

ON HOME-RANGE GAP-CROSSING

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ABSTRACT.—Gap-crossing may be defined as any movement by animals across swaths of inhospitable habitat. Such behavior is the least understood of the factors that control metapopulation dynamics. We differentiate among active and passive dispersal gap-crossing and active and passive home-range gap-crossing. From observations of active home-range gap-crossing by permanent-resident birds wintering in 47 woodlots in an agricultural landscape, we conclude that larger birds were more likely than smaller ones to cross gaps, and to cross wide gaps, and that proximity and prevalence of woodlands in the surrounding landscape were consistently positively related to the proportion of species that crossed gaps. We discuss these results in relation to the migration equation of Baker and the marginal value theorem of Charnov. Knowledge of decision rules relating active home-range gap-crossing to resource levels within individual habitat fragments and risk of movement among fragments appears to be important for valid calculations of local population densities and metapopulation persistence. *Received 8 May 1998, accepted 6 November 1998.*

METAPOPULATION DYNAMICS IN FRAGMENTED HABITATS (Opdam 1991) are thought to depend on interactions among four factors: (1) area requirements, (2) specialized-habitat requirements, (3) edge effects, and (4) gap-crossing ability (e.g. Dale et al. 1994). Here, we present records of gap-crossing by bird species residing within fragmented temperate-deciduous woodland habitat and then consider the consequences of home-range gap-crossing to metapopulation theory.

Gap-crossing has been defined as the ability to cross swaths of inhospitable habitat (Dale et al. 1994). Although "ability" implies physical ability, psychological constraints, rather than physical incompetence, appear to restrict gap-crossing in some species. Therefore, we define gap-crossing more generally as any movement across swaths of inhospitable habitat. We recognize two qualitatively distinct forms, "dispersal gap-crossing" and "home-range gap-crossing." Dispersal gap-crossing occurs during movement between natal and breeding sites; in many species, it operates only during one brief period per lifetime. Dispersal gap-crossing can involve movement across very wide gaps and has important implications for recolonization (Opdam 1991) and rescue effects (Brown and Kodric-Brown 1977) as functions of patch isolation. In contrast, home-range gap-crossing connects two or more habitat patches

within one home range, it may be engaged in repeatedly by the same animal, and it generally involves gaps much narrower than those crossed during dispersal. Home-range gap-crossing has important consequences for estimates of area requirements of individual animals and thus for distinguishing subpopulations within metapopulations (Rolstad 1991).

At the behavioral level, we distinguish between passive gap-crossing and active gap-crossing. Passive gap-crossing may or may not involve an active decision to leave a habitat patch, but the direction and rate of the crossing are not under an animal's control. For example, a young spider may actively decide when to "balloon" from its natal fragment but can disperse only in the direction of the wind and probably has little control over how far it travels during dispersal. Such passive gap-crossing is an implicit assumption underlying the island biogeography model of MacArthur and Wilson (1967).

Active gap-crossing (and any other active dispersal-like behavior) involves three separate decision processes: leaving a patch, deciding which way to go, and stopping at a second patch. Active gap-crossing assumes that individuals can move independently of the direction of movement of the medium that separates fragments, so that both the direction and distance of dispersal are under voluntary control. Thus, four types of gap-crossing behavior may be distinguished: (1) active dispersal gap-

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crossing, (2) passive dispersal gap-crossing, (3) active home-range gap-crossing, and (4) passive home-range gap-crossing. Examples of the first three types come readily to mind. Although a dispersing animal may not be in sensory contact with or otherwise have knowledge of its destination when it sets out across a gap, an active home-range gap-crosser should perceive its destination or know from previous experience that it is there. It is less easy to imagine a home range in any conventional sense in which constituent patches are reached only by passive gap-crossing, but examples may exist; e.g. fish are sometimes displaced by floods and then swim back upstream afterward (E. A. Marshall pers. comm.).

We recorded cases of gap-crossing that we observed during censuses of permanent-resident birds that wintered in very small forest fragments in an agricultural landscape. We had two principal objectives with regard to gap-crossing: (1) to determine whether such movements differed among species, and if so, whether such crossings were related to body size, as suggested by Dale et al. (1994); and (2) to determine whether prevalence of gap-crossing across an entire assemblage of resident birds was related to particular attributes of either the focal woodlot or the surrounding landscape. We expected that meeting these objectives would provide insight into which species might be more likely to incorporate several or more woodlots into multi-fragment home ranges, and what sort of woodlot might be more likely to be so incorporated. As we pursued field work during the winter hiatus between the autumn (i.e. juvenile) and spring (i.e. prebreeding) dispersal periods for these species, we assumed that our records represented active home-range gap-crossing.

STUDY AREA AND METHODS

We worked in the agricultural landscape of Crawford, Delaware, Marion, and Morrow counties, north-central Ohio. We surveyed 47 woodlots (0.54 to 6.01 ha) once each during three survey periods in the nonbreeding seasons of 1993-94 and 1994-95 (i.e. six visits per woodlot and a total of 288 visits; see below). We term these survey periods fall (28 October to 23 December 1993; 5 November to 15 December 1994), early winter (21 January to 9 February 1994; 24 January to 6 February 1995), and late winter (7 to 23 March 1994; 11 to 22 March 1995). Seven woodlots were composed of oak-hickory forest, 33 of beech-

maple forest, and 7 were a mix of the two forest types. Canopy height ranged from 10 to 15 m in 3 woodlots and exceeded 15 m in 44 woodlots. All 47 woodlots were absolute islands in that they were not connected by a fencerow or riparian corridor to any other woodland, and none contained bird feeders or any other source of supplemental food. We do not know the extent to which woodlands in the vicinity of each study woodlot contained supplemental food. We began data collection in 1993 in 50 woodlots, but abandoned three of them before repeating the surveys in 1994. In two of these three woodlots, a house (with a bird feeder) was built after the first winter of the study, and we discovered that birds in the third woodlot were flying substantial distances to a feeder in a neighboring farmyard. Because of certain implications of such home-range gap-crossing to supplemental food, we will consider this anecdote further in the Discussion.

Each survey entailed walking slowly around the perimeter of a woodlot once and then through the woodlot's interior along north-south transects set 50 m apart. Each woodlot was fringed by a band (5 to 6 m wide) of dense rose (*Rosa* sp.) and blackberry (*Rubus* sp.) shrub cover that would have hidden birds from observers on transects. Therefore, during the perimeter walk, we counted all birds within this fringe. During each of the interior transects, we counted all birds within 25 m of the transect line.

Instances of gap-crossing to and from woodlots were detected either while we walked across fields to a woodlot or while we walked around its perimeter. In cases where a bird's origin or destination could not be determined, we recorded the compass direction of the flight and later determined on a map the closest woodland or fencerow corridor in that direction. By assuming that all gap-crossings resembled each flight that we observed completely in being essentially linear, we incorporated such mapped distances into the data set. We counted each gap-crossing by a species as one record regardless of the number of individuals involved. Some analyses were restricted to gap-crossings out of woodlots and others also examined crossings into woodlots.

We indexed our observation efforts based on the distance that we walked across a field to reach a woodlot plus the perimeter of the woodlot around which we walked during censuses (Table 1). We assumed that the greater the value of this index, the more likely we were to observe gap-crossing.

For each woodlot, we recorded measures of size, structure, and degree of isolation and connectedness (Table 1). We measured woodlot area and perimeter from ground-truthed 7.5-min topographic maps and estimated to the nearest 5% the proportion of woodlot area composed of swamp, shrub, or herb/forb cover.

We defined isolation as how far apart woodlands were from each other and connectedness as how well

TABLE 1. Variables used in analysis of the proportion of species in a woodlot that were observed to gap-cross out of that woodlot ($n = 47$ woodlots). Values were either estimated during survey visits or taken from topographic maps.

Variable	$\bar{x} \pm SE$
Woodlot	
Perimeter (m)	630 \pm 258
Observation effort (perimeter plus distance walked to woodlot) (m)	946 \pm 333
Area (ha)	2.17 \pm 1.55
Shape index (woodlot perimeter/perimeter of circle of same area)	4.9 \pm 1.9
Topographical relief (maximum - minimum elevation in m)	5.1 \pm 1.3
Proportion of area in swamp	0.01 \pm 0.03
Proportion of area in shrub cover	0.55 \pm 0.30
Proportion of area in herbaceous cover	0.12 \pm 0.17
Landscape	
Distance to nearest woodlot (m)	386 \pm 245
Number of woodlots within 0.5 km	0.9 \pm 1.0
Number of woodlots within 1.0 km	3.5 \pm 2.1
Total woodland within 0.5 km (ha)	1.77 \pm 2.22
Total woodland within 1.0 km (ha)	12.62 \pm 12.21
Distance to nearest wooded fencerow or watercourse (m)	425 \pm 298
Total length of wooded fencerow or watercourse within 0.5 km (m)	267 \pm 403
Total length of wooded fencerow or watercourse within 1.0 km (m)	1,309 \pm 1,184

such woodlands were connected by potential movement corridors (e.g. wooded fencerows and watercourses). Isolation and connectedness of each woodlot within the landscape were characterized from topographic maps as distance to the nearest woodlot, area of woodland within 0.5 and 1.0 km, number of woodlots within 0.5 and 1.0 km, distance to the nearest wooded fencerow, and total length of fencerows within 0.5 and 1.0 km. To obtain composite estimates of the degrees of isolation and connectedness, we performed a principal components analysis using the eight landscape indices listed in Table 1. The first two principal components (PC1 and PC2) had eigenvalues greater than 1 and were deemed the most important based on the Kaiser criterion (Anonymous 1995). PC1 and PC2 accounted for 68% of the total variance in the landscape-level variables and therefore provided a good summary of the degree of isolation and connectedness of fragments (Table 2). PC1 showed moderate to high negative loadings for number of woodlots within 0.5 and 1.0 km, as well as for total area of woodland within 0.5 and 1.0 km. PC1 also had a high positive loading for distance to nearest woodlot. Therefore, we interpreted PC1 as an index of the amount and proximity of woodland in the landscape surrounding each fragment, with higher scores representing increased isolation.

PC2 had high positive loadings for the length of fencerow within 0.5 and 1.0 km and a high negative loading for distance to nearest fencerow. We interpreted PC2 as indicating connectedness to other woodlands in the landscape, higher scores representing increased connectedness. Each principal component beyond PC2 explained less than 10% of

the variance in landscape-level variables, and each was omitted from further analysis.

In general, our sample sizes were small and did not appear to be normally distributed; therefore, we primarily used nonparametric statistical tests (Hollander and Wolfe 1973). However, in examining the proportion of individuals of a species in a woodlot that gap-crossed, and the proportion of all species in a woodlot that gap-crossed, our sample sizes were >30 , so by the Central Limit Theorem, we assumed that our sampling distribution was approximately normal (Devore and Peck 1993) and employed multivariate parametric tests.

TABLE 2. Landscape variable scores and cumulative proportion of variation in eight indices of isolation and connectedness of 47 woodlots explained by the first two principal components. Eigenvalues were 3.37 for PC1 and 2.05 for PC2.

Landscape variable	PC1	PC2
Distance to nearest woodlot	0.409	0.259
Number of woodlots within 0.5 km	-0.453	-0.209
Number of woodlots within 1.0 km	-0.429	-0.029
Area of woodland within 0.5 km	-0.379	-0.214
Area of woodland within 1.0 km	-0.377	-0.158
Distance to nearest fencerow	0.262	-0.467
Length of fencerow within 0.5 km	-0.205	0.557
Length of fencerow within 1.0 km	-0.218	0.538
Proportion of variance explained	0.421	0.256

RESULTS

We present our results in the form of answers to six questions about gap-crossing.

Do species differ in the tendency to home-range gap-cross?—Only species detected in 25% or more of all woodlots were included in the analysis. Species differed in the tendency to gap-cross. Considering all instances of gap-crossing, both into and out of woodlots, Blue Jays (*Cyanocitta cristata*) and Red-bellied Woodpeckers (*Melanerpes carolinus*) were the most likely species to cross; Song Sparrows (*Melospiza melodia*) were the least likely; and Downy Woodpeckers (*Picoides pubescens*), Carolina Chickadees (*Poecile carolinensis*), Tufted Titmice (*Baeolophus bicolor*), White-breasted Nuthatches (*Sitta carolinensis*), and Northern Cardinals (*Cardinalis cardinalis*) were intermediate (Fig. 1).

It is possible that apparent differences among species in the tendency to cross gaps were due to differing numbers of individuals of the various species, or to a bias in observation effort. Restricting analysis to gap-crossing out of woodlots, we checked for such biases and for the possible influence of various woodlot and landscape variables. We used the arcsine-transformed proportion of individuals of each species that gap-crossed as the dependent variable to control for variation among woodlots and species in the number of individuals in a woodlot that could have gap-crossed.

Woodlot area was an important predictor of home-range gap-crossing, with birds of four species being significantly more likely to cross from small than from large woodlots (Table 3). The tendency of several species to leave a woodlot was also significantly higher if the woodlot had a large perimeter or extent of shrub cover (Table 3). Only the Downy Woodpecker seemed influenced by landscape-level factors, being more likely to leave woodlots farther from other woodlands (PC1) or more connected to other woodlands by wooded fence-rows (PC2; Table 3). The infrequent gap-crossing by White-Breasted Nuthatches and Song Sparrows (Fig. 1) was not significantly related to any environmental variable at either the habitat-patch or the landscape level. Finally, Northern Cardinals crossed gaps significantly less often as observer effort increased (Table 3).

Do species differ in the median distance crossed, and if so, is the difference associated with body

size?—We restricted our analysis (Jonckheere/Terpstra's distribution-free test for ordered alternatives using a one-way layout; Hollander and Wolfe 1973) to species in which we observed at least four crossings. These seven species, ranked by increasing body size (Dunning 1992), were Carolina Chickadee < White-breasted Nuthatch < Tufted Titmouse < Downy Woodpecker < Hairy Woodpecker (*Picoides villosus*) < Red-bellied Woodpecker < Blue Jay (Fig. 2). We used calculated average values of all crossings by each species for each woodlot and based our analysis on the medians of these average values. The species did differ in median gap-crossing distance, and the distance was significantly positively related to body mass ($P = 0.014$).

Do species differ in the maximum distance crossed, and if so, is the difference associated with body size?—Although closely related to the previous question, the issue of maximum gap-crossing has particular importance because it relates to how fragmented a home range could be tolerated by individuals of any given species. For analysis, we placed the same restrictions on the data set that we employed in studying the second question, but we also limited our attention to species seen crossing during at least four surveys. In testing the five species meeting these criteria, we used the maximum distance that an individual of each species was observed to cross during each survey. The median maximum distance was then taken as the median of the survey-specific maximum distances, so the sample sizes in Figure 3 are the number of surveys (>3) for each species for which we tallied at least one gap crossing. We employed Page's distribution-free test for ordered alternatives based on Friedman rank sums (Hollander and Wolfe 1973), blocking on census and ordering by body size (Carolina Chickadee < Red-breasted Nuthatch < Tufted Titmouse < Red-bellied Woodpecker < Blue Jay).

Similar to the results for median gap-crossing distance, maximum gap-crossing distance varied significantly among species and was positively related to body size ($P < 0.01$; Fig. 3). In Figure 3, the maxima for the woodpecker and the jay were derived from map locations, and therefore may be considered conservative estimates of the true maximum gap-crossing by these species.

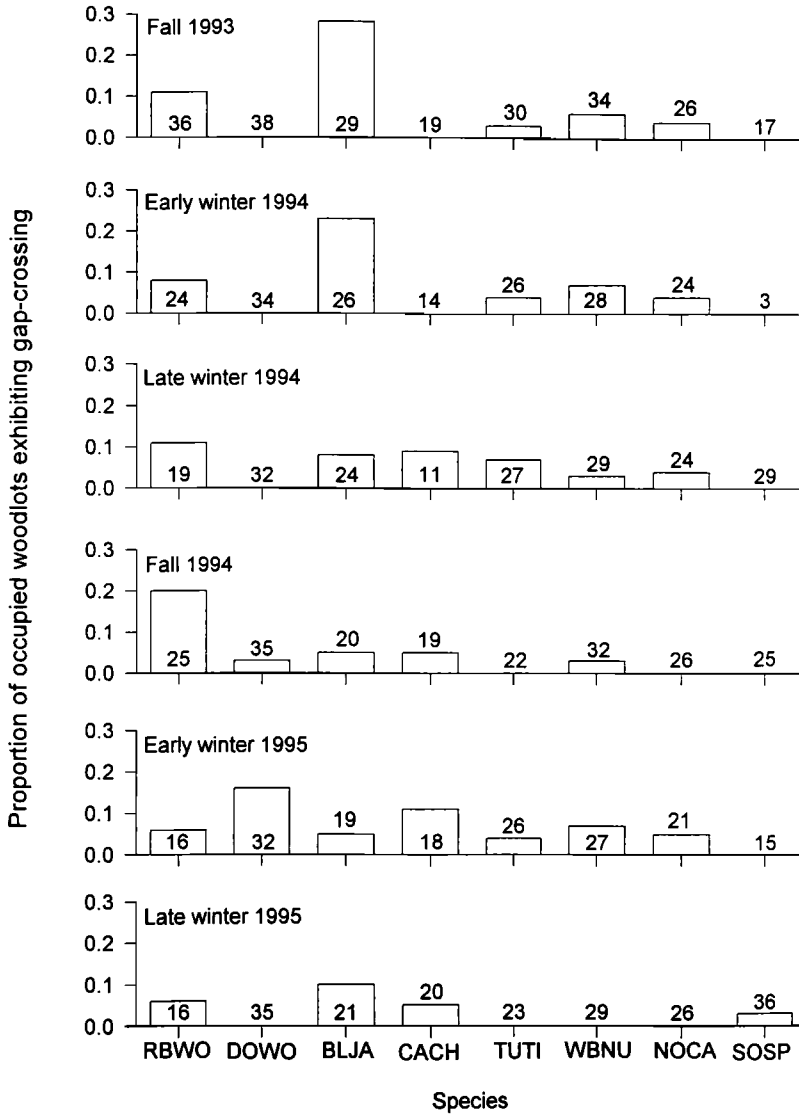


FIG. 1. Proportion of all woodlots occupied by a given bird species from or toward which individuals of that species were observed to fly across gaps. Results are from three surveys of 47 isolated woodlots during each of two nonbreeding seasons. Only species encountered in more than 25% of the woodlots are included. Numbers of woodlots occupied are shown in or above the bars. RBWO = Red-bellied Woodpecker, DOWO = Downy Woodpecker, BLJA = Blue Jay, CACH = Carolina Chickadee, TUTI = Tufted Titmouse, WBNU = White-breasted Nuthatch, NOCA = Northern Cardinal, SOSP = Song Sparrow.

Does gap-crossing distance vary with time of year?—To examine this question, we found the median distance crossed by each species during each of the three seasons, and compared these medians with a Friedman's test blocking on species. Median gap-crossing distance varied with season ($P = 0.005$; Fig. 4). Each species

crossed the widest gaps in fall and the narrowest gaps in late winter.

Did gap crossing distance vary between the two years of study?—Because median gap-crossing distances varied among species, we calculated species-specific median gap-crossing distances for each of the two winters. After subtracting,

TABLE 3. General linear models for the proportion of individuals of a species in a woodlot that crossed a gap out of that woodlot. Shown are significant *F*-values, with the direction of the relationship in parentheses (e.g. a minus for Area indicates that birds moved from smaller to larger woodlots). Independent variables listed in Table 2, but not in this table, were not significantly related to gap-crossing by any species.

Species ^a	Area	Edge	Shrub	PC1	PC2	Observer effort
Red-bellied Woodpecker	6.43 (-)*	10.49 (+)**	5.19 (+)*	—	—	—
Downy Woodpecker	—	—	—	4.45 (+)*	6.56 (+)*	—
Blue Jay	7.33 (-)*	23.52 (+)**	6.77 (+)*	—	—	—
Carolina Chickadee	18.30 (-)**	58.48 (+)**	—	—	—	—
Tufted Titmouse	—	4.50 (+)**	—	—	—	—
White-breasted Nuthatch	—	—	—	—	—	—
Northern Cardinal	27.64 (-)**	87.73 (+)**	—	—	—	6.32 (-)*
Song Sparrow	—	—	—	—	—	—

*, 0.05 > *P* > 0.01; **, *P* < 0.01.

^a *df* = 1 and 21 for Red-bellied Woodpecker, Blue Jay, and Carolina Chickadee; 1 and 27 for Downy Woodpecker; 1 and 23 for Tufted Titmouse; and 1 and 19 for Northern Cardinal.

for each species, the second winter's median from the first winter's, we searched for significant variation with a one-sample Wilcoxon test. The result was nonsignificant variation between years (*P* = 0.14).

Is the proportion of species in a woodlot that cross to or from the woodlot related to features of the woodlot itself or the surrounding landscape?—We investigated this question by regressing the woodlot and landscape variables with the proportions of species found in a woodlot that were observed to cross out of the lot.

After having been adjusted for the number of species present in the woodlot, the number of species observed to gap-cross out of a woodlot was significantly positively related only to the total area of woodland within 0.5 km (adjusted *r*² = 0.100, *df* = 1 and 46, *P* = 0.017). Considered in the aggregate, the variables we employed to describe woodlot and landscape features were poor predictors of centrifugal gap-crossing.

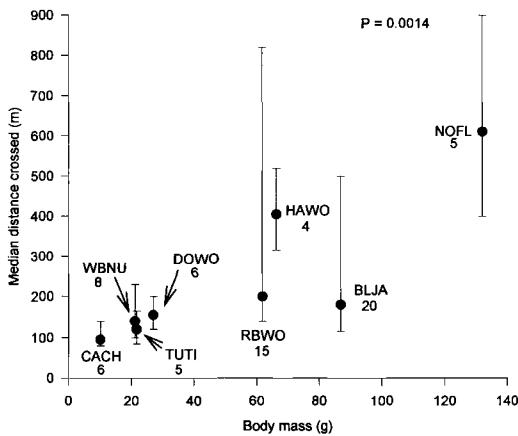


FIG. 2. Relationship between median gap-crossing distance and body mass in permanent-resident birds species wintering in an agricultural landscape. Analysis was restricted to species with at least four observed crossings. Numerals denote number of crossings, and whiskers are quartile deviations above and below the medians. HAWO = Hairy Woodpecker, NOFL = Northern Flicker (*Colaptes auratus*); other species abbreviations are as in Figure 1.

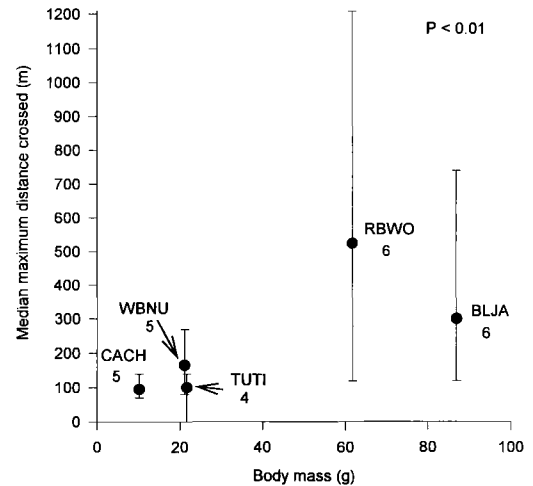


FIG. 3. Relationship between median maximum gap-crossing distance and body mass in permanent-resident bird species wintering in an agricultural landscape. Numerals denote number of surveys during which each species was observed to gap-cross at least once, and whiskers are quartile deviations above and below the medians. Species abbreviations as in Figure 1.

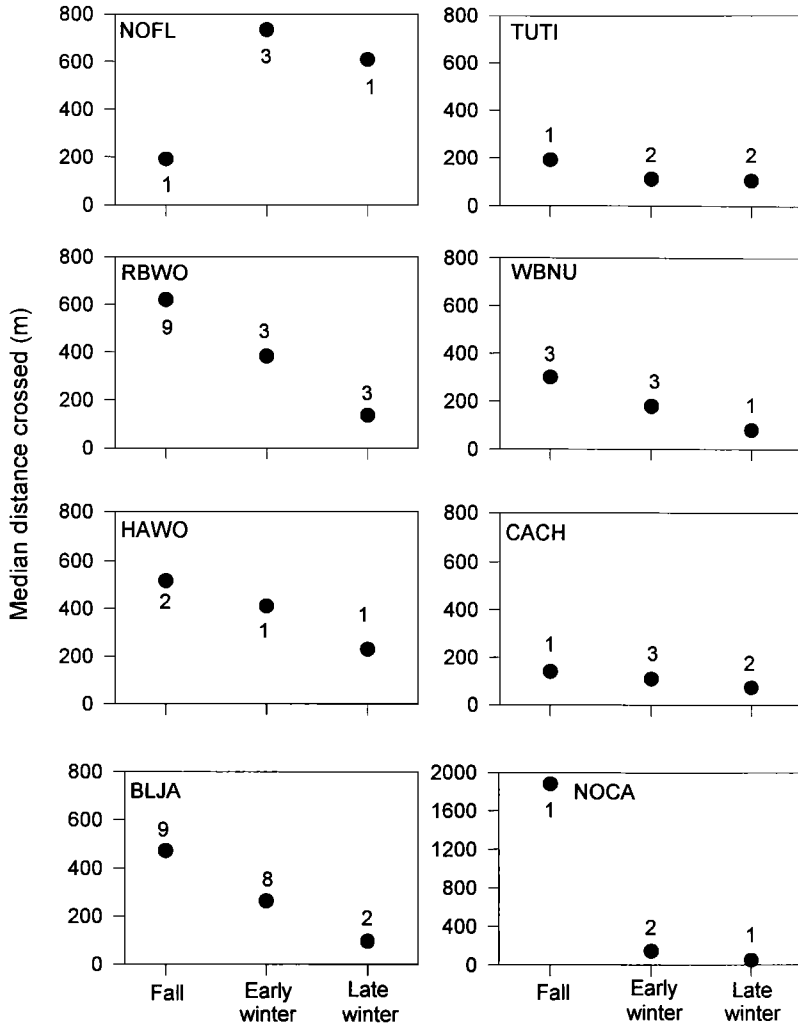


FIG. 4. Relationship between median distance of gap crossed and season for eight bird species. Numerals denote the number of observations in each season. We judged the sample sizes insufficient for determining quartile deviations from the median. Species abbreviations as in Figures 1 and 2. Note the unique abscissa scale for Northern Cardinal.

DISCUSSION

Our main findings were that larger species of birds were more likely than smaller ones to cross gaps (Fig. 1) and to cross wide gaps (Figs. 2 and 3), that gap-crossing was more likely to occur in fall than in early or late winter (Fig. 4), and that the prevalence of woodlands in the surrounding landscape was consistently related to the proportion of species that crossed gaps.

Here, we discuss our results in conjunction with two theoretical constructs that appear to

have relevance to active home-range gap-crossing, namely Baker's (1978) "migration equation" and Charnov's (1976) "marginal value theorem." Although both are incomplete in explanatory power, considered together, they provide considerable insight into a direction that future research might take to obtain a clearer picture of the causes of home-range gap-crossing.

Although Baker terms his construct a migration equation, it is meant to be applied to any movement between two points in space. Thus, it applies to gap-crossing between habitat

patches. The model is intended to provide a general explanation for the conditions under which any movement would be favored by natural selection. For our purposes, the mathematical preamble may be dispensed with and the migration equation itself presented:

$$h_1 < h_2 M, \quad (1)$$

where h_1 and h_2 are habitat suitabilities (i.e. fitness payoffs) in habitats 1 and 2, respectively, and M is the effect on fitness (usually negative) of the actual movement from habitat 1 to habitat 2. In essence, the migration equation states that movement between habitats (i.e. locations) 1 and 2 is adaptive whenever the fitness payoff in habitat 1 is lower than that in habitat 2 discounted by the cost of the movement.

For example, in the comparison between Blue Jays and Carolina Chickadees, one possibility is that the fitness cost associated with flying between gaps is higher for the smaller bird. Chickadees appear to have lower flight speed than jays, so perhaps they are more vulnerable to predation by hawks while en route, or perhaps the relative metabolic cost of long flights in cold weather is higher for the smaller bird. In addition, the winter-long energy requirement of a bird should be roughly proportional to body size. Small birds such as chickadees tend to require smaller home ranges during the winter, so they may be less likely to increase their fitness by crossing a gap than are larger birds.

In a similar vein, Baker's equation warns us to be cautious when ascribing cause in cases where animals appear to be unwilling to cross gaps of a particular width. An often-quoted example that may involve a misinterpretation is the disappearance of ant-following bird species after fragmentation of a lowland Neotropical rainforest (e.g. Bierregaard et al. 1992). Shortly after fragmentation, understory species that normally forage on prey flushed by raiding army ants disappeared from fragments separated from the parent forest by as little as 80 m. This disappearance has been widely interpreted as demonstrating an unwillingness of individuals of these species to cross an apparently inconsequential gap, even though all of the species seemed quite capable anatomically and physiologically of doing so. However, if crossing such a narrow gap involves considerable predation risk from resident accipitrine hawks,

for example, then h_2 would need to be very much higher than h_1 for the crossing to be adaptive. Such might be the case if h_1 suddenly were to drop precipitously, as presumably was the case in the newly fragmented plots. We would be surprised to learn that the ant-following birds disappearing from the new fragments actually had died there rather than crossing the 80-m gap to the parent forest. Assuming that for antbirds the drop in habitat suitability in the new fragments was more or less permanent, the migration equation would predict that crossing from the parent forest back into the fragments would never be adaptive. Similar arguments based on the high fitness costs of crossing gaps not being overcompensated by differences in habitat suitability can be invoked to explain the apparently very pronounced reluctance of many Neotropical understory birds to cross other gaps, such as rivers.

One of the three woodlots that we dropped from our survey was located 150 m from an isolated farmhouse that had in its yard a sunflower-seed feeder and two leafless trees. At approximately 30-min intervals on 28 October 1993, chickadees, titmice, and nuthatches flew from the woodlot to the feeder, husked and ate seeds while perched in the two trees, then flew back to the woodlot. In terms of Baker's model, the rich food supply at the farmhouse had made $h_2 M$ higher than h_1 for birds in the woodlot, whereas the presumably lower predation risk in the woodlot had made $h_2 M$ higher than h_1 for birds at the farm whose crops and stomachs were full. Thus, the birds flying back and forth throughout the day could have been responding to two comparisons of habitat suitabilities depending on their trophic state.

A second construct relevant to active home-range gap-crossing is the marginal value theorem (Charnov 1976). This model predicts how long a forager should stay in each patch within its home range. An important assumption of the model is that while in a patch, a forager continually depresses the level of its prey there, so that its rate of energy intake steadily decreases. When that rate reaches the overall net energy intake rate for all patches in its home range (the marginal value), the animal should move to another patch. Between visits by the forager, the food supply in each patch is assumed to recover.

It may not be immediately clear how the

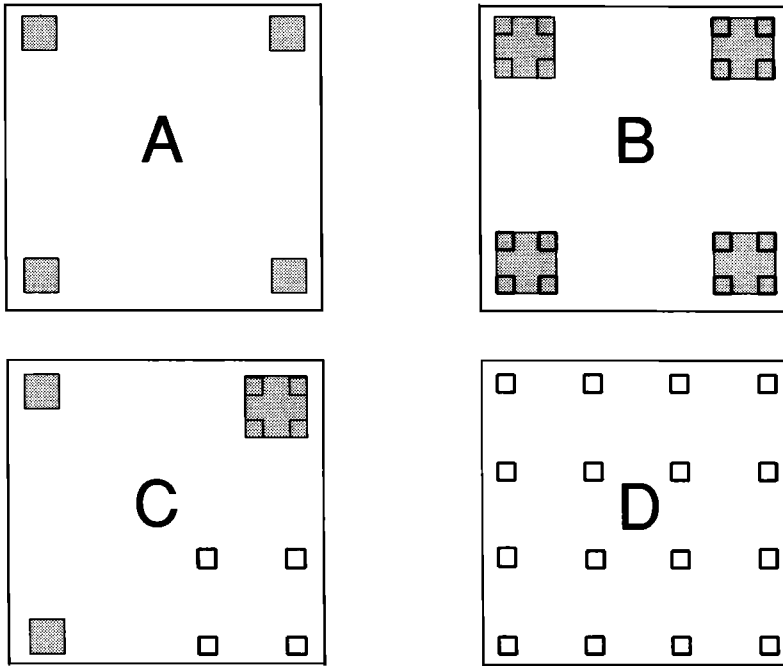


FIG. 5. Schematic patterns of occurrence of White-breasted Nuthatches as a function of woodland fragment size and gap distance. Woodland fragments (heavy lines) total 16 ha in each of the four landscapes. In A, each woodland of 4 ha is large enough to constitute a home range (stippled) for one nuthatch. In B, four 1-ha woodlots closer together than the maximum home range gap-crossing distance (200 m) of nuthatches are incorporated into each of four home ranges. In C, one set of four 1-ha woodlots is spread too far apart to furnish a home range, whereas in D, all 16 1-ha woodlots are too widely dispersed to be incorporated into nuthatch home ranges.

marginal value theorem might apply to gap-crossing in the wintering temperate-zone birds we studied because their food supplies are thought to decrease continually, thus failing to satisfy the assumptions about food depression and recovery. However, it seems possible that some forms of food could meet the criteria. In particular, prey availability at ant colonies visited by Hairy Woodpeckers may be temporarily reduced within the birds' reach, but the ants may recolonize such areas on warm days between visits by the woodpeckers.

It is also possible to conceive of woodlots as automatically fluctuating in net energy return during the winter, in effect diminishing and replenishing a net energy supply. In cold weather during winter, the species in our study are known to move horizontally in response to wind direction, favoring leeward and sheltered locations during high winds (Grubb 1977). One can imagine that within a matrix of woodlots in an agricultural landscape, some patches are

sheltered from the wind by other patches or are themselves large enough to provide a sheltered side. Whether gap-crossing might be directed toward sheltered patches is unknown, but birds that commute to woodlots that provide more thermal protection in any particular wind direction should realize an energy benefit, perhaps remaining longer above the "marginal value."

One shortcoming of the marginal value theorem was that it did not consider predation risk as a causal factor. Subsequent modifications have considered how differences in predation risk among patches could affect patch choice (e.g. Gilliam and Fraser 1987), but the effect of differential predation risk while a bird is in transit between patches has not been considered in patch-choice models. Such consideration would be useful to the development of a theory of gap-crossing.

We anticipate that future studies will follow the movements of individually marked animals

within a matrix of habitat fragments. Such a procedure will furnish much more opportunity to understand both the behavioral decisions made by active gap-crossers in response to a suite of potentially causal factors, and the fitness consequences of those decisions. For example, the greater gap-crossing distances exhibited during fall than during the two subsequent periods each year (Fig. 4) may have been in response to differing relative suitabilities of habitats 1 and 2, or to differing transit costs. Alternatively, our assumption may have been incorrect that by the first sampling period, the late-summer and early-autumn dispersal of juvenals had been completed. Also, as the winter wore on, mortality would have continually reduced the number of gap-crossers that we could have detected.

Home-range gap-crossing and metapopulations.—Rolstad (1991) recently pointed out that metapopulation dynamics can be affected by what we are terming home-range gap-crossing within subpopulations as well as by what we are terming dispersal gap-crossing among subpopulations. In his extended discussion of hierarchical patterns of animal responses to habitat fragmentation, Rolstad imagined a primary level of response resulting in mosaics of individual fragments incorporated into the home ranges of individual gap-crossing animals. A secondary level of response consisted of dispersal gap-crossing among such home ranges. Distinctive attributes of metapopulations (e.g. asynchronous extinctions and recolonizations among subpopulations) characterized this secondary level.

Figure 5 portrays the combined effects of home-range requirements and active home-range gap-crossing within a schematic metapopulation of one of our study species, the White-breasted Nuthatch. In constructing the figure, we used 4 ha (Pravosudov and Grubb 1993) and 200 m (Fig. 3) as the species' minimum home-range size and maximum home-range gap-crossing distance, respectively. Although all four landscapes in Figure 5 occupy the same area and have similar total areas of woodland available to nuthatches, limits to gap-crossing determine that A to D contain 4, 4, 3, and 0 nuthatches, respectively. If there is a distinct primary level of metapopulation organization that involves the incorporation of disjoint patches into home ranges, knowledge of

behavioral decisions relating active home-range gap-crossing to resource levels within patches, and of risk of movement among patches, will be important for calculations of local population densities and metapopulation persistence.

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