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Source: The Auk, 123(2) : 301-312

Published By: American Ornithological Society

URL: https://doi.org/10.1642/0004-8038(2006)123[301:AHMMCA]2.0.CO;2

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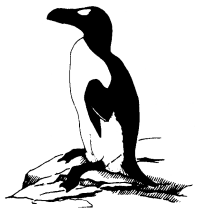
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The Auk

A Quarterly
Journal of Ornithology

Vol. 123 No. 2 April 2006



The Auk 123(2):301–312, 2006

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Printed in USA.

PERSPECTIVES IN ORNITHOLOGY

AVIAN HABITAT MANAGEMENT MEETS CONSPECIFIC ATTRACTION: IF YOU BUILD IT, WILL THEY COME?

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THE ESSENCE OF management for any animal, including birds, is habitat management. Even with endangered species that require intensive measures such as captive breeding, successful habitat management is ultimately judged by the successful release and subsequent establishment of these species in their appropriate natural or restored habitat. In the earliest days of wildlife management, the focus was on manipulating habitat disturbance regimes (such as forest succession or grassland burning) to provide the appropriate habitats for the target species, often with an emphasis on maximizing the edge between different habitat stages (Leopold 1933). Because the focal species were mostly game species that preferred edge habitat, little effort was put into categorizing habitats once they matured past the early successional stages. As late as the 1980s, many wildlife management schemes tended to lump mature forest habitats and their resident species into a single category of "mature forest," with the implication that diversity in these habitats was low and their resident species of somewhat less value, reflecting the focus on harvestable species prevalent at the time (Faaborg 1980, Noss 1983).

Of course, good birders knew that mature forest involved a variety of microhabitat types supporting diverse species, depending on variation in habitat structure and composition. James (1971) and James and Shugart (1970) were the first to measure the structure of a bird's habitat and describe it using multivariate statistical techniques. James's methodology quickly spread through the ornithological world, and habitat structural measures are a part of most research projects even today. Her work initiated what one might call the "era of habitat structure," as quantitative habitat suitability index (HSI) models for many species were developed (Kahl et al. 1985). The logic behind these models was simple: by knowing the detailed habitat structure required by a target species, forest managers could manipulate habitat to favor such structures and, thus, that species. For example, in parts of Missouri, mature oak forests protected from fire develop thick understory growth that is preferred by Kentucky Warblers (*Oporornis formosus*); with fire, the understory disappears and Ovenbirds (*Seiurus aurocapilla*) become common.

In the late 1980s, a focus on forest fragmentation and the development of landscape ecology reduced the use of HSI models. Fragmentation studies began to show how, despite the occurrence of acceptable habitat according to the HSI models (Robbins et al. 1989), area-sensitive species disappeared from a location as habitat size was reduced. Studies incorporating landscape- and local-level effects demonstrated that the severity of the local response to patch size

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could be modulated by landscape-level factors, such as amount of habitat in the area surrounding the study site (Donovan et al. 1997). Demographic studies accentuated the effects of fragmentation by showing that many bird species living in fragmented habitats were not producing enough young to sustain populations (Robinson et al. 1995), which supported concepts of regional population regulation and source–sink models (Pulliam 1988). Perhaps because the broad landscape approaches painted such a bleak picture for bird populations, managers in fragmented regions may have believed that attempts at detailed habitat manipulations for target species were futile. Only recently have studies shown that populations of many species living in fragmented landscapes respond to both local habitat structure and regional habitat distribution (Howell et al. 2000, Thompson et al. 2002). Habitat models, including HSI models, now incorporate both local- and landscape-scale effects in these models (Marzluff et al. 2002, Larson et al. 2003). This trend culminated in what are now called hierarchical models that combine a variety of spatial scales from the tiny vegetation plots of James (1971) to broad landscape patterns (introduced by Kristan and Scott [2006]). A special section in *The Condor* (volume 108, 2006) highlighted these hierarchical models.

An underlying assumption in avian habitat management is that if the manager can provide habitat with appropriate structure at all relevant scales, the target bird species will find and use it. Many of us call this the "Field of Dreams" hypothesis, referring to the movie of that name in which the character played by Kevin Costner hears a voice saying, "If you build it, they will come." Costner's character builds his baseball field and long-dead ballplayers show up, though it takes a while, and not all humans can see the ballplayers, which perhaps has parallels with current Ivory-billed Woodpecker (*Campephilus principalis*) management. Several recent observations have made it clear to us and others (Parker et al. 2005, Fletcher and Miller 2006) that we may need to reconsider the Field of Dreams hypothesis. Avian social behavior may be working in such a way that birds do not always use all available sites with optimal habitat structure for breeding. We suggest that some formerly confusing patterns of habitat selection might become clearer with a broad reconsideration of the behavior behind habitat selection in birds.

Conspecific Attraction to Fields (or Forests) of Dreams

For years, members of the Avian Ecology Laboratory at the University of Missouri, Columbia, have discussed the problem of measuring and modeling habitat selection while conducting a variety of studies on avian responses to habitat fragmentation. Three patterns in the data puzzled us: (1) some large forest fragments did not support otherwise abundant migrant birds (Hayden et al. 1985); (2) sex ratios were heavily male-biased in the smallest populations occurring in fragments (Gibbs and Faaborg 1990, Van Horn et al. 1995); and (3) young male Ovenbirds that did not attract a mate all season were as site faithful as successful males, whereas males that failed in what we assume were multiple attempts dispersed the next year (Porneluzi and Faaborg 1999). For example, in a five-county survey for Ovenbirds in mid-Missouri, we found that our smallest populations had at least five males, even though some of these populations apparently did not attract a female all summer (Van Horn et al. 1995).

Some of our ideas about habitat selection have recently crystallized after seeing the experiments of Ward and Schlossberg (2004) on conspecific attraction in the Black-capped Vireo (*Vireo atricapilla*). They used playbacks of song at sites they believed were empty in previous years and had immediate and sometimes impressive responses: 73 individuals established territories on the five experimental sites in the first year. Because many of these birds were successful and returned to the site the following year, song playbacks were necessary in these sites only once. This experimental evidence demonstrates that a cue, such as presence of conspecifics, may play an important role in the habitat-selection process by attracting individuals and stimulating them to establish adjacent territories (Muller et al. 1997, Parker et al. 2005). This response, commonly known as conspecific attraction, suggests that some birds, in the process of selecting habitats, may also be cueing in on singing males rather than searching only for an appropriately structured breeding site.

The success of Ward and Schlossberg's (2004) study, and observations that Baird's Sparrows (*Ammodramus bairdii*), along with many other species of grassland birds, tend to exhibit clumped distributions across the landscape

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(Green et al. 2002), prompted M.A. to conduct a similar experiment with the Baird's Sparrow in North Dakota (Ahlering 2005). She played back song on three sites at each of two locations where Baird's Sparrows had not been observed the previous two years. Males colonized three of the six playback sites and none of the control sites. The three colonized plots had one, two, and three males for a total of six individuals establishing territories for the duration of the breeding season. Although these numbers seem low, the densities on these small experimental sites (9 ha) were comparable with the natural low-density situation observed in many species of grassland birds (Cody 1985). Habitat assessment indicated no difference in structure between the control and experimental plots. The willingness of a few Baird's Sparrow males to establish territories adjacent to, and countersing with, the playbacks suggests that conspecific attraction may be influencing their habitat-selection decisions and that this response might be elicited in both grassland and forest birds.

Conspecific attraction is known to occur in colonial-nesting species and has been used in management of seabird populations for several years (Kotliar and Burger 1984, Kress and Nettleship 1988, Danchin et al. 1998, Serrano et al. 2004). Here, we focus on the potential implications of conspecific attraction for territorial species; however, even in this context, the concept of conspecific attraction is not new. Hildén's (1965) classic paper on habitat selection in birds stated that territorial aggregation and sociality were common among many bird species, with associated observations on the loose aggregations formed by many territorial European passerines. Since then, though, discussions combining social behavior and habitat selection have been somewhat limited. Klopfer and Ganzhorn (1985) discussed some behavioral aspects of habitat selection, but they focused on behavioral methods used by birds to circumvent physiological constraints on habitat selection and perception. In Europe, Alatalo et al.'s (1982) work on Pied Flycatchers (*Ficedula hypoleuca*) and Pöysä et al.'s (1998) work on Mallards (*Anas platyrhynchos*) supported the use of conspecific attraction as a cue for resource selection. In North America, observational studies on a diverse group of territorial species have demonstrated some support for the use of conspecific attraction in territory or nest placement (Muller et al. 1997, Lahaye et al. 2001, Etterson 2003). In the symposium volume that stimulated much of the recent work on migrant bird ecology and conservation, Morton (1992) noted the conservation importance of understanding these patterns for migratory birds, though few of the researchers focusing on this group have expanded on his ideas. Although scientists are increasingly aware of the importance of understanding the role of behavior in resource use (Lima and Zollner 1996, Sutherland 1998, Cooper and Millspaugh 2001, Marzluff et al. 2001), the role of social cues like conspecific attraction in the actual behavioral process of habitat selection is just beginning to be appreciated in the science and management of territorial birds.

Many explanations for the adaptive value of conspecific attraction exist, and they are often not mutually exclusive. Stamps and her students (Stamps 1988, Muller et al. 1997) have demonstrated the advantages of establishing a territory that abuts an already-established neighbor, a pattern that would lead to clustering of territories when habitat is not saturated. However, many of the more recent explanations for conspecific attraction in birds can be placed in two categories: (1) the use of other birds as a source of information about habitat quality and (2) the potential to increase mating success.

Males may use conspecifics as a source of information about previous or current habitat quality (Doligez et al. 2002, Sergio and Penteriani 2005). Dispersing birds may use already-established birds as a source of information about habitat quality. Models have suggested that following such cues may reduce search costs, settlement costs, or the costs of the "Allee effect" (Greene and Stamps 2001). If successful males are more likely to be site-faithful (Porneluzi 2003), dispersing males could use these site-faithful males as an additional indication of habitat quality beyond structural habitat cues. This would be most beneficial for juvenile males that may be less proficient in identifying suitable breeding habitat. In fact, Ward and Schlossberg (2004) showed that second-year Black-capped Vireos comprised a greater proportion of the experimental population than in the population as a whole. In species with low levels of site-fidelity, such as many species of grassland birds (Zimmerman 1992, Igl and Johnson 1999, Winter et al. 2005), juveniles may be cueing on older males that may have gained

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more reliable knowledge about suitable types of habitat for breeding from previous experiences, even though they are not from that particular location. However, even low rates of return may be enough to result in clustering.

Similarly, dispersing males that fail in a given year can use the breeding success of other birds as a source of information by prospecting reproductive success of conspecifics at the end of the breeding season (Reed et al. 1999, Pärt and Doligez 2003). This type of conspecific attraction is known as performance-based conspecific attraction or public information, and has been shown to occur in some species (Doligez et al. 2002, Danchin et al. 2004, Serrano et al. 2004). Birds may use the previous year's breeding success to settle near successful conspecifics in the following breeding season, as suggested in the studies above; however, some birds, especially juveniles with no previous breeding experience, may use information about the location of adults across the landscape gathered at the end of the breeding season to establish territories in the following year. Using song playbacks with Bobolinks (*Dolichonyx oryzivorus*) in Nova Scotia, Nocera et al. (2006) recently demonstrated that first-time breeders use information about the location of adults at the end of the breeding season in making settlement decisions during their first breeding season the following year. Public information theory and the playback study with Bobolinks suggest that for some site-faithful species, conspecific cues assessed at the end of the breeding season can be incorporated into the habitat-selection decisions of birds the following year.

Conspecific attraction also could be driven by the potential to increase mating success. Recent work with conspecific attraction has focused on the motivation of settling in an aggregation to obtain extrapair copulations and fertilizations (Ramsay et al. 1999, Mennill et al. 2004, Tarof and Ratcliffe 2004). This response may be driven by males that want to establish a territory adjacent to conspecifics to increase their potential for extrapair fertilizations, or by females that prefer to mate with males in an aggregation rather than males in an isolated territory to increase their opportunity for extrapair copulations. In these cases, subordinate males may pay a cost in terms of paternity early in life, but may be rewarded in later years if they live long enough to become dominant males preferred by local females. Several studies have developed the idea of hidden leks within aggregations of classically territorial and socially monogamous species (Wagner 1998, Fletcher and Miller 2006).

As we continue to learn more about conspecific attraction, its potential use in conservation will become more apparent. There may be habitats available that only need an artificial stimulus to attract populations and establish site-faithful resident birds to serve as natural attractants to maintain the population. In these cases, manipulating the existing population into using available habitat may be a more effective approach than increasing the amount of available habitat. In species where conspecific attraction is strong, simply providing habitat may not be enough to overcome a behavioral constraint involving settling near neighbors. Some aspect of the social cues provided by settled males may be necessary to stimulate a male to settle at a site, even if the only cue provided is vocal. If such strong presence–absence patterns exist because of conspecific attraction, there may be other, more subtle situations where the occurrence of conspecific attraction may explain patterns of avian distribution and provide a potential means of increasing local or regional populations through a mixture of habitat management and behavioral manipulations.

Below, we discuss some potential management implications of conspecific attraction for territorial songbirds, but as we point out again in the end, there is still much we do not know about the prevalence of this behavior, the mechanisms behind it, and the effects the use of this manipulation in management situations may have on the population as a whole. We suggest that conspecific attraction is an important aspect of avian behavior to consider, but we cannot lose sight of our still-limited understanding of habitat needs and the importance of providing high-quality habitat.

Large Minimum Area Requirements in Fragmented Landscapes

Of the hundreds of studies done on animal responses to habitat fragmentation, virtually all show increasing diversity of species with increasing fragment size, in part because some species are present only on fragments of a certain minimum size or larger. These "minimum area requirements" were a major focus of

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studies in the mid-1980s (Villard et al. 1992), but became less important as the paradigm shifted to regional landscapes and source–sink demographics (Pulliam 1988). The most area-sensitive species (those requiring the largest minimum area) were often long-distance migrants, which seemed counterintuitive, given that these species could travel such long distances between breeding and wintering grounds. The literature discussing these requirements often marveled at the fact that a forest that looked structurally perfect would not support a species, though it seemed to have space for dozens of territories. For example, in the 1980s, a survey for Ovenbirds in Boone County, Missouri, found several forest tracts that were larger than the observed minimum area of species occurrence and appeared to have perfect habitat, yet lacked Ovenbirds (Gentry 1989).

Given the growing evidence that conspecific attraction may be important for some species (discussed above), scenarios involving the absence of conspecific attraction on these sites could potentially explain the local absence of these species. Two mechanisms associated with the fragmentation process possibly explain these empty sites. First, if resident birds were patchily distributed and site-faithful across the contiguous landscape before fragmentation, remaining fragments that did not initially support any breeding birds would be empty following the loss of surrounding habitat. Alternatively, if all fragments had some breeding birds, small fragments with high probabilities of local extinction might also end up empty. In both scenarios, the absence of any males faithful to these sites could keep them empty for prolonged periods. The possible need for an established male to attract other males changes the structure of metapopulation and source–sink models once local extinction has occurred by limiting what is termed the "rescue effect" (Brown and Kodric-Brown 1977). Strong conspecific attraction could decrease the number of occupied habitats across the landscape by decreasing colonization and recruitment of empty habitats and encouraging dispersal to already-occupied habitats (Smith and Peacock 1990, Ray et al. 1991, Reed and Dobson 1993, Reed 1999, Parker et al. 2005).

In either situation, populations that are small or isolated or both would be most susceptible to having all males fail and disperse or die in a given year through stochastic processes, leaving a habitat patch without an individual of that species fixed on returning to that site the following spring. Although maintaining these small populations may most often involve successful males returning to the site of their previous success, it is interesting to note that Porneluzi (2003) found that unpaired Ovenbirds returned to their territorial areas at the same rate as successful males, which may buffer these populations somewhat. He also found, though, that males that attracted mates but failed all summer tended to disperse. Consequently, a couple of years of high nest loss could also lead to an empty habitat island. To the extent that a population avoids the edge of the habitat (as is particularly pronounced in the Ovenbird, which often will not establish a territory within 200–300 m of the habitat edge; Van Horn et al. 1995), remarkably large habitat fragments could end up lacking species, which has been shown repeatedly in studies of area sensitivity (Hayden et al. 1985, Robbins et al. 1989, Robinson 1992). Therefore, the extent to which conspecific attraction may influence these patterns of minimum area of occurrence merits further study.

Is Conspecific Attraction at Work in Large Populations?

Although the absence of conspecific attraction might cause an acceptable habitat to lack a species for some period, conspecific attraction's relative importance in maintaining a natural population may decline rather rapidly as population size increases and the number of potential returning males becomes large. However, without an understanding of the mechanisms behind conspecific attraction or its effects after the initial settlement of breeding males on an area, it is difficult to discuss any effect of density dependence that might occur with regard to the behavior of conspecific attraction. Do the advantages of being adjacent to others increase as population size increases, or do these advantages reach some sort of saturation level rather quickly? These are important questions that need to be addressed. How a bird balances conspecific attraction with the range of its innate habitat-selection cues could influence the breadth of habitat use in large populations. It is likely that birds use a variety of cues, both social and structural, to select territories, but if conspecifics are an important aspect of a species'

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mating strategy, optimal habitat for that species might include both habitat and social needs. For example, if birds use conspecifics as a cue to increase mating success (i.e. extrapair copulations), they may be willing to use a wider range of habitat structurally to obtain the advantages of being next to conspecifics.

Although we know of few studies attempting to test a hypothesis that nesting birds compromise habitat selection to be near other nesting birds, studies directed at other aspects of habitat use have produced situations where a greater population size within a landscape seems to have resulted in individuals using territories with a wider range of habitat structure. The pattern of Baird's Sparrow habitat use at a site in Saskatchewan near the center of the species' geographic distribution suggests that males at this site establish territories in a wider range of habitats to be near conspecifics (Ahlering 2005). Habitat use was evaluated for three different populations of Baird's Sparrows in North Dakota and Saskatchewan, and the range of habitat use for all parameters measured was the greatest in Saskatchewan, the site with by far the highest density of birds. Given that Baird's Sparrows in North Dakota exhibited a conspecific attraction response to playbacks, this pattern suggests that birds may broaden their habitat requirements to establish a territory near neighbors.

A study in the forested habitat of the Missouri Ozarks suggests a similar pattern. In this case, we have been doing an experiment on the effects of forest management on bird populations (Gram et al. 2003). The study started with nine separate study areas of ~400 ha each, all of which supported mature oak–hickory forest and all of which were surveyed for birds for five years before treatment. Not surprisingly, the Indigo Bunting (*Passerina cyanea*) was not common, because the study areas had few of the clearings that the species requires for nesting. We recorded, on average, only ~10 pairs per 100 ha within all nine study sites during 1991–1995, mostly along old logging roads. In 1996, three of the sites had trees removed by even-aged management (clearcutting) over ~10% of the area, three sites had an equivalent amount of timber removed by single-tree and group-selection cutting over ~70% of those areas, and three sites were treated as controls with no harvest (Gram et al. 2003). Because both types of harvest produce clearings attractive to Indigo Buntings, populations within both treatment sites skyrocketed over the next few years, with both treatments exceeding 100 pairs per 100 ha at their peak. Not surprisingly, the control sites showed no increase in numbers for the first two years, but then increased dramatically, with nearly five times the density of the mean pretreatment years despite no change in the habitat offered on these sites. In nearly all cases, the treatments were adjacent to one another, so the distances involved were not large. As local populations became large, breeding Indigo Buntings apparently chose to use habitats that had been unacceptable for nearly a decade, perhaps because of the advantages of being a part of this larger population. Interestingly, other second-growth species that became abundant in the openings created by forest management—White-eyed Vireo (*Vireo griseus*), Prairie Warbler (*Dendroica discolor*), and Yellow-breasted Chat (*Icteria virens*)—were never recorded in the control sites (Gram et al. 2003), which suggests that we must be careful when generalizing about this response.

On the basis of these obviously speculative observations, it appears that in high-density populations there may be some relaxation in the habitat cues used. If we could show that a certain level of intensive habitat treatment stimulates a target species also to use habitats in neighboring vegetation, thereby increasing the overall total population effect when compared with smaller treatments spread over a broader area, we would know something very important for management, even if we did not understand the behavioral basis behind it. Understanding such a pattern would be of great value for understanding basic behavior; however, we also need to understand the long-term effects of these manipulations on the demographics of these populations. If the desire to settle near conspecifics is driven by the desire to obtain extrapair copulations, then we may need to rethink how we evaluate habitat suitability for species. From a bird's perspective, there must be a balance between the appropriate habitat structure and nearest-neighbor distance. Certainly, we need to go back and examine our Ozark data to see the extent to which the increase in Indigo Buntings occurs on the parts of the control sites closest to the treatment areas.

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Are All Species Clustered and Is All Clustering Conspecific Attraction?

As noted earlier, several studies of territorial birds in contiguous habitats have shown a clustering of territories that seems to be independent of actual variation in habitat structure (Herremans 1993, Tarof and Ratcliffe 2004). If the independence from habitat patterns is real, then we must deal with the potential consequences of this behavior and resulting issues such as reproductive strategies (e.g. hidden leks). To date, published observations of conspecific attraction are mostly anecdotal in nature. However, rather than assume that conspecific attraction is widespread, we need to do the appropriate searches for patterns that show clusters of territories; species that do not cluster probably do not use conspecific attraction as an important part of their habitat-selection behavior. Additionally, even if a species shows clustered territories, this cannot automatically be explained by conspecific attraction.

For example, recent work by Bourque and Desrochers (2006) examined the degree of aggregation in 17 forest songbirds at various spatial scales before and after accounting for the effects of vegetation structure. Nine species showed aggregated territories in at least one spatial scale, and eight were aggregated at all scales. This trend suggests that only about half the species show clustering that could be explained by conspecific attraction. On the other hand, removal experiments by Bourque (2005) with Ovenbirds, a species observed to cluster, suggested that conspecific presence was not important to settlement within vacated territories.

Other factors involved in the habitat-selection process could result in clustered territories without invoking conspecific attraction as a cause. For example, several recent studies have shown that many forest breeding birds shift their habitat use to some sort of alternative, usually younger, vegetation type after independence (for fledglings) or breeding (for adults) (Anders et al. 1998, Pagen et al. 2000, Suedkamp Wells 2005, White et al. 2005). In at least two species that make this habitat shift, our experimental work has shown that they seem to select breeding territories that fulfill their structural habitat requirements of mature forest but that are in proximity to this alternative habitat, which is used by both young and adults after breeding. In the Ozark experiment described above, we found that both the Wood Thrush (*Hylocichla mustelina*) and Worm-eating Warbler (*Helmitheros vermivorum*) have shifted their breeding territories in such a way that they are closer to large openings such as clearcuts (M. J. Wallendorf et al. unpubl. data). This shift to high breeding densities around clearcuts has resulted in lower densities away from such clearcuts, and the Wood Thrush has almost completely left our control sites, which are distant from any alternative habitat, even though these sites have changed little in the past decade. Studies of postfledging Wood Thrush in the Ozarks showed that there was an increase in mortality as juveniles became independent and wandered through the forest looking for these alternative sites (Anders et al. 1998), whereas Wood Thrush living in fragments in central Missouri did not have to wander far to find brushy habitats (which are part of fragment edges) and did not show a similar increase in mortality (Fink 2003). A logical conclusion from these studies is that Wood Thrush may have lower annual reproductive success when they nest far from thickets and other habitats required by the young after independence.

Although this example of a habitat shift may seem distinctly different from the conspecific attraction described earlier, the reality is that we have recorded a local shift in distribution where breeding birds seem to be concentrating in some locations (around clearcuts) and becoming sparse or absent from similarly structured sites where they formerly bred, a clustered distributional pattern that, when examined at a large scale, could easily be attributed to conspecific attraction. Such a distribution seems to fit the basic attraction model we described earlier, but in this case we can see that a "nearness to clearcut" parameter has been added to the other structural components, recognizing that a nearby alternative habitat may be part of the overall selection process to produce young successfully through the summer.

Perhaps we should revisit all those species that have shown patterns explained by conspecific attraction to see whether alternative explanations for these distributions can be found. In particular, few species have been examined for the importance of alternative habitats for postfledging and postbreeding birds, yet this

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parameter may be critical in understanding distributional patterns and may even explain regional population declines whose causes have been related to other factors. For example, the Wood Thrush has been shown to be declining throughout much of its eastern range (Peterjohn et al. 1995), including such well-studied sites as Hubbard Brook in New England (Holmes and Sherry 1988). Hames et al. (2002) have developed a model to explain this decline that invokes the effects of acid rain on calcium levels in this region, where reduced calcium leads to fewer snails, which leads to thinner egg shells, which leads to low reproductive success. We suggest that a viable alternative model involves the growing maturation and homogeneity of deciduous forests in the east, where mature forest next to clearings has become increasingly rare, leading to a decline in Wood Thrush. It is noteworthy that Wood Thrush are gone from Hubbard Brook and its surroundings in New Hampshire, but if you visit forests near second-growth or clearings in that region, you can still find Wood Thrush (R. T. Holmes pers. comm). In this example, it is clear that building the appropriate habitat is still important for all species, and it is critical that we continue to further our understanding of habitat selection and use for all species' behavioral needs and stages of their life cycle. Just as in the past we expanded our descriptions of breeding habitat to include both local structural cues and regional landscape cues, we now must recognize that, for some species, a second habitat is needed during the breeding season, and both the structural cues of this habitat and its proximity to the breeding site may be critical parameters. When these locations are limited, we may see clusters of territories; are these attributable to conspecific attraction or convergence on a location, which includes both optimal breeding and postbreeding habitat?

Research Needs: Habitat Building versus Conspecific Attraction

At a minimum, the growing evidence suggests that conspecific attraction may play a role in habitat selection for some species and that suitable habitats may exist that require some sort of behavioral manipulation to attract colonists and establish sustainable populations. The potential conservation value of this response has been emphasized for some endangered species through presence or increased abundance (or both) on a local scale (Jeffries and Brunton 2001, Ward and Schlossberg 2004); however, our understanding of the possible costs and benefits of such behavioral manipulations to all the existing populations of a species is far from complete. Simply moving a limited number of breeding birds around is a zero-sum game; if empty habitats are empty for good reasons, such movements could be detrimental. Obviously, we need to make sure we do not create ecological traps with these manipulations and attract birds into sink habitats where they have little chance of breeding successfully. We have discussed situations where conspecific attraction may be important in large populations and might alter patterns of habitat use. Finally, we presented the possibility that some distributions that appear to result from conspecific attraction may actually reflect concentrations of breeding birds near an alternate habitat type used later in the season.

Before managers attempt to manipulate conspecific attraction in larger populations and at greater spatial scales, we must fill in the numerous gaps in our knowledge about the prevalence of this response within and among groups of species, the strength of behavioral cues in relation to innate cues of habitat quality, and the mechanisms behind these responses. Regardless of whether conspecific attraction is occurring with songbirds, it is still important to focus on creating optimal habitat, especially if males are using other individuals as cues about habitat quality. However, if males prefer to settle near conspecifics because of social advantages such as extrapair copulations, then the resources that birds use include both habitat and other individuals, and conspecific attraction may need to be given attention in these instances. As an extension of this, if birds are using the presence of conspecifics as a cue in selecting breeding habitat, it is also possible that migratory birds use this response to select habitat on the wintering grounds. Adequate understanding of how conspecific attraction affects total populations will require research at spatial scales much larger than usually associated with behavioral studies. To make things even more complex, several recent studies have suggested that some birds may consider both conspecific and heterospecific

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cues when choosing habitat (Parejo et al. 2004, R. J. Fletcher unpubl. data).

It is almost mind-boggling to contemplate all the possible factors involved in a bird's choice of habitat and how challenging the study of such behavior will be at the spatial scale required. For example, Fletcher (2006) uses simulations to model different habitat-selection strategies and their potential effects on survival, reproduction, and bird distribution in different landscapes. These simulations produce distributions that could lead to testable predictions for addressing the effects and prevalence of different habitat-selection strategies in the field. As studies of habitat selection have progressed over the decades from considering habitat at a local level to the larger landscape matrix and even the regional level, we have gained a broader understanding of how these different scales influence habitat selection and use. However, the recent surge in observations and evidence that social cues may influence habitat selection for territorial songbirds makes it clear that we need to begin to incorporate these social issues in our habitat- selection framework. As future human development inevitably results in avian populations that are smaller and more isolated, we will have to be as efficient as possible with the space available. This may mean that we go beyond the "if you build it" stage and recognize the constraints and the opportunities that occur with the "they will come" part of the equation.

Acknowledgments

As noted, the ideas incorporated in this paper have been discussed by members of the Avian Ecology Laboratory at the University of Missouri-Columbia for over two decades. We thank all those past members whose thoughts and data have contributed to this work. The manuscript was reviewed by present members of the Lab, including J. Toms, A. Cox, W. Bailey, J. Reidy, E. Ruelas Inzunza, and C. Rittenhouse. R. Fletcher and F. Thompson III also reviewed an early draft of this manuscript. Finally, we thank R. Fletcher, J. Bourque, and A. Desrochers for access to unpublished material that aided greatly in developing this paper. We apologize to anyone working in this field whose manuscripts we were not able to access in our search for current research.

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