Behavioral barriers to non-migratory movements of birds

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Although effects of physical barriers to animal movement are well established, the behavioral inhibition of individuals moving across habitat gaps, ecotones, and inter-patch (matrix) habitat has received little attention. Birds are often cited as a taxon in which movements should not be disrupted by gaps in landscape connectivity. Here we synthesize evidence from the literature for behavioral inhibition of movements by birds, and find that a wide variety of behavioral inhibitions to movements have been observed. We also present a model for describing edge or gap permeability that incorporates the propensity of an individual to cross an ecotone or enter a gap, and the effect of gap width. From published observations, we propose five ecologically based patterns of behavioral inhibition of bird movements as hypotheses: that habitat specialists, understory-dwellers, tropical species, solitary species, and non-migratory species are more inhibited than are species that are their ecological counterparts. Understanding what animals perceive as impediments to movement will contribute to efforts to maintain populations through landscape design, and will allow us to predict the types and degrees of habitat fragmentation that will cause persistence problems for various species.

Introduction

Physical barriers to movements such as dispersal and migration are widely recognized for birds. For example, movements can be inhibited by large geographic features, such as mountain ranges (Baker 1978, Leshem & Yomtov 1996), which can play a role in speciation (Nelson & Rosen 1981, Gascon *et al.* 2000). Long-distance movement also can be restricted by physiologi-cal constraints, such as the need to acquire fat reserves before crossing a water body or desert (Baker 1978, Akesson 1999). Our interest is in relatively subtle barriers to movements, where an animal is physically capable of crossing a particular distance or habitat but does not do so, indicating a behavioral restriction of movement (e.g., Mayr 1942, Ehrlich 1961). We also focus on movements at the landscape scale, typical of dispersal, rather than at the larger spatial scale of

migration. In this paper we refer to barriers that restrict movement behaviorally as behavioral barriers to movement.

Some bird species migrate vast distances over unfamiliar terrain, yet the same species can have relatively short dispersal distances that are affected by behavioral decisions (Rolstad 1991, Villard & Merriam 1995, Reed *et al*. 1999). Evidence of behavioral barriers to movement of birds comes from a wide variety of sources, ranging from species distribution patterns (Willis 1974, Terborgh 1985, Capparella 1988, Robinson 1999) to observations of habitat gap crossing (Desrochers & Hannon 1997, St. Clair *et al*. 1998, Harris & Reed 2001). These behavioral inhibitions often coincide with landscape features such as ecotones, habitat gaps, and matrix habitat types (Stamps *et al*. 1987, Hansson 1991, Hansen & di Castri 1992, Rickets 2001, Vandermeer & Carvajal 2001), and can vary among individuals within a species (Fraser *et al*. 2001). Few ecologically based patterns across species of barriers to movement have been proposed. It has been suggested that Neotropical migrant forest birds are more sensitive to habitat loss and fragmentation than are temperate resident species, in that they are less likely to occupy fragmented landscapes (e.g., Blake 1986, Robbins *et al*. 1989). It has been suggested that this sensitivity might be due to a greater inhibition of movement across habitat unsuitable for breeding (Whitcomb *et al*. 1981, Lynch & Whigham 1984, Machtans *et al*. 1996). However, some forest-breeding, Neotropical migrants readily cross wide gaps in forests (Norris & Stutchbury 2001), and there is evidence that Neotropical migrants are less susceptible to other potential effects of fragmentation such as lack of nesting cavities (Imbeau *et al*. 2001).

Behavioral barriers to movement become more important to population persistence when habitats are fragmented (Hanski & Gilpin 1991, Wu *et al*. 1993, Daily & Ehrlich 1996, Reed 1999). The practical advantage of understanding the behavioral basis of movement decisions is that landscapes might be designed to allow species to move among otherwise isolated patches of habitat (Saunders & Hobbs 1991, Hansson *et al*. 1992, Beier & Noss 1998, Reed 2002).

The impacts of habitat fragmentation and the potential ameliorating effects of corridors would be better predicted by understanding the behaviors inherent in dispersal (Lima & Zollner 1996, Yahner & Mahan 1997, Sutherland 1998, Haddad 1999, Reed 1999, 2002). The importance of an organism's dispersal capability, independent of distance, only recently has been incorporated into models of subdivided populations (Taylor *et al*. 1993, Fahrig & Merriam 1994, Donovan *et al*. 1995).

Our goals here are to quantify gap-crossing abilities and types of behavioral barriers to non-migratory movements by birds. These movements are primarily for dispersal, seasonal shifts in home range, and within home range movements, so they encompass local and landscape-level movements.

Barrier permeability

Potential behavioral barriers to dispersal generally take the form of a gap in habitat. The barrier can be crossing the ecotone itself, or it can be some feature of the gap habitat, such as its width or the type of habitat that makes up the gap. It is useful to characterize potential barriers by their permeability, or the propensity of an individual of a particular species to cross the barrier (Stamps *et al*. 1987). Permeability can be key to persistence of populations in fragmented landscapes. Using a simulation model, Stamps *et al*. (1987) found that even slight changes in edge permeability could alter migration (i.e., dispersal) rates dramatically, which strongly influenced metapopulation persistence. Barrier permeability has been described qualitatively as ranging from soft, those that are crossed readily, to hard, which dispersing individuals virtually never cross (e.g., Stamps *et al*. 1987). Wiens (1992) offers a model based on diffusion equations to describe permeability of a landscape to a dispersing individual, expressing permeability in terms of "thickness" of the boundary and the contrast between adjacent patches.

Perceptions of ecotone and gap permeability, and therefore predicted impacts of habitat fragmentation, can vary by species (Wiens 1995).

Even for the same type of ecotone, reduced contrast in vegetation structure and increased understory density in habitat gaps consistently reduce forest birds' perceptions of edges as barriers. For example, DeGraaf (1992) found that edge avoidance by forest birds was most pronounced where forest stands creating the edges were farthest apart in age (i.e., greatest for mature forest-clearcut edges) (*see also* Machtans *et al.* 1996, Sieving *et al.* 1996, Harris & Reed 2001). The early successional habitats used by juvenile wood thrushes (*Hylocichla mustelina*), a forest species, exhibit dense understory and ground cover (Anders *et al.* 1998, Vega Rivera *et al.* 1998). Clumped regenerating vegetation also appears to facilitate movement of forest birds crossing clearcuts (Machtans *et al.* 1996). One implication of these observations is that the transient nature of regenerating clearcuts should reduce their long-term impact on population persistence of forest birds compared to other habitat types that fragment forests, such as agricultural fields and roads (Askins 1994). Comparable information is unavailable for non-forest birds.

One influence on gap permeability not included in Wiens' (1992) model is gap width, and whether or not there is a species-specific threshold distance beyond which individuals will not cross (Table 1). A threshold distance is one where a small change in distance produces an abrupt reduction in the probability of movement (With & Crist 1995). Investigations of gap permeability to birds using song playback often result in a graded response with distance, as with habitat cover, with some maximum distance individuals will not travel (e.g., Rail *et al.* 1997). Desrochers and Hannon (1997), Rail *et al.* (1997), and St. Clair *et al.* (1998) provide species-specific data on the probability of crossing gaps of different widths. All species' probabilities declined with distance; although a threshold was not generally apparent, most species exhibited a maximum distance beyond which they would not cross. Brooker *et al.* (1999) also provide data on maximum gap distances some species were recorded crossing. A forest species that appeared to be particularly uninhibited in crossing open habitat was the hooded warbler (*Wilsonia citrina*), where males searching for extra-pair copulations can cross

a gap of open habitat > 400 m across (Norris & Stutchbury 2001). It should be noted, however, that the stimulus to cross gaps is different between these studies; birds in Brooker *et al.*'s (1999) study were dispersing. Also, several species of wintering residents in temperate woodlots crossed large gaps, with median maximum distances of up to approximately 550 m (Grubb & Doherty 1999).

Ecotone permeability that includes discontinuities or gaps is not readily described by Wiens' (1992) diffusion model of landscape permeability. As an alternative, we offer a model for describing ecotone or gap permeability:

$$f(g) = \frac{h}{1 + \left(\dfrac{g}{b}\right)^n}. \qquad (1)$$

Here, h is a measure of the tendency of an individual to attempt to cross a gap of a particular width (g). This value can be a characteristic of a species or an individual, and will probably differ depending on stimulus. Consequently if $h < 1$, then an individual will not always enter a gap when it is encountered. For example, we estimated h for black-throated blue warblers (*Dendroica caerulescens*) by using song playback (Harris & Reed 2001). We found 33% of the individuals evaluated would not enter the clearcut from where the playback emanated, so $h = 0.67$. As b increases, an animal's tendency to cross gaps, once the gap is entered, increases. Specifically, b is the gap size for which an animal has a 50% probability of moving if $g = b$ and $h = 1$. Finally, n determines the steepness of the transition from high to low probability of crossing as gap width increases. As n approaches infinity, the probability of crossing becomes a step function with a threshold at the value $g = b$. This equation can describe a variety of gap-crossing probability functions (Fig. 1), and it can be combined with other rules. For example, the above equation might describe the probability of crossing a gap up to a certain width, beyond which an animal will not cross (Fig. 1B). The model also can incorporate the underlying processes that might affect both h and b, such as season and life history characteristics.

To demonstrate the application of this

Table 1. Possible threshold distances to movement across gaps, reported in or estimated from published papers.

Species	Threshold distance (m)	Gap type	Season or reason for movement	Method	Reference
North temperate residents					
Black-capped chickadee (*Poecile atricapillus*)	50[a]	clearcuts; forest detour available	winter	direct observation: mobbing call playback	St. Clair *et al.* (1998), Bélisle & Desrochers (2002)
	120[a]	clearcuts; forest detour not available	winter	direct observation: mobbing call playback	St. Clair *et al.* (1998)
	< 50[a]	clearcuts, fields	late summer–fall	direct observation: mobbing call playback	Desrochers & Hannon (1997)
Red-breasted nuthatch (*Sitta canadensis*)	50	clearcuts, fields	summer–fall	direct observation: mobbing call playback	Desrochers & Hannon (1997)
White-breasted nuthatch (*Sitta carolinensis*)	150[a]	clearcuts, fields	fall–winter	direct observation	Grubb & Doherty (1999)
Caroline chickadee (*Poecile carolinensis*)	90	clearcuts, fields	fall–winter	direct observation	Grubb & Doherty (1999)
Tufted titmouse (*Baeolophus bicolor*)	115	clearcuts, fields	fall–winter	direct observation	Grubb & Doherty (1999)
Downy woodpecker (*Picoides pubescens*)	160	clearcuts, fields	fall–winter	direct observation	Grubb & Doherty (1999)
Red-bellied woodpecker (*Melanerpes carolinus*)	200	clearcuts, fields	fall–winter	direct observation	Grubb & Doherty (1999)
Hairy woodpecker (*Picoides villosus*)	400	clearcuts, fields	fall–winter	direct observation	Grubb & Doherty (1999)
Blue jay (*Cyanocitta cristata*)	175	clearcuts, fields	fall–winter	direct observation	Grubb & Doherty (1999)
Northern flicker (*Colaptes auratus*)	600	clearcuts, fields	fall–winter	direct observation	Grubb & Doherty (1999)
South temperate residents					
Blue-breasted fairy wren (*Malurus pulcherrimus*)	< 60[b]	agricultural fields	dispersal	indirect: banding	Brooker *et al.* (1999)
White-browed babbler (*Pomatostomus superciliosus*)	270	agricultural fields	dispersal	indirect: banding	Brooker *et al.* (1999)
Magellanic tapaculo (*Scytalopus m. magellanicus*)	0[c]/≥ 20	open field/field with cover	breeding	direct observation: song playback	Sieving *et al.* (1996)
Ochre-flanked tapaculo (*Eugralla paradoxa*)	0/≥ 20	open field/field with cover	breeding	direct observation: song playback	Sieving *et al.* (1996)

Species					Reference
Chucao tapaculo (*Scelorchilus rubecula*)	0/≥20	open field/field with cover	breeding	direct observation: song playback	Sieving *et al.* (1996)
Black-throated huet-huet (*Pteroptochos tarnii*)	0/≥20	open field/field with cover	breeding	direct observation: song playback	Sieving *et al.* (1996)
Des Murs' wiretail (*Sylviorthorhynchus desmursii*)	0/≥20	open field/field with cover	breeding	direct observation: song playback	Sieving *et al.* (1996)
Short-distance migrants (north temperate)					
White-throated sparrow (*Zonotrichia albicollis*)	65–70 [a]	trails, dirt roads, clearcuts	summer	direct observation: song playback	Rail *et al.* (1997)
Golden-crowned kinglet (*Regulus satrapa*)	40	trails, dirt roads, clearcuts	summer	direct observation: song playback	Rail *et al.* (1997)
	30	fields, clearcuts	summer–fall	direct observation: mobbing call playback	Desrochers & Hannon (1997)
Long-distance migrants (Neotropical)					
Red-eyed vireo (*Vireo olivaceus*)	30	fields, clearcuts	summer–fall	direct observation: mobbing call playback	Desrochers & Hannon (1997)
Swainson's thrush (*Catharus ustulatus*)	50	trails, dirt roads, clearcuts	summer	direct observation: mobbing call playback	Rail *et al.* (1997)
Black-throated green warbler (*Dendroica virens*)	25	trails, dirt roads, clearcuts	summer	direct observation: mobbing call playback	Rail *et al.* (1997)
Yellow-rumped warbler (*Dendroica coronata*)	35–40	trails, dirt roads, clearcuts	summer	direct observation: mobbing call playback	Rail *et al.* (1997)
Ovenbird (*Seiurus aurocapillus*)	40–50	clearcuts, fields	summer–fall	direct observation: mobbing call playback	Desrochers & Hannon (1997)
	< 25 [d]	roads, powerline gaps	late summer: males alone or with offspring	direct: transmitters	Bayne & Hobson (2001)
	100–300	agriculture fields	late summer: males alone	direct: transmitters	Bayne & Hobson (2001)
Hooded warbler (*Wilsonia citrina*)	465 [e]	agriculture fields	summer: males seeking extra-pair copulations	direct: transmitters	Norris & Stutchbury (2001)

[a] Values were reported as threshold distances or extrapolated from data using inflection point or median gap distance crossed.

[b] Values were reported as distances above which birds' dispersal movements were inhibited.

[c] Threshold values were not measured; birds either approached speakers at a maximum distance of 20 m or not, therefore, it is assumed that the threshold distance is ≥ 20 m or 0.

[d] Threshold values were not measured; about 30% of birds crossed small roads or powerline gaps, and the minimum gap distance crossed by males without young was 100–300 m.

[e] Threshold values were not measured; the frequency of movements across open fields to neighboring woodlots was not diminished at distances of up to 465 m from a male's resident patch.
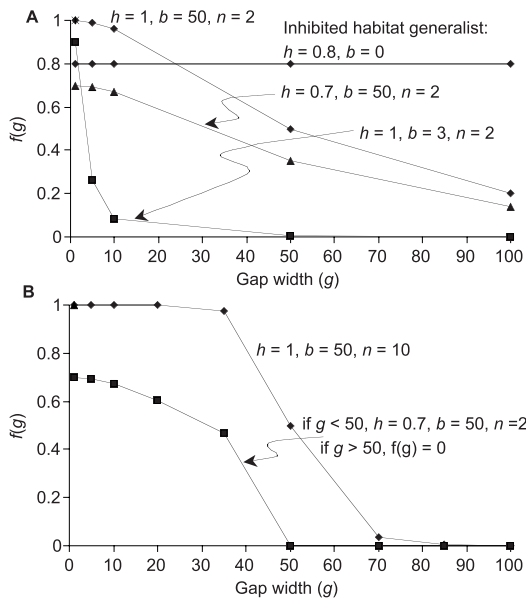
Fig. 1. — **A**: Gap-crossing probabilities for four different combinations of values for parameters in Eq. 1. — **B**: gap-crossing probability as step functions using a single set of values in Eq. 1 (upper curve) and as multiple rules for gap crossing based on distance (lower curve).
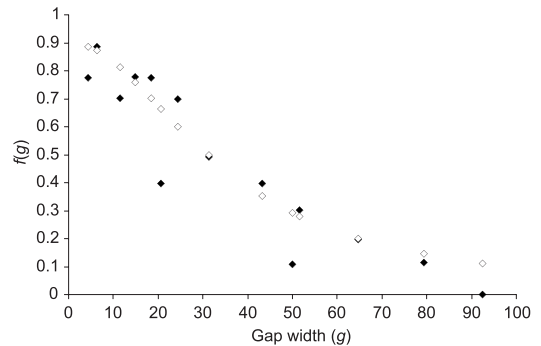

Fig. 2. Data from Rail *et al.* (1997) on gap crossing probabilities, relative to gap width, by golden-crowned kinglets (*Regulus satrapa*) (closed diamonds), and our fit to these data using Eq. 1, and parameter values of *h* = 0.9, *b* = 34.7, and *n* = 2 (open diamonds).

model, we fit Eq. 1 to gap crossing probabilities by golden-crowned kinglets (*Regulus satrapa*) published by Rail *et al.* (1997), using data we extracted from their Fig. 2b. From their graph, a 50% probability of crossing a gap corresponds to a gap of ~31.25 m; this value would be *b* if *h* =1. However, kinglets in this study had a response rate of 90% to tape playback from 100 m (Rail *et al.* 1997), so *h* = 0.9. Consequently we standardize *b* using *h*, so *b* = 31.25/0.9 = 34.7. From the plot, the relationship between probability of crossing and gap width is shallow, so we let *n* = 2 as a first estimate (*see* Fig. 1A). From this, Eq. 1 becomes

$$f(g) = \frac{0.9}{1 + \left(\dfrac{g}{34.7}\right)^2}.$$

When we calculate predicted gap crossing probabilities using the distance values corresponding to the data points in Rail *et al.*'s (1997) figure, we find that this model fits the presented data

well ($r^2 = 0.94$; Fig. 2). Because we only guessed at an appropriate value for *n*, we reran the model with *n* = 1.5, 3, and 4, and found model fits of $r^2 = -0.7$, 0.94, and 0.93, respectively. Consequently, *n* = 2–3 is the best fit.

Other behavioral barriers to movement

Until now, we have focused on habitat gaps and ecotones as potential behavioral barriers to movement. Most of the available evidence comes from forest species whose movement is restricted by forest/non-forest transition zones. There are also examples of habitat gaps or changes in habitat structure within forest that result in a behavioral barrier to movement (Enoksson *et al.* 1995). The Bachman's sparrow (*Aimophila aestivalis*) is a songbird that specializes in open longleaf pine forest maintained by fire or other disturbance. For this species, closed canopy forest is a barrier that can inhibit dispersal between patches of suitable breeding habitat (Dunning *et al.* 1995). Some open-habitat specialists such as yellowhammers (*Emberiza citrinella*) avoid moving near forest edges, just as some forest-interior species do (Hansson 1983).

Rivers are barriers to dispersal for some species, often forming borders of avian species' and

subspecies' distributions, particularly in the tropics (Mayr 1942, Ford 1978, Capparella 1988, Gascon *et al.* 2000). The impeding effects of water boundaries on avian movement may be more prevalent than is apparent from speciation events, however, since genotypic changes have been identified across water boundaries even where phenotypic differences are not obvious (Capparella 1988). Colonization and extinctions of species on islands also provide evidence that water inhibits movements of temperate (Grubb & Pravosudov 1994) and tropical (Robinson 1999) bird species. Avian extinctions on Barro Colorado Island, Panama, indicate that water can be a barrier to immigration (Willis 1974, Karr 1982, Robinson 1999). Another example of extinctions on islands comes from a human-made lake in South Africa, where islands lost bird species while land-bridge islands maintained all of their original species, even where bridges consisted of a thin strip of muddy lake bottom (Dean & Bond 1994). For some species, water appears to be a more impermeable barrier to movement than is land of similar width. Machtans *et al.* (1996) observed birds flying across a 100–300 m-wide lake less frequently than across a 200 m-wide clearcut, and forest specialists were never observed flying over the lake (*see also* Hodges & Krementz 1996).

Finally, social interactions can be behavioral barriers to movement, particularly to dispersal (Brandt 1985). Intraspecific competition can reduce movements of songbirds via territoriality, aggression, and social dominance (e.g., Sherry & Holmes 1996), and interspecific competition can limit movements through corridors and into edge habitat (Catterall *et al.* 1991, Bentley & Catterall 1997). Even local song dialects have the potential to inhibit immigration (Baker & Mewaldt 1978, Baker 1981, Chilton & Ross 1996, Miyasato & Baker 1999). Particularly for colonial-nesters, the absence of conspecifics at an otherwise suitable breeding site also can be enough to discourage movement to that site, thus acting as a behavioral barrier to dispersal (Smith & Peacock 1989, Reed & Dobson 1993, Reed *et al.* 1999). Conspecific attraction, and even heterospecific attraction (Mönkkönen *et al.* 1996, 1999), also may attract birds across an otherwise unsuitable habitat gap.

Dispersal, home range, and post-fledging movements

Details of avian movements during dispersal are limited, but we find evidence in the literature for the existence of behavioral barriers to both natal and breeding dispersal for forest species. Much of this comes from movements detected in connected (intact) landscapes, with corresponding lack of movement in unconnected habitat interpreted as evidence of a barrier. For example, riparian buffer strips can enhance movements of juveniles and adults dispersing through fragmented boreal forests (Machtans *et al.* 1996, Desrochers & Hannon 1997). In some studies, forest birds often take woodland routes rather than crossing clearcuts, even when the path through the forest is two to three times longer than the direct route (Desrochers & Hannon 1997, Bélisle & Desrochers 2002). The authors hypothesized that predation risk may be a driving factor in a bird's decision to take the longer, less exposed route. The predation risk hypothesis may be particularly relevant when evaluating birds dispersing with young; male ovenbirds (*Seiurus aurocapillus*) with fledglings were much more reluctant to cross large (100–300 m) gaps than males dispersing alone (Bayne & Hobson 2001). Two Australian habitat specialists, the blue-breasted fairy wren (*Malurus pulcherrimus*) and the white-browed babbler (*Pomatostomus superciliosus*), readily used corridors of native vegetation during dispersal (Brooker *et al.* 1999). In studies of fragmented and intact forests at a larger spatial scale, dispersal patterns are altered by fragmentation. Juvenile crested tits (*Parus cristatus*) in fragmented habitat delay dispersal compared to those in continuous forest (Lens & Dhondt 1994). In a study of wood nuthatch (*Sitta europaea*) dispersal, adults were less likely to disperse from their territories in fragmented habitat than were adults in intact habitat (Matthysen & Currie 1996). The authors proposed higher search costs for suitable habitat and perceived increased mortality risk among birds that ventured into open areas to move between fragments; the latter hypothesis is a behavioral barrier to dispersal. Behavioral constraints on adults crossing open habitat has been

reported for other species as well. For example, breeding dispersal of American robins (*Turdus migratorius*) is greater between connected sites than between unconnected sites, suggesting woody draws act as corridors or stepping stones (Haas 1995).

Dispersal can be a product of expanding home range movements followed by a shift in activity and subsequent home range retraction (Rolstad 1991). Consequently, we investigated home range behaviors to determine what evidence was available for behavioral barriers. A home range is the area within which an animal forages, breeds, and otherwise spends time during a given time interval (Baker 1978). Studies of home range use are not normally capable of providing evidence of behavioral barriers to movement, per se; rather, they provide indirect evidence. Specifically, the inclusion of a habitat gap in a home range demonstrates that the gap size and its matrix habitat do not constitute a behavioral barrier to movement. For example, individuals sometimes include unusable habitat within their home range, regularly crossing gaps in suitable habitat (Ims 1995, Grubb & Doherty 1999). Birds might also move across ecotones and habitat gaps to seek extra-pair copulations (Norris & Stutchbury 2001). These observations constitute evidence that the ecotones or gaps being crossed do not constitute barriers to movement. Conversely, the observation of habitat patches in fragmented landscapes not being included in home ranges (e.g., Matthysen & Currie 1996, Schmiegelow *et al*. 1997) is not sufficient evidence of a barrier to dispersal because exclusion could be due to other factors, such as reduced habitat quality (Recher *et al*. 1987, Bierregaard *et al*. 1992), predation risk (Lima & Dill 1990), or energetic inefficiency (Redpath 1995). Habitat borders also can serve as conduits for movement, with increased activity near edges potentially indicating a boundary effect of those edges (Desrochers and Fortin 2000). Possibly the best evidence from home range studies of what does and does not constitute a behavioral barrier to movement comes from comparative and experimental studies. Ims (1995) experimentally fragmented a landscape, and found home range sizes of capercaillie (*Tetrao urogallus*) expanded to encompass habi-

tat between patches. Again, this provides information on what gap size and matrix type did not constitute a barrier to movement.

Similar examples of habitat types unsuitable for breeding being included in home ranges come from forest-interior birds that sometimes use snags and remnant trees in open areas as perches (e.g., McClanahan & Wolfe 1993, King *et al*. 1997). Grubb and Doherty (1999) studied inter-patch movements within the home ranges of eight temperate-forest species during late fall and winter. They found variability among species in gap-crossing tendencies, with large birds such as blue jays (*Cyanocitta cristata*) and red-bellied woodpeckers (*Melanerpes carolinus*) more likely to cross, and song sparrows (*Melospiza melodia*) the least likely. They also found that larger gaps were crossed in the fall than in early or late winter, and suggest that fall movements might have been dispersal to wintering areas while later movements were not. It is important to distinguish between dispersal and home range movements because if a species is more prone to behavioral inhibition of movement during the breeding season than at any other time, landscape structure of breeding habitat might limit local population size.

Field studies show that behavioral barriers to movement apparently change by season, being more restricted during the breeding season and less so post-fledging. Late in the breeding season, non-riparian songbirds use shrub corridors to travel to riparian areas, using unconnected riparian habitat minimally (Dmowski & Kozakiewcz 1990). During the post-breeding season, forest-interior species, such as wood thrushes, readily use and move through early- and mid-successional habitats, which are avoided in other seasons (Anders *et al*. 1998, Vega Rivera *et al*. 1998). However, the most open habitats, such as fields and clearcuts, still act as barriers to movements of these thrushes. Several species that breed exclusively in interior forest expand their habitat use during fall to include a wide variety of habitats, including recent clearcuts, presumably due to a concomitant shift to frugivory. In fact, a fall survey in the southeastern U.S. showed the greatest abundance of Neotropical migrant interior-forest specialists in large (80 m-wide) clearcut gaps (Kilgo *et al*.

1999). Species that treat open areas as barriers to movement during the breeding season, particularly Neotropical migrants, readily use open areas during winter months as well (Hutto 1985, Böhning-Gaese *et al.* 1993). Bentley and Catterall (1997) hypothesized that increased use of remnant habitat by wintering migrant bushland birds in Australia indicates a greater flexibility in moving across open space during the winter than during the breeding season. Gap-crossing experiments on resident birds in logged boreal forests reveal a similar pattern (Desrochers & Hannon 1997, St. Clair *et al.* 1998), although seasonal differences are not always evident (Bélisle & Desrochers 2002).

Discussion

Birds are often cited as a taxon in which movements should not be disrupted by gaps in the structural connectivity of the landscape (e.g., Bennett 1990, With *et al.* 1997). Based on our literature review, however, a wide variety of behavioral inhibitions to movements by birds have been observed. Ecotones, gaps in habitat, and water commonly act as behavioral barriers to movement by birds. We were surprised, however, to find no evidence of paved roads acting as barriers to avian movement, beyond the obvious physical risks to crossing (e.g., Mader 1984, Massemin *et al.* 1998). Roads are known to be barriers to movement for other taxa (e.g., Oxley *et al.* 1974, Baur & Baur 1990, Trombulak & Frissell 2000), but road avoidance by birds appears to be a function of low quality habitat for breeding rather than inhibition of movement (Reijnen *et al.* 1997).

The mechanisms driving observed behavioral inhibitions to cross landscape features that do not constitute physical barriers are unknown. It is possible that observed behavioral inhibitions to crossing gaps of open habitat are genetically based (cf. Fraser *et al.* 2001) ancillary to adaptations for other purposes, such as habitat and foraging specialization (Huhta *et al.* 1999), lack of behavioral flexibility (cf. Sol & Lefebvre 2000), and neophobia (Greenberg 1983, 1989, Schaden 1993), or from direct pressures like predator avoidance (Lima & Dill 1990). Regard-

less, one consequence of behavioral barriers to movement is that fragmenting a landscape can have a greater impact on species persistence than previously thought. Models of landscape connectivity (e.g., Metzger & Decamps 1997, With *et al.* 1997, With & King 1999, reviewed by Tischendorf & Fahrig 2000) would be improved by incorporating behavioral inhibitions to movement to accurately assess potential dispersal. For example, models of habitat loss and fragmentation predict thresholds in habitat loss below which persistence declines dramatically (e.g., Gardner *et al.* 1987, Keitt *et al.* 1997, Hill & Caswell 1999; *see* Fahrig 1998 for model predicting thresholds to be uncommon). Empirical support of critical threshold relationships between habitat cover and patch occupancy or population density, however, is debated (Andrén 1994, Bender *et al.* 1998, Mönkkönen & Reunanen 1999). Incorporating behaviorally based gap permeability might decrease disparity between theoretical and empirical results.

Corridors might ameliorate the effects of habitat fragmentation and behavioral barriers to movement (e.g., Noss 1987, Beier & Noss 1998), but this solution must be tested. In addition, corridors are not the only potential way to reduce the impacts of habitat fragmentation. Our review indicates that for forest species, organizing a landscape to reduce contrasts between adjacent patches and maintain gap distances below species-specific crossing thresholds would encourage more movement across the landscape. In a recent experimental study, Bélisle *et al.* (2001) displaced black-throated blue warblers, ovenbirds, and black-capped chickadees (*Poecile atricapillus*), all forest species, from territories in landscapes that varied in their forest cover and fragmentation. They found greater return rates correlated with forest cover, but not with mean inter-patch distances, ostensibly demonstrating behavioral constraints to movement at the landscape level caused by habitat fragmentation. In another study that controlled for forest cover, a more complex pattern was observed. Bélisle and St. Clair (2001) found whether or not landscape features such as rivers acted as a movement barrier depended on migratory strategy and perhaps on navigational ability. The importance of habitat cover is supported by

a study by Ricketts (2001), where matrix habitat affected inter-patch movement in four of six taxa of butterfly, showing another physiologically mobile group to exhibit behavioral inhibition to movements.

It is important to realize that reported gap-crossing tendencies and patterns (Table 1 and above) can be affected by landscape features, evaluation methods, and the motivational state of the individual, as well as by the reason for moving (e.g., foraging, dispersal, seeking extra-pair copulations). This has the potential to hide ecologically significant patterns among species. Movements can be inferred from indirect evidence or observed directly (Turchin 1998). The different methods used for assessing movement vary in their capacity to provide details of what might constitute a barrier to dispersal, and may work only seasonally. For example, song playback during the breeding season would target only movements associated with territorial defense. Because this literature has been reviewed recently (Desrochers *et al.* 1999), we will only highlight key issues.

Assumptions are often made about movement paths and about responses to experimental stimuli, and limitations exist for all methods of evaluating movement. However, these should not deter research on behavioral inhibitions to movement because suitable experimental design can allow strong arguments to be made for the presence or absence of inhibitions. Indirect methods for assessing movement across various habitats include censuses, capture-recapture studies, and genetic comparisons. Indirect methods often provide a large amount of data per unit effort, and can be done at a large spatial scale, but normally cannot reveal the movement path taken. For example, census data provided the basis for early investigations of corridors facilitating movement, where movement through a corridor was inferred from species compositions in connected patches, but there was no evidence that birds would not have moved in the absence of corridors (MacClintock *et al.* 1977). Schmiegelow *et al.* (1997) improved on this experimental design by comparing species richness in connected and unconnected areas, and they supported the idea that corridors facilitate movement of birds between otherwise isolated patches. Generally, movement patterns relative to landscape features assessed by indirect methods must be inferred, and these assumptions play critical roles in determining connectedness of a landscape (Metzger & Décamps 1997, With & King 1999). However, given adequate replication, and perhaps experimental landscape manipulation, indirect methods can provide strong evidence for or against behavioral inhibitions to movement.

Direct methods can be as simple as observing unmarked individuals flying across ecotones or habitat gaps (e.g., Wegner & Merriam 1979) or as sophisticated as tracking individuals using satellite radio transmitters (Brodeur *et al.* 1996, Britten *et al.* 1999). Possibly the most common approach is to sequentially survey populations for individually marked individuals to quantify dispersal events across different landscape features. These longitudinal studies provide excellent data on short-distance movements, but become more difficult as distance increases due to the area researchers are required to search (Barrowclough 1980, Faaborg *et al.* 1998). A less intensive method to determine if behavioral barriers to movement exist is to use recorded playback of conspecific songs or alarm calls to assess propensity to cross ecotones or enter different types of habitat. However, responses are dependent on the motivation provided by the stimulus, such as a bird showing a territorial reaction (e.g., Titus & Haas 1990). Consequently, if a suitable playback is determined, a great deal of relevant information can be gathered quickly (Desrochers & Hannon 1997, St. Clair *et al.* 1998).

Recent research using ground-based radio telemetry (Bélisle & St. Clair 2001, Norris & Stutchbury 2001) and return patterns of displaced birds (Bélisle *et al.* 2001) provide excellent information on landscape use, although behavioral decisions during movement are unknown.

Based on our literature review, we find some evidence of ecologically based patterns in behavioral barriers to movement. We present these patterns as hypotheses because studies are sparse, so the evidence for each hypothesis is only suggestive. Consequently, these hypotheses should be viewed as heuristic tools to stimulate interest in research on behavioral barriers to movement.

Hypothesis 1: Habitat specialists are more

likely than are habitat generalists to be inhib-ited in crossing ecotones or habitat gaps. Stud-ies of forest birds show that habitat specialists are unlikely to cross large gaps between forest patches (Desrochers & Hannon 1997, Rail *et al.* 1997, St. Clair *et al.* 1998), and when habi-tat is fragmented, corridors increase movement and colonization rates (Machtans *et al.* 1996, Schmiegelow *et al.* 1997, Brooker *et al.* 1999). In one study, forest specialists were more reluc-tant to cross large gaps than were generalist species such as white-throated sparrows (*Zonot-richia albicollis*) (Rail *et al.* 1997). Habitat spe-cialists are defined as such because they restrict their habitat use. Consequently, these species might be relatively sensitive to habitat fragmen-tation (e.g., Hansson 1991, Ims 1995).

Hypothesis 2: Forest understory species are less likely to enter open areas than are canopy species. This hypothesis arises from studies of extinction, speciation, and colonization patterns of isolated habitat and examples exist from temperate and tropical forests (Willis 1979, Karr 1982, Capparella 1988, Newmark 1991, Bierre-gaard *et al.* 1992). These observations are sup-ported by playback experiments in which canopy species tended to show less inhibition to moving across gaps than did understory species (Deroch-ers & Hannon 1997, St. Clair *et al.* 1999). Species used to open, exposed microhabitats like treetops might be more prepared to avoid the predation threats that exist in open areas (Derochers & Hannon 1997). There is con-siderable overlap between this hypothesis and hypothesis 1 because some understory species are specialists on that stratum, while canopy species occupy a wider vertical range in forests (Terborgh & Weske 1969).

Hypothesis 3: Tropical species are more inhibited in their movements than are temper-ate species. Tropical birds are thought to have shorter dispersal and colonization distances than their temperate counterparts, although direct evidence is limited (Terborgh 1975). Smaller specific and subspecific range sizes in the trop-ics and distributions that often end at waterways (Mayr 1942, Capparella 1988, Gascon *et al.* 2000) are consistent with this assertion. Because of high diversity and population densities, social factors may also act more frequently as barri-ers to movement in the tropics in the form of competitive interactions, particularly where the centers of multiple species' distributions overlap (Terborgh 1985). If this hypothesis were sup-ported, it would imply that habitat fragmenta-tion has a greater impact on tropical species than on temperate species. Again, specializations are likely play an additional role in this sensitivity to fragmentation in tropical species; Neotropi-cal forest birds are generally more specialized in their foraging techniques and use narrower habitats and microhabitats than temperate forest birds (Willis 1974, Stouffer & Bierregaard 1995, Robinson 1999).

Hypothesis 4: Species that tend to be socially solitary are more inhibited in their movements than are flocking species. According to predic-tions from predation risk theory, birds should be more likely to venture into unfamiliar, usu-ally open, areas if they are in groups (Lima & Dill 1990, Van Vuren 1998). For example, in yellow-eyed juncos (*Junco phaeonotus*), group size increases with the distance to cover during foraging (Caraco *et al.* 1980). Greater flocking tendency and larger home range size of black-capped chickadees might explain their greater likelihood of entering narrow corridors than white-breasted nuthatches (*Sitta carolinensis*) and hairy woodpeckers (*Picoides villosus*) (St. Clair *et al.* 1998). In addition, animals tend to be most vulnerable to predators when in unfamiliar environments and when alone (Van Vuren 1998). However, this hypothesis is not supported for all comparisons. For forest birds moving across agricultural fields, interspecific group size only affects distances birds move from forest edges during winter (Bélisle & Desrochers 2002), and conspecific group size has no influence on forest bird tendency to enter open areas (St. Clair *et al.* 1998, Bélisle & Desrochers 2002).

Hypothesis 5: Non-migratory species are more inhibited behaviorally in their movements than are migratory species. This hypothesis has been proposed before (e.g., Udvardy 1981, Paradis *et al.* 1998), although there is little evidence supporting it (Whitcomb *et al.* 1981, Lynch & Whigham 1984, Böhning-Gaese *et al.* 1998). Migrants might exhibit less restrictive foraging specialization, allowing use of differ-ent habitats during breeding and non-breeding

seasons, which might result in less inhibition of movement among habitat types (Greenberg 1983). Consistent with the idea that migrants might be less restricted in movements, analysis of banding data for British birds shows that migrants disperse farther than do resident birds (Paradis *et al*. 1998). Recent translocation experiments yield some evidence to suggest that this hypothesis may be valid. Resident red-breasted nuthatches (*Sitta Canadensis*) had a 57% return rate when displaced from their territories, whereas short-distance migrants (golden-crowned kinglets) and long-distance migrants (yellow-rumped warblers, *Dendroica coronata*) had return rates of 100% and 86%, respectively (Bélisle & St. Clair 2001). These results, however, cannot distinguish this hypothesis from the alternatives that return rates reflect navigational ability, motivation, or opportunity, such as birds stopping at the first open territory in an unsaturated landscape.

Clearly investigations of behavioral barriers to movement are in early stages of development, and they are in need of both observational and experimental research. Given the importance of dispersal and connectivity to species persistence in recently fragmented landscapes, it is an important research problem.

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