in only 6.4% of tests. Partial congruence (i.e., some habitat preferences were positively associated with success) was observed in 37.2% of tests, with no relationships between the two in 56.4% of cases. Specifically, the percentage of preferences positively associated with success averaged 20.0 ± 2.98% across all tests, with 72.2 ± 3.51% being neutral and 6.7 ± 1.93% negative.

Congruence varied across geographic locations (Table 1), albeit not significantly (Table 2). The highest values were observed in North America and Europe, where sample sizes for tests were also the largest. Variation in congruence was also observed across major habitat types (Table 2 and Fig. 1A), although only forest and shrubland differed significantly (LSD post hoc test, $P = 0.02$). Congruence tended to be higher when analyzed at the patch than at the nest-substrate scale (Table 2 and Fig. 1B). Tests of cavity-nesters tended to produce lower congruence (Table 2 and Fig. 1C), which is not surprising given that cavity-nesting birds generally experience relatively high nest survival (Ricklefs 1969, Martin 1988), potentially relaxing the selection on cavity nest sites to limit predation, parasitism, or both. Studies with larger nest sample sizes tended to find more congruence, though those of longer duration did not (Table 2).

Proposed Explanations and Mechanisms for Mismatches

Following Table 1, we group proposed mechanisms for incongruence between nest-site preferences and success into three broad categories: anthropogenic, methodological, and ecological–evolutionary, and discuss each in turn with an emphasis on ecological and evolutionary mechanisms. Although understanding anthropogenic and methodological causes for patterns of incongruence is necessary for evaluating nesting habitat dynamics in altered landscapes and under different sampling scenarios, we emphasize the need for a shift toward framing ecological and evolutionary hypotheses whose predictions can ultimately be subjected to empirical and experimental testing.

Anthropogenic explanations.—Mismatches between habitat preferences and reproductive performance may, in some cases, be attributable to ecological–evolutionary traps in which historical settlement cues become decoupled from their historical outcomes, usually because of anthropogenic habitat change (Table 3). Very few study areas have not been altered in some way by human
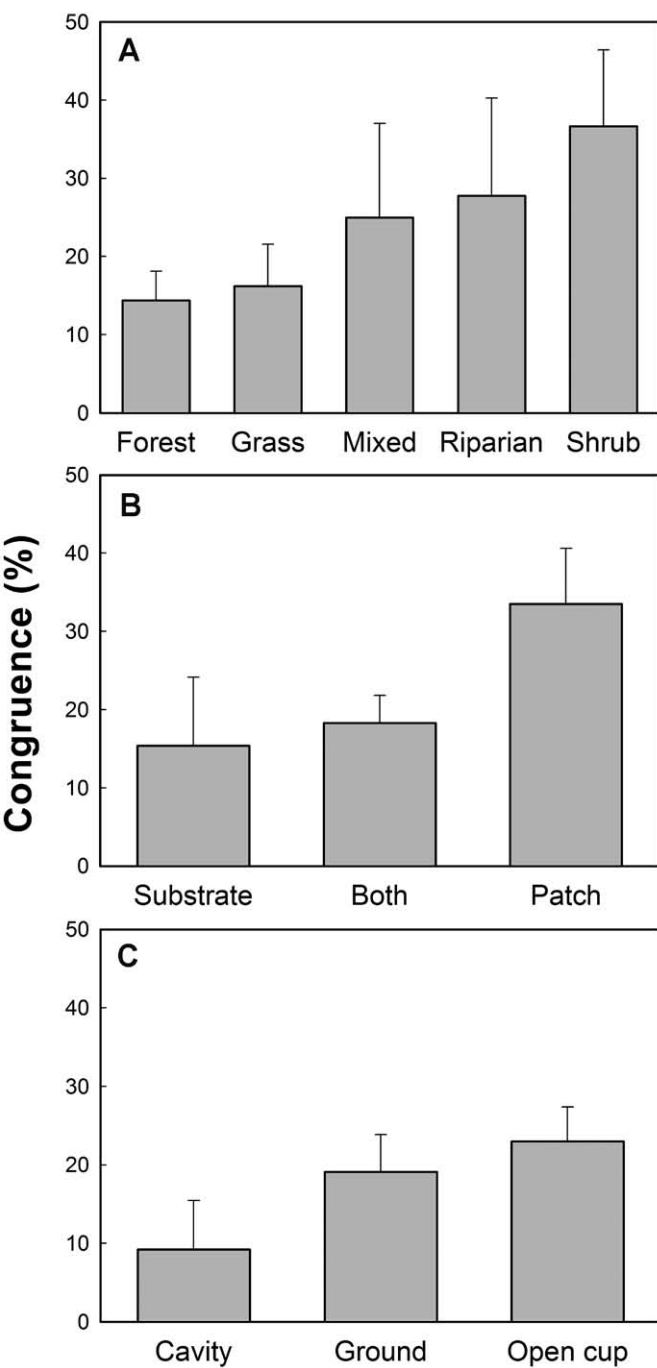
FIG. 1. Percentage of cases in which assessed habitat preferences paralleled nesting success with respect to the same habitat metrics (congruence) in relation to (A) general habitat type, (B) scale at which tests were conducted, and (C) nest type.

TABLE 3. Hypotheses proposed for observed lack of congruence between assessed avian nest-site preferences and nest success with respect to the same habitat metrics in reviewed studies (see text for specific inclusion criteria; n = number of papers in which the hypothesis was suggested).

Hypothesis for discordance	n
Anthropogenic	
Swamping by influx of generalist–novel nest predators	10
Ecological traps; preferences evolved under historical, not current, habitat conditions	19
Methodological	
Small sample size or lack of power	5
Intercorrelated habitat variables leading to confounding of factors	7
Critical habitat features not measured	12
Ecological–evolutionary	
(a) Poor nest sites already selected out	4
(b) Preferences also shaped by other fitness components (e.g., adult survival)	5
(c) Adaptive preferences depend on adult experience or quality	6
(d) Optimal nest sites not always limited	6
(e) Competition can limit access to ideal nest sites	7
(f) Intra- and interspecific variation in nest sites favored, so predators cannot develop search images; and/or plasticity in choices favored	7
(g) Tradeoffs with concealment and view of surroundings or ability for escape	7
(h) Risk dependent on parental behavior at nest (defense, activity)	8
(i) Spatial variation in selection pressures	10
(j) Preferences reflect long-term optima; temporal variation in selective pressures	12
(k) Depends on type and foraging strategies of dominant nest predators	15
(l) Complex or diverse nest-predator assemblages ("no site is safe")	16
(m) Nest predation is random, incidental, opportunistic, or stochastic (no directional selection)	20
(n) Tradeoffs with other selective pressures such as microclimate, access to food, and extrapair copulations	24

One form of ecological trap that is relevant and has been commonly proposed (Table 3) is an increase in generalist predators that elevate nest predation risk along habitat edges in landscapes fragmented by land uses such as row-crop agriculture that provide subsidies to predator populations (Gates and Gysel 1978, Chalfoun et al. 2002). Clearly, ecological and evolutionary traps are a pervasive issue in wildlife–habitat relationships, given the scope of human-induced habitat change worldwide.

Methodological explanations.—Several methodological and sampling issues have been put forth as potential explanations for lack of congruence in nest-site preferences and success (Table 3). In some cases, substantial numbers of nests may be required to tease apart relationships if the effect size of habitat choice on the probability of success is low and/or if multiple habitat metrics operate simultaneously to influence habitat-selection strategies.

activities, and such habitat changes can outpace the ability of natural selection to produce viable adaptations to the novel conditions. However, traps are not our major focus, and we direct the reader who is interested in a fuller discussion elsewhere (e.g., Schlaepfer et al. 2002, Battin 2004, Robertson and Hutto 2006).

A potentially pervasive issue in habitat selection studies is correlations among assessed habitat metrics that can obscure which habitat characteristics are actually driving preferences and success. In other words, some habitat metrics are causal in terms of habitat selection and some are simply correlated with the causal metric (Battin and Lawler 2006, Morrison et al. 2006). For example, Chalfoun and Martin (2009) documented that both Big Sagebrush (*Artemisia tridentata*) shrub density and the density of potential nest shrubs (PNS) were correlated with each other and with nest-site choice in Brewer's Sparrow (*Spizella breweri*), but only the experimental removal of PNS increased nest predation risk. Such interrelationships of habitat metrics render the common practice of including a large number of variables in models and letting statistical packages parse out the most "significant" ones without careful *a priori*, biologically relevant hypotheses problematic. Finally, several authors in our review (Table 3) indicated that they may not have included all of the potentially important habitat variables in their analyses. As an example, if authors focus on attributes of nest concealment but the major nest predators within the study area primarily use other sensory modalities for foraging such as olfactory or heat-sensing rather than visual, the assessed habitat attributes may not match reproductive outcomes (Murphy et al. 1997, Conover et al. 2010). Although this is seemingly intuitive, authors rarely provide justification for why the habitat attributes included in their models are the most relevant according to the ecology and natural history of their focal species (Jones 2001, Fisher and Davis 2010).

A second methodological issue that can potentially obfuscate adaptive patterns of habitat selection concerns the spatial and temporal domain of data collection. As we discuss below, natural selection may operate at spatial and temporal scales that differ from those at which data are often collected (Wiens 1989). Authors commonly acknowledge that habitat selection is a hierarchical process that occurs across multiple spatial scales (cf. Hildén 1965, Johnson 1980, Hutto 1985). Selective pressures can vary across scales that may favor the selection of different habitat characteristics at different scales (Orians and Wittenberger 1991, Battin and Lawler 2006, Chalfoun and Martin 2007, Mayor et al. 2009). Moreover, different selective pressures and their associated optimal habitat characteristics may influence specific components of fitness more strongly, which means that estimates of habitat preference and quality based on different fitness metrics can lead to very different conclusions (Pidgeon et al. 2006, Arlt and Pärt 2007, Chalfoun and Martin 2007). For example, breeding female Yellow-headed Blackbirds (*Xanthocephalus xanthocephalus*) preferentially settled in marshes with greater availability of the invertebrate prey fed to nestlings, but they selected nest sites on the basis of microhabitat structure to avoid nest predation (Orians and Wittenberger 1991). Simply measuring the same suite of habitat covariates at concentrically larger radii around breeding territories or nest sites with respect to nest survival is therefore unlikely to reveal the mechanisms underlying patterns of breeding-habitat use (Battin and Lawler 2006).

In general, very few investigations have evaluated habitat selection across multiple spatial scales with respect to relevant habitat attributes and multiple associated components of fitness. Approaches that concentrate on single scales and/or fitness components could miss interesting tradeoffs that occur across

scales and different fitness metrics that are integrated within the overall strategy for breeding-habitat selection. For example, Brewer's Sparrows that settled in high-shrub-cover landscapes experienced higher nest predation rates but fledged larger young, whereas the opposite was typically true in lower-shrub-cover landscapes (Chalfoun and Martin 2007). In such a scenario, because larger fledglings often have higher postfledging survival prospects (Naef-Daenzer et al. 2001), the overall number of individuals that survive to breed could theoretically be equal in the two landscape types or even higher for the one with lower fledging rates, depending on postbreeding-season stressors (Fig. 2). In other words, individuals may have multiple pathways available to maximize reproductive fitness. However, assessments of concurrent or subsequent survival parameters in relation to patterns of avian breeding-habitat use (let alone preferences) are rare (Johnson 2007; but see Holmes et al. 1996, Murphy 2001).

In systems with high temporal variability in selective pressures, preferences may reflect long-term rather than proximate optima (Table 3; Clark and Shutler 1999, Garshelis 2000), which suggests that evaluation of the mean and variance of congruence between preferences and performance over time may prove insightful. In variable systems, moreover, studies of very short duration may paint a very incomplete picture of the selection pressures driving habitat choices. A final temporal methodological consideration concerns site settlement order by nesting birds within a season. Assuming that optimal nest sites are limited within an area, the best areas should be occupied first (i.e., preferred; Robertson and Hutto 2006), often by more experienced and/or dominant individuals (Block and Brennan 1993, Holmes 2007, Johnson 2007). Yet studies rarely parse out the congruence between the attributes of the earliest versus later nest sites chosen within a year
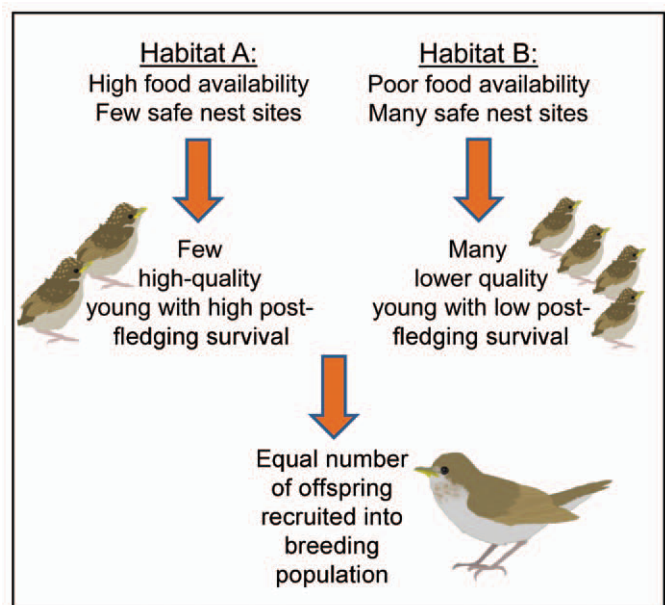

Fig. 2. Potential reproductive outcomes of selecting between two hypothetical breeding habitats that differ in the availablity of food resources and safe nest sites. In theory, both choices could lead to similar fitness via resource variation and selection on different fitness components.

and resulting success. Thus, the resulting comparison is average attributes selected versus nest fates, which may help explain the large number of apparently neutral relationships between nest-site preferences and reproductive performance documented in our review.

Evolutionary and ecological mechanisms.—Numerous ecological and evolutionary explanations have been put forward to explain observed lack of preference–performance congruence (Table 3). Note that many of these can jointly be considered methodological explanations. For example, explanations b and g suggest that adult survival and nest concealment, respectively, influence the relationship between preference and nest success. It is equally valid to consider this a methodological limitation for an individual study. However, because it is not conceivable to measure every possible influence, there will always be such post hoc reasoning to contend with. Second, the explanations fall into some general categories that partly overlap with one another. Explanations may focus on why a preference exists that does not match the highest nest success (e.g., b, c, j), for example, because there are additional (unmeasured) selection pressures such as adult survival (explanation b) that are omitted. Another set of explanations focus on the outcome, that is, on nest success (e.g., i, l, m). In this case they trend toward invoking spatial and/or temporal variation (randomness or unpredictability), implying that birds or natural selection have difficulty tracking a moving optimum. Still other explanations suggest that nest predators and competitors (inter- and intraspecific, e.g., e) constrain habitat choice or select for flexible phenotypes (e.g., to retard the development of search images by predators; e.g., f). Finally, tradeoffs are frequently invoked (e.g., g, l, n) but seldom documented. For example, one tradeoff that may be common within diverse nest-predator assemblages is predator facilitation (Kotler et al. 1992).

Somewhat surprising is how avian ecologists have proffered explanations at different extremes. For example, the lack of congruence in some studies has prompted the suggestion that nest-site selection is random with respect to nest success because predation risk is inherently unpredictable (Filliater et al. 1994, Cooper et al. 1999). By contrast, others have argued that when evolutionary selective pressures are consistent in time and space, organisms may show little flexibility because they currently occupy an adaptive peak (or plateau). Thus, within the range of natural variation, preferences may not be correlated with fitness, as shown in the Yellow Warbler (*Setophaga petechia*; Latif et al. 2012; see below). These explanations seem to be at opposite ends of a continuum. However, Filliater et al. (1994) and Cooper et al. (1999) were observational studies, whereas Latif et al. (2012) was experimental, which may partially explain the very different interpretations. For instance, the lack of fitness differences measured in two habitats utilized under the "rules" of an ideal free distribution does not belie the fact that the habitats are quantitatively different (Schmidt and Whelan 1999). One obtains this conclusion by considering an appropriate conceptual framework and testing it, preferably experimentally. To this end, we turn our attention to potentially useful, if incomplete, frameworks and how a combination of experimental and observational studies based on information hold much promise for understanding the circumstances and mechanisms of when and why breeding-habitat selection is likely to be adaptive.

Adaptation to spatiotemporal variation.—Evolutionary selection pressures that are consistent in time and space can produce relatively fixed habitat preferences. Indeed, evolution can produce organisms that behave as if they have knowledge of the types, frequency, and quality of habitats (McNamara et al. 2006). This evolutionary "information" may form the basis of individuals' prior probabilities in the Bayesian sense (see McNamara et al. 2006). A given species may always nest on the ground or at a level of nest concealment because by doing so they realize, all else being equal, the lowest possible nest mortality. They occupy an adaptive peak, and, over the observed range of preferences, variation does not correlate with fitness (Latif et al. 2012).

Most ecological systems, however, are characterized by considerable variation in time and space. For example, as a nest substrate, Japanese Barberry (*Berberis thunbergii*) affords some protection against nest predation in the Veery (*Catharus fuscescens*). However, the benefit is largely limited to (1) years with high densities of ground-foraging predators (Schmidt et al. 2005), whose abundance can vary by two orders of magnitude across breeding seasons through annual variation in acorn mast (Schmidt and Ostfeld 2008); (2) particular spatial locations (e.g., mesic drainages) where Japanese Barberry is common; and (3) drier seasons, because heavy spring precipitation causes Veeries to shift to more xeric sites with different nesting-substrate options. Finally, the reduction in nest mortality rates in Japanese Barberry in comparison to alternative substrates is greatest in high rodent years—years with the lowest mean nest success, making Japanese Barberry the best option in an otherwise very bad year.

Selective pressures are also likely to vary in ecological and evolutionary time because of variation in the breeding assemblage, the collective nest-site decisions of coexisting species, and predator behavioral responses to nests as prey (Martin 1993, 1996; Schmidt and Whelan 1998). In a study of apparent competition, Schmidt and Whelan (1998) found that nest mortality in Wood Thrush (*Hylocichla mustelina*) nesting in *Lonicera* and *Rhamnus* was influenced by the number of American Robins (*Turdus migratorius*) also nesting in these substrates. Martin and Martin (2001) used reciprocal removal experiments to show that interference competition with Orange-crowned Warblers (*Oreothlypis celata*) produced suboptimal selection and lower nest survivorship in Virginia's Warbler (*O. virginiae*). Moreover, when Orange-crowned Warblers were removed, sites occupied by Virginia's Warblers were indistinguishable from their interference competitor. In both studies, interspecific competition was asymmetric: American Robins and Orange-crowned Warblers were unaffected by their competitor. Not only are heterospecific interactions largely ignored in field studies of nest-site selection (a potential methodological drawback), but breeding birds may also be limited in their ability to assess the strength of interspecific interactions prior to choosing breeding sites (explanations e and f). However, playback experiments suggest that some species may use vocal cues to assess interspecific competition when choosing breeding habitat (Fletcher 2008).

Breeding birds may use a bet-hedging strategy as an evolutionary mechanism for coping with uncertainty and spatiotemporal variability in selective pressures. The term "bet-hedging" actually refers to one of three different strategies discussed in the literature: conservative bet-hedging (play it safe), diversified

bet-hedging (risk-spreading), and adaptive coin-flipping (i.e., random "flipping" between strategies that may outperform a fixed generalist strategy). Olofsson et al. (2009) demonstrated that individuals may actually use a mixture of all three types. If the habitat characteristics that favor nest success vary unpredictably among years, bet-hedging may be a means to maximize long-term fitness, but may only be perceived as adaptive at the appropriate temporal scale. Variation within and between clutch sizes has been attributed to bet-hedging (Boyce and Perrins 1987, Morris and Lundberg 2011), and there is little reason to think that it should be restricted to clutch size. Thus, low congruence (in the short term; see explanation j) and considerable plasticity (both within and among individuals) in breeding-habitat selection should be expected. This topic is ripe for future investigation.

If variation in space (i.e., habitat) exists and fitness maps differently in each habitat to nest-site or nest-patch features (termed a fitness-mapping function), the optimal strategy is one that maximizes the weighted mean fitness function (Cohen 2006). Cohen's analysis shows that the optimal strategy may perform poorly in specific or even most habitats (Fig. 3); rather, the population should be better adapted to more abundant and productive habitats (also see Holt 2003). Second, species are predicted to exploit habitats with positively correlated fitness functions. By contrast, species will be poorly adapted to habitats with negatively correlated fitness functions (e.g., high nest survival is correlated to low food abundance or low juvenile survival). These predictions are ultimately testable in the field. Returning to an earlier example, Brewer's Sparrows settled earlier and in higher densities in landscapes with higher shrub cover and height, which was not associated with higher fledging probability per nest but did result in larger offspring size and renesting propensity (Chalfoun and Martin 2007). Conversely, at the scale of the nest site, females preferred patches with higher densities of potential nest shrubs, which resulted in lower nest predation risk. Food availability was likely driving choices at larger scales, whereas nest predation risk was the important selective pressure at the nest patch scale. This example may fit what Cohen (2006) refers to as negatively correlated fitness functions, where fitness has been partitioned into surviving one of three different periods (nest, fledgling, and adult), and tradeoffs exist among them. Maximizing long-term fitness need not correspond to minimizing mortality associated with any single stage (and accounting for age-specific fecundity, of course) (explanations b and n).

Lastly, perceived habitat quality and patterns of avian settlement at individual sites may be influenced by the characteristics (i.e., risk of predation) of neighboring sites, what Resetarits and Binckley (2009) refer to as spatial contagion of predation risk. Working with aquatic beetles within experimental pools, these authors demonstrated how colonization rates of beetles declined as a function of the risk and proximity of surrounding pools stocked with predators. The mechanism for this effect is not understood, but it may represent a sequential Bayesian updating process in which individuals lowered their estimate of perceived quality on the basis of sampling previously visited (and predator-occupied) sites. Wonderful and accessible overviews on this topic can be found in Bradbury and Vehrencamp (1998) and McNamara et al. (2006). If birds sequentially sample prospective territories prior to settling at a particular site (or on the basis of nest fate; see Schmidt and Whelan 2010), we should see spatial contagion effects.

Fig. 3. Mean fitness across five habitats (a–e; light curves and small arrows) and the mixed population's fitness (bold curve and arrow) illustrated in terms of the number of fledglings produced (substituting the probability of nest predation would not alter the conclusion). "Trait value" may refer to one or more nest-site or patch characteristics, nest height, etc. The optimal trait value does not maximize fitness within any individual habitat (top). This model assumes that individuals lack information on habitat type or phenotypic plasticity in nesting behavior (e.g., site selection). Although these assumptions are not likely to be valid, neither is perfect information likely. Given plasticity, habitat-specific and performance-based cues can allow individuals to better match traits to habitat. Adopted from Cohen (2006).

Cues as proximate indicators of habitat quality.—Good times and good places to breed are likely to have their "tell" (to use a gambling analogy). In other words, information is frequently, if not always, available to guide habitat choices. Indeed, adaptive habitat selection is often most strongly inferred when the focus is on behavioral (e.g., territory settlement and nest-site decision) and life-history responses to specific cues that indicate quality, rather than on quantifying metrics of habitat structure, which too frequently operates within an information vacuum. For instance, cues of predator or brood-parasite presence–activity have been experimentally manipulated through the addition of vocalizations (Eggers et al. 2006, Forsman and Martin 2009, Emmering and Schmidt 2011, Zanette et al. 2011, Parejo et al. 2012), models (Peluc et al. 2008), and odors (Mönkkönen et al. 2009). Such experiments have demonstrated resulting shifts in nest-site selection (Eggers et al. 2006, Peluc et al. 2008, Zanette et al. 2011, Kelly 2012), reduced site occupancy, increased mean nest distance from the source of the cue, and altered life-history traits, such as investment in current reproductive success (Eggers et al. 2006, Zanette et al. 2011, Parejo et al. 2012). Likewise, lack of direct predator cues may explain the strong community pattern of recruitment in response to predator removals by Fontaine and Martin (2006).

Breeding outcomes also produce information (intended or unintended) that may be both private, unless parental care is absent, and public, particularly when reproduction is successful. Given the low vagility of young shortly after leaving the nest,

information regarding breeding success is often spatially explicit. The availability of private and public information has likely led to two performance-based breeding-site-selection strategies commonly observed in birds, the win–stay:lose–switch rule (WSLS; based on the outcome of personal breeding success) and prospecting behavior that contributes to resettlement where conspecific, and in some cases heterospecific, success was observed. A third, but less understood, performance-based strategy is natal habitat imprinting. In this case, however, an individual's own survival is the performance cue that may guide future breeding-habitat selection toward habitats that resemble its natal environment. Before we briefly review these three types of cues, it is worth pointing out that ecologists frequently view cues as inseparable from an appropriate rule of thumb that is thought to approximate an optimal solution to a complex process. This approximation may hold in many circumstances, but rules may have far-reaching consequences outside normal situations (Schmidt 2001, Stephens and Anderson 2001) that harken back to ecological traps.

Informed fidelity.—Personal information based on an individual's own breeding success is a well-recognized pattern in avian habitat selection (Switzer 1997, Stamps 2001, Porneluzi 2003, Schmidt and Whelan 2010), most recently reviewed under the broader theme of habitat familiarity by Piper (2011). The WSLS rule is the simplest manifestation of an individual vacating a site if reproduction is unsuccessful there but remaining at the site (or returning to it) otherwise. This often is seen at the territory level (Hoover 2003) because data are readily tractable from a population of uniquely marked individuals. However, this informed fidelity may be to the territory, to a habitat patch (as in Kokko and Sutherland 2001, Schmidt 2004), or even to general physical characteristics. The WSLS rule likely underperforms in relation to a Bayesian assessment rule (Schmidt and Whelan 2010), which in principle behaves the same way but which accounts for information from all breeding attempts within a season, or even among seasons, and the probability distribution of site quality. For the moment, the Bayesian assessment rule remains untested.

Informed fidelity or switching after nest failure may apply within seasons as well as across seasons (Powell and Frasch 2000, Chalfoun and Martin 2010). Chalfoun and Martin (2010) demonstrated that Brewer's Sparrows change nest-patch characteristics, such as height and potential nest shrub density, between nest attempts within a season. Changes in nest-site characteristics that followed a predation event were greater than those that followed nest success, and pairs that changed nest-patch attributes to a greater extent after failure had higher renesting success, which suggests an adaptive strategy. Similarly, Betts et al. (2008b) observed movement up a habitat-quality gradient inferred from within-season dispersal to sites with greater shrub density—shrub density being correlated with higher survival and nest success. This latter study is based on weak inference, as limited information may have simply led to nonideal habitat choice early in the season. Nonetheless, individual movements within a season may reveal adaptive patterns of habitat selection that are contingent on information availability. Interestingly, informed fidelity could greatly weaken site selection based on current assessment of habitat features when played out as an evolutionary game (see below).

Prospecting.—Typically, predator abundance—and, hence, reproductive success—varies across breeding territories and habitat patches (Morton 2005, Schmidt et al. 2006, Schmitt and Holbrook 2007, Silberbush and Blaustein 2011). Provided there is a moderate level of temporal correlation between years (Doligez et al. 2003, Schmidt 2004), conspecific success can be used as a performance-based cue of site (territory, patch) quality. Since Reed et al.'s (1999) review of prospecting behavior (under the heading of "informed dispersal"), the literature has seen a marked increase in the number of experimental demonstrations of conspecific information use (e.g., Valone 2007, Schmidt et al. 2010). Experiments have directly manipulated breeding success through nestling-transplant experiments at one or more spatial scales (e.g., Doligez et al. 2002, Aparicio et al. 2007, Parejo et al. 2007) or manipulated cues of conspecific breeding success, such as late-season song and fledgling vocalizations (Betts et al 2008a, Kelly 2012). Collectively, these experiments have demonstrated that dispersal, occupancy rates, and settlement times are influenced by direct and indirect information on conspecific breeding success. Although not all studies demonstrate the use of conspecific cues, at least one of the "negative" results makes sense in light of the absence of temporal correlation in site quality among breeding Barn Swallows (*Hirundo rustica*; Safran 2004), which instead use an adaptive site-selection rule based on reusing previously constructed nests and not conspecific nesting success.

Imprinting.—Survival from egg to independence provides information about the quality of the natal habitat and could potentially form the basis for underlying habitat preferences. One form this may take is another rule of thumb: natal habitat imprinting (or natal habitat preference induction, NHPI; Davis and Stamps 2004). Using an optimization approach, Stamps et al. (2009) showed that surviving to the age of dispersal can increase the expected relative attractiveness of cues from natal habitat over the same cue to naive dispersers. Conditions necessary to promote NHPI are that (1) greater natal survivorship must be associated with habitat quality, (2) temporal correlation must exist in quality (or rank quality) within the territory or patch, and (3) habitat quality must rarely be high. All three of these conditions are frequently satisfied in avian breeding systems or, more generally, in empirical studies of predator-free space (Stamps et al. 2009). However, Davis and Stamps's (2004) review cited few experimental demonstrations of NHI in birds. This may be more of an observational limitation or lack of knowledge about the particular habitat attributes on which birds imprint. Our conclusion is that the conditions for NHPI may frequently occur in breeding birds but are grossly understudied, especially in the field.

To summarize this section, cues, many of them performance-based, provide some of the strongest evidence we have that breeding-habitat selection across multiple scales is adaptive. One last note to highlight an often neglected point: An individual breeding attempt may or may not produce offspring, but it always produces information. This habitat-sampling component of breeding behavior may be incredibly important within a season (e.g., moving up a habitat gradient) or between seasons (e.g., directing fidelity versus dispersal). Furthermore, as studies of prospecting have shown, information from even a single breeding attempt may reach, and thereby benefit, a much larger audience than the genetic parents. However, up to this point we have only considered the fitness benefit of information to individuals and have ignored population dynamics. A consideration of density- and frequency-dependent feedback can yield new

insights into the use and benefits of information and reveal additional complexities of breeding-habitat selection.

Adaptive habitat selection when density and frequency dependence operate.—Lack of information or using rules of thumb to guide habitat choice will necessarily lead to imperfect choices or decision making, but they may still represent an adaptive (i.e., fitness-maximizing) solution within the set of constraints under which individuals operate. However, adaptive choices can take on different characteristics in an evolutionary context that involves density and frequency dependence where the fitness consequence of an individual's strategy (habitat preferences or rules of thumb) depends on the density and strategies played by its competitors. This eco-evolutionary dynamic must be considered if we are to fully understand adaptive habitat selection. Specifically, evolutionary games select for strategies that are invasion resistant and, thus, may promote individual success at the expense of producing negative consequences at the population level (Rankin and López-Sepulcre 2005, Rankin et al. 2007).

Consider the "territory game" (K. A. Schmidt unpubl. data) played out among migratory birds sampling breeding sites (i.e., prospective territories) that differ in their inherent risk of nest predation, say the number of predators or density of stems for concealing a nest. Individuals attempt to occupy areas of low risk by sequentially sampling sites and applying an acceptance threshold (Real 1990) to determine whether the site will be rejected or occupied. The threshold, the strategy μ, specifies the site of minimal acceptable quality, and it evolves within a frequency-dependent context. By setting a threshold of high minimum quality, an individual biases settlement to high-quality sites; however, it must sample more sites, on average, to find one that it considers acceptable. A second individual with a slightly less selective nature accepts, on average, slightly lower-quality sites but searches fewer sites. If individuals bias settlement to high-quality sites, the quality of remaining unoccupied sites necessarily declines with each additional round of sampling. This punishes the overly selective strategy. Hence, there is a tradeoff between a minimal acceptable quality (requiring a high μ) and the number of rounds to find an acceptable site.

When μ is free to evolve under perfect information of sampled sites and in a scenario where the number of territories far outnumber individuals (i.e., weak density-dependence), good sites remain unoccupied even at later rounds, so individuals evolve to be very selective: the evolutionary stable strategy (ESS; μ^*) is well above mean quality. By contrast, when individuals fill up most territories (strong density-dependence), thresholds are set near the average ($\mu^* \sim$ mean quality). Imperfect information further decreases selectivity. More interesting is how the coexisting strategy, WSLS, influences the results. High-quality sites are, on average, successful more often and hence reoccupied by surviving incumbents using WSLS. In effect, these high-quality sites are "taken off the market" as long as incumbent replacement is infrequent (e.g., Pärt et al. 2011, Piper 2011). In this scenario, competition for territories is more intense and an individual pays a higher cost, on average, in future rounds if it rejects a site. In this case, μ^* can evolve to be very unselective (Fig. 4).

The above model is applied at the territory scale, and if this is the scale of critical heterogeneity in nest success, it has large repercussions for whether we expect to see congruence or a lack thereof. The model also suggests ways out of the territory game. For
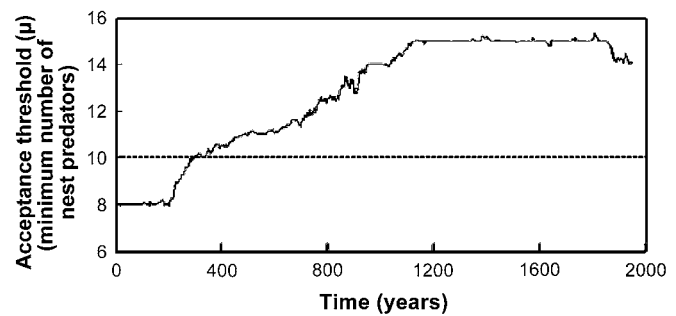

Fig. 4. Results of the "territory game," in which a simulated population of birds evolves an acceptance threshold (μ^*) of minimum site quality. In this example, the threshold represents the minimum number of nest predators per site that the individual can occupy; therefore, μ is inversely correlated with mean acceptable quality. In this simulation, individuals also use the coexisting win-stay:lose-switch strategy. Only individuals without prior nest success (first-time breeders or unsuccessful breeders in the previous year) accept or reject sites on the basis of their threshold. If an individual has failed to find an acceptable site after 5 sampling rounds it occupies the next randomly sampled site. All individuals reproduce, and nest success is based on the number of nest predators at their site. Mean number of nest predators across sites is 10 (dotted line) and standard deviation is 3.0. The threshold (μ) evolves from an initial value that is selective on sites of quality greater than the mean to a strategy that is unselective. For example, at $\mu = 14$, individuals will accept a site with as many as 14 nest predators, or a 28% higher probability of nest predation than the average site (each predator has an additive risk of predation of 7%). Population size also varies as a function of μ, which in turn produces dynamic feedback on μ (results not shown).

example, sequential settlement and partial migration stagger settlement in time and reduce competition for sites at any given moment. Yet these strategies come with their own costs. If early arrival is better for first choice of territory, advancement of settlement dates may occur. But if information is limited in early spring, early arrival gives the individual first choice, but with limited information on which to make a decision. This may occur in systems in which predators are also migratory or have a winter dormancy phase, such as Edible Dormice (*Glis glis*; Adamík and Král 2008) and chipmunks (*Tamias* spp.; Morton 2005, Emmering and Schmidt 2011), and where vegetation development provide cues to site quality (e.g., Arlt and Pärt 2007). There are certainly more factors driving territory choice than competition alone, and these may all play out as an evolutionary game (e.g., for another game-theoretic approach to settlement, see Johansson and Jonzén 2012). Ultimately, theoretical development that moves lock-step with empirical studies will best help push the field forward.

General Discussion

The high level of apparent mismatches in our review of empirical studies might recall the former debate on the question of whether nest-site selection is random or nonrandom with respect to nest predation risk (Filliater et al. 1994, Wilson and Cooper 1998, Cooper et al. 1999, Schmidt and Whelan 1999). But this is a nonstarter. There are certainly processes that make optimization difficult. Density

and frequency dependence can select for strategies that would give the impression that birds are poor judges of habitat quality, even when they can perfectly assess the quality of individual sites. However, the adaptive nature of these strategies may not emerge until we have a broader understanding of how the physical environment, predators, conspecifics and heterospecifics, information, and behavioral plasticity interact. Habitat selection may be an individual (or breeding pair) decision, but it is played out in a game with other individuals all operating with imperfect information. Even if evolution can select for a strategy that makes a "best" choice under uncertainty and ecological constraints, at best it may only be a good choice on average. Even when individuals are able to perfectly assess the quality of individual sites they sample, the frequency-dependent nature of competing strategies among individuals is unlikely to maximize fitness. Certainly, the classic assumption in models of habitat selection that animals are "ideal" in their ability to differentiate among habitats of different quality (i.e., Fretwell and Lucas 1970) is simplistic and insufficient in terms of our understanding of overall habitat-selection strategies. We expect that future tests of many of the hypotheses for nonideal breeding-habitat selection proposed here should contribute to a more holistic understanding of habitat-selection strategies. Such improved understanding is critical in light of the rate at which habitats are changing globally, thereby necessitating rapid assessments about which habitats are "optimal" in terms of evolved preferences and fitness outcomes.

Acknowledgments

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