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Interception of moving organisms: influences of patch shape, size, and orientation on community structure

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Abstract

Island biogeographers have predicted that in oceanic systems, oblong islands oriented perpendicular to the dispersal paths of organisms should intercept more species and individuals than (1) circular islands of the same size, and **(2)** oblong islands of equal area oriented parallel to the direction of travel. Landscape ecologists expect similar relations with habitat patches in a terrestrial matrix. Yet in neither situation is there adequate empirical information to permit conclusions about the prevalence of such effects. To test the hypothesis that intercept-related patch variables influence community structure on the landscape scale, we studied relations between the richness and abundance of cavity-nesting birds and patch shape, size, and orientation relative to a northerly migration path. The influences of other patch features on nest abundances were removed analytically. Multiple regression indicated that the mean and total number of nesting species, and nest abundances for migrants were significantly associated with patch orientation or a patch area x orientation interaction, but not patch shape. Nest abundances for permanent residents were not associated with patch shape or orientation, although area effects, possibly reflecting dispersal interception, were evident. These results are consistent with the hypothesis that stochastic interception of migrating or dispersing organisms influences patch community structure. In addition to richness and abundance effects apparent in this analysis, the sex ratio, age structure, growth rate, social structure, and genetic features of patch populations may also be influenced. The interception of moving organisms by patches may thus be a key factor influencing population and community persistence in reserves. If so, landscape structure could be manipulated to maximize the interception of dispersing or migrating organisms, or minimize it if the effects are undesirable.

Introduction

In oceanic systems, long narrow islands oriented perpendicular to the dispersal paths of organisms are expected to intercept more species and individuals than comparable islands oriented parallel to the line of travel (Game 1980: **630).** If greater interception leads to increased immigration or reduced extinction, then (all else being equal) perpendicular islands should support more species and individuals than parallel islands. Very little empirical support exists for these seemingly logical patterns though. Blouin and Connor (1985) examined the relation between island shape and the species richness of

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five taxa (plants, insects, amphibians and reptiles, mammals, and birds) in **14** archipelagos from around the world. No significant island-shape effects were evident. The species richness of seaborne plant propagules on island beaches does appear, however, to be positively associated with the size of the intercept (beach length) (Buckley and Knedlhans **1986).**

It is reasonable to predict similar interception effects for terrestrial habitat patches (e.g., Forman and Godron **1986: 107,** 412**),** but here also there have been too few studies to warrant conclusions. The single study we are aware of considered wind-borne insect interception relative to patch shape; after Faeth and Kane **(1978)** controlled analytically for patch area, no significant shape effects on species diversity were apparent. The 'angle of interaction,' defined by Forman and Godron (1**986: 410)** as 'the spatial orientation of a landscape structure relative to the direction of flow of objects,' indicates how the shape, size and orientation of a patch may influence its community structure. These dimensions relative to the lines of travel across a landscape are what would influence interception, not necessarily these features *per se.*

Apart from interception effects, patch shape influences community structure and physical conditions within patches apparently through edge effects (Forman and Godron **1986: 108–**111; Temple **1986).** For example, long narrow patches with lower interior-to-edge ratios usually support more edge species, and their interiors are subject to higher windspeeds, whereas circular patches of the same size, having higher interior-to-edge ratios, typically support more interior species and their core areas experience lower windspeeds. Patch shape is important in determining the extent to which physical, ecological, and sociological phenomena in the surrounding matrix influence conditions within the patch (Schonewald-Cox and Bayless **1986: 314–315).** And based on simulations and field evidence, a patch's perimeter length-to-area ratio (a measure of shape) may affect the direction and amount of animal movement across its perimeter (Buechner **1987, 1989).** Absent from all patch shape studies to date, however, are explicit empirical tests for interception effects on community structure.

If through interception, patch shape, size and orientation are pervasive influences on patch community structure, these effects should be detectable at various spatial scales. Further, these relations should be evident for organisms that move through landscapes passively (e.g., wind- and water-borne insects and seeds) and for those that disperse or migrate under their own power. Interception effects are not likely to be important, however, unless patch sizes are large relative to species' body sizes. Migrant organisms appear to use a variety of cues (e.g., sun, polarized light, stars, wind direction, Earth's magnetic field) to reach their general destinations (Abel 1980: **283–373).** But the specific sites within these regions that are eventually used may depend, in part, on the stochastic interception of migrants by acceptable patches. Similar interception of dispersing organisms also seems likely (Forman and Godron **1986: 412).** Thus an element of chance may affect the specific places in which dispersing and migrating organisms actually settle in a landscape. Large intercepts are expected to 'sample' moving organisms more 'efficiently' (*sensu* Haila **1983);** they therefore should have more species and individuals than patches with less interceptive surface, all else being equal. If this is correct, then the shape, size, and orientation of a patch should influence its community structure significantly.

To test this idea, we examined the richness and abundance of cavity-nesting birds relative to patch shape, orientation, their interaction, and their two-way interactions involving patch area. The species studied included permanent and summer residents. We assumed, before collecting our data, that summer residents migrated to our study area along a northerly migration path. Our ***a** priori* hypothesis was that larger, more oblong patches oriented perpendicular to a northerly migration path would be occupied by more nesting species and individuals than smaller, less oblong patches oriented parallel to this line of movement. We expected such relations for richness and migrant abundance, but not resident abundance. The results indicate interception effects that, if evident for a variety of organisms, will be important in efforts to design reserve systems and manage landscapes to preserve biodiversity.

Methods

Study area

From mid May to mid August 1983 and 1984, we studied cavity-nesting bird communities in 34 cottonwood-willow (*Populus-Salix*) patches along 22.2 km of the North Platte River in Wyoming (42" 18′ N, 104"37′ **W).** Patches were separated by irrigated cropland and pastureland and were remnants of a once continuous corridor. The floodplain was approximately 1 km wide, bordered on both sides by rolling short-grass prairie, and oriented in a west-northwest to east-southeast direction. Vegetation structure and floristic composition of patches and adjacent areas are described in Table 1 and in Gutzwiller and Anderson (1987a).

Nest abundances

Every two weeks (four times each nesting season) KJG searched the entire area of each patch for active nests at a rate of 15 min/ha. To avoid daily and seasonal biases associated with bird activity, the time of daily searches was randomized, and the sequences of searches were reversed between years. We judged our search method to be adequate and time-efficient because doubling the search periods did not affect the number of nests found (Gutzwiller 1985: 95–96). Patches were defined as groups of trees (≥ 10.2 cm dbh) separated from all other such patches or individual trees by at least 30 m (Gutzwiller and Anderson 1987a). Territories of some individuals in small patches may have included parts of nearby patches. But our observations indicated that individuals tended one nest in only one patch at any given time. Thus, our estimates of nest abundance for patches were independent. Differential nest detectability among species was negligible, and competitive and commensalistic relations among species for nest trees and nest cavities appeared very weak (Gutzwiller and Anderson 1988). In the present analysis, we included only those nests that could be verified as active; dummy nests, roost holes, and abandoned cavities, for example, were excluded. To avoid the problem of artifacts from single-season analyses (see Wiens 1981), we combined the nest-abundance data from 1983 and 1984 and studied relations for the two-year period as a whole. Most species' nest abundances across all patches were not significantly different between years; only the number of northern flicker *(Colaptes auratus)* nests differed slightly (mean difference = 0.38 nests) between 1983 and 1984 (Gutzwiller and Anderson 1987b). Nest abundances were recorded for six residents (downy woodpecker *[Picoides pubescens]*, hairy woodpecker *[P. villosus]*, northern flicker, American kestrel [*Falco sparverius*], black-capped chickadee [*Parus atricapillus*], European starling [*Sturnus vulgaris]),*and four migrants (house wren *[Troglodytes aedon],* tree swallow *[Tachycineta bicolor*], common grackle [*Quiscalus quiscula*], red-headed woodpecker [*Melanerpes erythrocephalus*]).

Statistical analyses

Data for all ten species were used to estimate the mean number of nesting species (MEANSP) and the total number of nesting species (TOTSP) for each patch. Ordinary least squares regression **(OLSR)** was used to study the relation between these continuous variables and patch features. Four species (common grackle, hairy woodpecker, black-capped chickadee, tree swallow) nested in too few of the 34 patches to permit separate analyses of their nest abundance. Four species (red-headed woodpecker, downy woodpecker, American kestrel, northern flicker) nested frequently enough to estimate logistic regression models relating their probability (presence/absence) of nesting to patch features. The mean number of nests for house wrens and European starlings was continuous enough for us to use OLSR to study relations between patch dimensions and nest abundance.

Earlier work (Gutzwiller and Anderson 1987a) indicated nest abundances were significantly associated with several patch features: area (AREA); perimeter length of edge/ha (EPHA); size of the nearest streamside habitat patch (SIZEH); the frequency of snags > 85 cm dbh (SNAG6); presence or absence of adjacent palustrine wetland (PALUS); the frequency of healthy plants > 2.5 m in height and 41–70 cm dbh (PSC5); distance to

Table 1. Summary statistics for habitat variables measured at 34 *Populus-Salix* patches in southeastern Wyoming.[a]

Variable	$\bar{X}$	*SD*	Range
Patch area (AREA), ha	7.17	8.50	0.12–32.27
Patch shape (SHAPE)	2.97	1.56	1.3–7.6
Patch orientation relative to true E-W line (OTL),°	39.1	23.9	1.5–86.5
Patch orientation relative to magnetic E-W line (OML),°	33.4	23.0	0.5–77.0
SHAPE x OTL interactionb	113.7	83.9	2.1–281.2
SHAPE x **OML** interaction[b]	101.1	90.8	1.0–391.4
SHAPE x AREA interactionb	20.7	24.6	0.2–81.2
OTL x AREA interactionb	291.0	437.9	4.5–1694.2
OML x AREA interaction[b]	257.8	382.1	0.7–1311.0
Distance to nearest streamside patch, m	121.62	106.59	35–492
Perimeter length of edge/ha,m/ha	794.76	421.00	391.60–2127.50
Size of nearest streamside patch, ha	14.19	9.98	0.20–32.27
Mean number of snag-diameter classes represented per 60-m^2 sampling plot	0.26	0.10	0.05–0.49
Mean number of plant strata represented per 60 m^2 sampling plot	2.01	0.69	0.65–3.05
Frequency of snags 10.2–25 cm dbh	0.12	0.08	0.0–0.34
Frequency of snags 26–40 cm dbh	0.09	0.07	0.0–0.27
Frequency of snags 41–55 cm dbh	0.03	0.03	0.0–0.13
Frequency of snags 56–70 cm dbh	0.01	0.01	0.0–0.06
Frequency of snags 71–85 cm dbh	0.01	0.03	0.0–0.19
Frequency of snags > 85 cm dbh	0.01	0.02	0.0–0.09
Frequency of healthy plants ■ 0.5 m in height	0.59	0.27	0.0–1.0
Frequency of healthy plants > 0.5 m and ≤ 2.5 m in height	0.62	0.26	0.0–1.0
Frequency of healthy plants > 2.5 m in height and ■ 15.2 cm dbh	0.26	0.20	0.0–0.71
Frequency of healthy plants > 2.5 m in height and 15.3–40 cm dbh	0.32	0.18	0.0–0.74
Frequency of healthy plants > 2.5 m in height and 41–70 cm dbh	0.16	0.11	0.0–0.44
Frequency of healthy plants > 2.5 m in height and > 70 cm dbh	0.05	0.06	0.0–0.25
Number of snag-diameter classes represented per patch	3.18	1.29	1–6
Number of healthy plant strata represented per patch	5.41	0.66	4–6
Presence or absence of adjacent palustrine wetland[c]	0.29	0.46	0–1
Presence or absence of adjacent riverine wetland[c]	0.56	0.50	0–1
Presence or absence of adjacent mixed rangeland[c]	0.21	0.41	0–1
Presence or absence or adjacent irrigated cropland[c]	0.35	0.49	0–1
Presence or absence or adjacent roads (dirt, paved, or **rail)**[c]	0.47	0.51	0–1
Number of adjoining land-use types[d]	1.88	1.25	0–5

[a] Partially from Gutzwiller and Anderson (1987b); definitions and methods of measurement are in Gutzwiller (1985), Gutzwiller and Anderson (1987a), and in the text.

[b] Cross-product terms used to test for interactions.

[c] Indicator variables; presence coded as 1, absence coded as 0. Means can be interpreted as the proportion of the 34 patches bordered by the associated land-use types.

[d] Some patches were bordered solely by herbaceous rangeland (i.e., none of the other five land-use types adjoined these patches); the presence or absence of herbaceous rangeland was not, however, considered a variable because it bordered all patches to some extent.

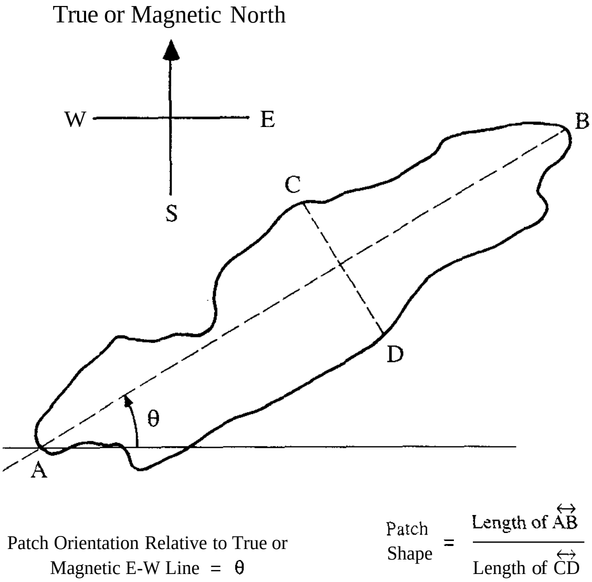

Fig. 1. Illustration of methods used **to** measure patch shape, patch orientation relative to a true (geographic) E-W line, and patch orientation relative to a magnetic E-W line.

nearest streamside habitat patch. The actual patch characteristics that were important varied with the specific dependent variable. In the present study, we tested whether additional patch features associated with interception effects were significantly related to nest abundance, after controlling for explanatory variables found to be significant in the earlier work. The new features considered were: patch shape, patch orientation, their interaction, and their two-way interactions involving patch area.

Patch shape (SHAPE) was defined as the maximum length of the patch divided by its maximum width (perpendicular to the maximum length chord) (Fig. 1); SHAPE measured deviation from circularity and did not depend on perimeter irregularities (Blouin and Connor 1985: 280) as other measures do (Game 1980: 630). We measured orientation in two ways. One involved the angle between the long axis of each patch and a true (geographic) east-west (E-W) line (OTL). The other was measured similarly but for a magnetic E-W line (OML) (Fig. 1). Migrants (house wrens, red-headed woodpeckers, tree swallows, and common grackles) may have used the sun, stars, or magnetic cues to orient in a northerly direction toward our study area (Abel 1980: 283–373). These angles measured the orientation of the long axis of the patches relative to northerly migration paths; very small angles indicated patches were nearly perpendicular (E-W) to a northward path, and large angles (near 90°) indicated patches were oriented parallel (north-south [N-S]) to a northerly line of travel. Patch shape and orientation were measured with topographic maps, aerial photographs, and a protractor. Interactions of these variables (SHAPE x OTL, SHAPE x OML) and their two-way interactions with patch area (SHAPE x AREA, OTL x AREA, **OML** x AREA) were studied as cross-product terms (Neter and Wasserman 1974: 219–224). Summary statistics for these and other patch features are presented in Table 1.

For the OLSR models, Proc Rsquare (**SAS** Institute 1985a: 711–724) was used to determine which patch variables made the largest contribution to R^2; for these analyses we required that the explanatory variables from the original models be included in every regression fit. Proc Reg (SAS Institute 1985a: 655–709) was used to ensure that new variables had significant ($P < 0.05$) t ratios (Neter and Wasserman 1974: 61) and variance inflation factors < 5 (Montgomery and Peck 1982: 300). Final models had to have F statistics that were significant ($P < 0.05$). Partial regression residual plots (Proc Reg, SAS Institute [1985a: 678–6821) confirmed the statistical assumption that there were linear relations between dependent variables and all explanatory variables. For the logistic regression analyses, BMDPLR was used to identify variables that had significant ($P < 0.05$) improvement chi-square values, and final models with nonsignificant ($P \geq 0.05$) goodness-of-fit (Brown) statistics; the latter are used to test for lack of fit of the logistic model. In these analyses too we included original explanatory variables in each fit. The maximum-likelihood method was used to assess the significance of explanatory variables in the stepwise process (Dixon 1985: 330–344).

When additive and interaction terms in a model involved the same patch feature (e.g., AREA), we interpreted the interaction effect (Sokal and Rohlf 1987: 195–198). To represent relations between nest abundances and intercept-related patch features, we used Proc **G3D** (SAS Institute **1985b: 399–412)** to plot the predicted number of nesting species, mean number of nests, or the probability of nesting versus explanatory variables. Predicted values were computed from **(1)** regression equations that involved only the coefficients for new explanatory variables from the final models, and **(2)** data that spanned the range of values observed in this study for these variables. This was the clearest way to demonstrate the significant relations addressed in this paper. Graphs of observed nest abundances versus intercept-related variables would have been uninformative because substantial fractions of the variation in nest abundances were associated with the other patch features in the models. Because spurious correlations are possible, inferences from regression analyses can be problematic; the possibility of this was minimal here be cause relations were reasonable on statistical and biological grounds, and parsimonious.

Results

With EPHA, AREA, SIZEH, SNAG6, and PALUS in the model for MEANSP, the OTL × AREA interaction was significant ($t = -2.753, P = 0.010$), and it increased R^2 by **3%** to **0.90.** After controlling for the same five explanatory variables, we observed similar relations for TOTSP and the OTL × AREA interaction ($t = -2.582, P = 0.016$; R^2 increased **3%** to **0.89).** The mean number of house wren (HOWR) nests was significantly associated with the OML × AREA interaction ($t = -3.506, P = 0.001$; R^2 increased **10%** to 0.75), after controlling for AREA. With AREA and PSC5 in the model, the probability of nesting by red-headed woodpeckers was negatively associated with OTL (improvement $X^2 = 4.201$, $P = 0.040$; Brown's goodness-of-fit $X^2 = 0.893, P = 0.640$). OTL thus had additive (not interaction) effects on the probability of nesting by red-headed woodpeckers. No other new patch features were significant in these analyses. And none of the new intercept-related patch variables were correlated with nest abundances for European starlings, downy woodpeckers, or northern flickers. For American kestrels the OTL × AREA effect approached significance (improvement $X^2 = 3.816, P = 0.051$; Brown's goodness-of-fit $X^2 = 3.922, P = 0.141$) after accounting for AREA.

More species and more house wrens nested in patches that were large and oriented in an E-W direction; fewer species and fewer house wrens nested in smaller, N-S patches. The slopes of the MEANSP-AREA, TOTSP-AREA, and HOWR-AREA relations for E-W patches were steeper than those for N-S patches (Figs. **2–4).** The threshold of the influence of patch area on the probability of nesting by red-headed woodpeckers was lower for E-W patches than for **N-S** patches (Fig. 5). For the original variables in these relations, there were no changes in the signs of the coefficients, and there were negligible changes in attained significance levels of the coefficients, after the new patch variables were included. This indicates that multicollinearity was not a problem in these analyses (Montgomery and Peck **1982: 305–306).** Further, coefficients for the new patch variables were negative (as expected for interception effects), and all of the original coefficients had signs that were predictable from the biology of the organisms involved. These results indicate important patch variables have probably not been left out of the models (see Montgomery and Peck **1982: 384–386).** None of the coefficients for patch orientation, or associated interactions with AREA, were positive.

Discussion

The results indicate that patch orientation influences the richness and abundance of cavity-nesting birds that breed in them. Based on our observations and published breeding and winter distributions (Farrand **1983;** Root 1988), to reach our study area red-headed woodpeckers migrated from the south or southeast, and house wrens migrated from the southwest, south, or southeast. In our study area, downy woodpeckers and European starlings were sedentary residents, whereas populations of American kestrels and northern flickers

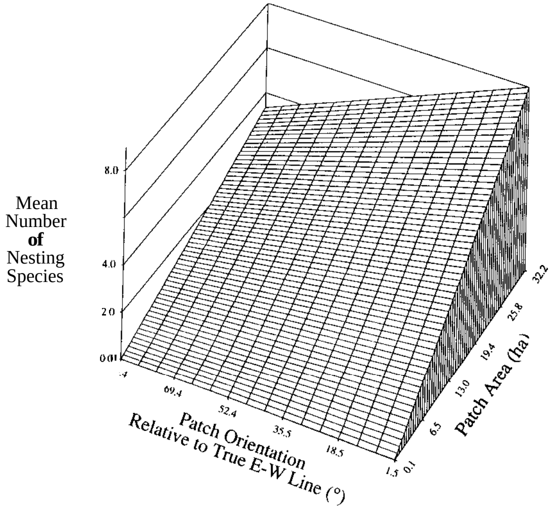

Fig. 2. Relation between the mean number of nesting species and the interaction of patch area and patch orientation relative to a true (geographic) E-W line.

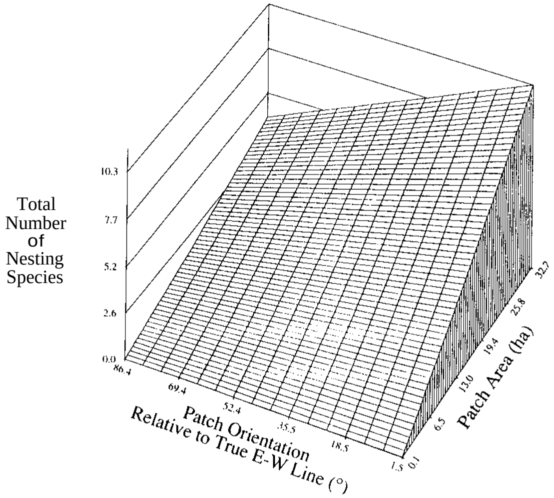

Fig. 3. Relation between the total number of nesting species and the interaction of patch area and patch orientation relative to a true (geographic) E-W line.

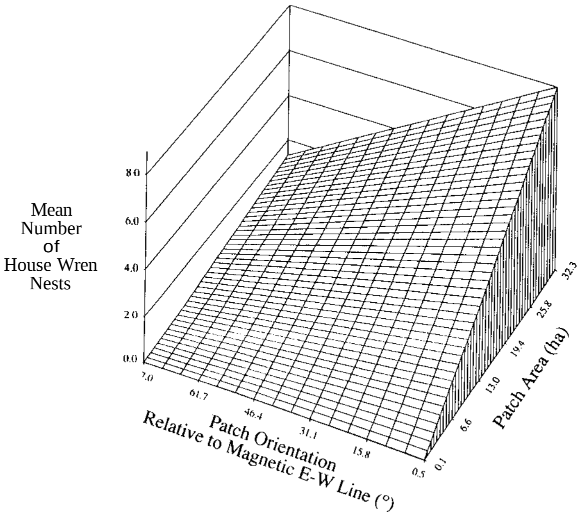

Fig. 4. Relation between the mean number of house wren nests and the interaction of patch area and patch orientation relative to a magnetic E-W line.

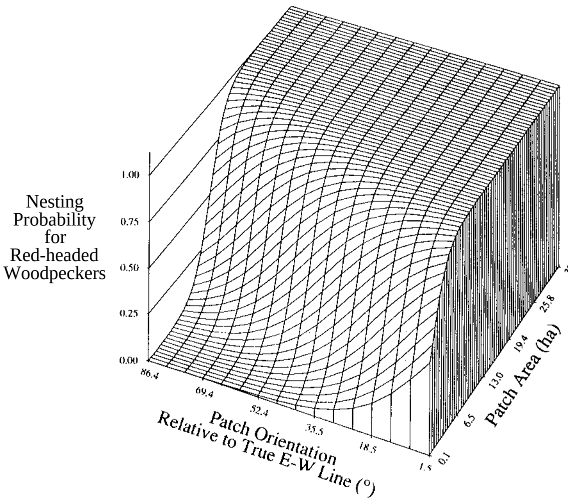

Fig. 5. Relation between the probability of nesting by red-headed woodpeckers and the additive effects of patch area and patch orientation relative to a true (geographic) E-W line.

may have contained some migratory individuals, even though these latter two species are year-round residents there (Farrand 1983). One would expect obligate migrants moving along northerly lines of travel to be intercepted by patches oriented in an E-W direction and to thus exhibit a relation between nest abundance and patch orientation. Such patterns should not be evident for sedentary species, and they should be weak or absent for species with both sedentary and migratory individuals. For species richness (involving six residents and four migrants), we observed significant relations consistent with our hypothesis concerning orientation. Orientation effects were absent for sedentary species and weak or absent for species whose populations may have contained both sedentary and migratory individuals. The absence of positive regression coefficients for patch orientation, and orientation × area interactions, suggests birds were not intercepted appreciably during movements they may have made along the corridor (i.e., parallel to the river), or at least that little subsequent nesting occurred due to such movements.

The importance of these results lies primarily in the collective pattern of relations we detected, and less in the individual increases in R^2 (3–10%, $P = 0.001–0.016$) or the magnitude of X^2 statistics (4.201, $P = 0.040$) associated with patch orientation. Considering the numerous other biological and physical factors that affect nest-site selection, the high variability typical of field data, and that we studied a single guild, one would expect it to be difficult to detect effects of patch orientation. That we discovered these relations at all indicates interception may be more important than our results imply. Otherwise, under these conditions the patterns may have remained inconspicuous. Undoubtedly, our use of covariates improved the statistical power of the analysis and hence our ability to detect the associations. The significant relations between nesting species richness, migrant nest abundance, and patch orientation were far more common than one would expect by chance alone; we detected all four of the expected associations. Further, all of these relations were negative, as hypothesized. In accord with the interception hypothesis, there were no relations between nest abundance for sedentary residents and patch orientation. For American kestrels and northern flickers, both sedentary and migratory individuals may have comprised the populations. We thus expected relations between their nest abundances and patch orientation to be weak or absent, and this is what we observed.

For some of the relations we studied previously (Gutzwiller and Anderson 1987a), EPHA, the perimeter length-to-area ratio for patches, emerged as a significant variable. We accounted for this analytically in the present analysis to obtain a clearer understanding of the role of SHAPE *per se*. EPHA is a correlate of shape that reflects edge and boundary-form effects, which by themselves can be important determinants of community structure (e.g., Forman *et al.* 1976; Temple and Cary 1988; Yahner 1988; Hardt and Forman 1989). Controlling for this variation enabled us to assess the relation between SHAPE and patch community structure in the absence of confounding edge effects. Apparently, neither SHAPE nor its interactions with OTL, OML, or AREA were important influences (cf. Blouin and Connor 1985).

Heat, wind, nutrients, and floristic composition may vary in patches depending on patch orientation relative to the sources of these inputs (Ranney *et al.* 1981, Forman and Godron 1986: 410–412). If oriented in different directions, patches of even the same size and shape could have very different biotic and abiotic conditions. Do the patterns we observed reflect interception effects, or are they merely a consequence of associations between environmental conditions and patch orientation? Patches oriented in an E-W direction, one might argue, may simply support better conditions for cavity-nesting birds. Perhaps, for example, sunlight is more intense and plant and hence insect biomass are higher in E-W patches. Or wind damage may occur more often in such patches, creating more dead limbs and trees that attract cavity-nesting birds. In the present study, we controlled statistically for conditions (and concomitantly for other variables related to them) that we previously found to be correlated with MEANSP, TOTSP, and nest abundances for individual species (see above). The remaining patch features in our earlier work (Table 1), many of which would reflect environmental conditions associated with patch orientation, were not correlated with nest abundances. The possibility that intercept-related variables simply reflect the influences of associated patch conditions, and not interception ***per se***, thus seems minimal. In addition, following these controls, there would have to have been an incredible coincidence in the associations among variables to produce the different patterns we observed for breeding migrants and permanent residents. That is, improved conditions for cavity nesters in E-W patches should have attracted all species, not just migrants. One cannot explain the patterns on the basis of like habitat associations within migrants and within residents either; the habitat relations for the species differed significantly within each group (Gutzwiller and Anderson 1987a). Our results are consistent with the far simpler hypothesis of interception.

To explain species-area relations, 'sampling' models have been proposed (e.g., Connor and McCoy 1979; Coleman 1981), wherein a patch's species richness represents a random sample of the regional biota and is directly related to patch area ('sample size'). But constraints arising from site tenacity, habitat composition and species abundance indicate that wholly random models are unrealistic (Haila 1983, 1986). Consistent with these conclusions, our earlier work (Gutzwiller and Anderson 1987a) indicates that although some 'sampling' effect attributable to AREA may occur, it does not adequately explain the patterns we observed because, after accounting for AREA, several other patch features (see above) were important (see Boecklen 1986; Nilsson 1986; and Møller 1987 too). In the present paper we also demonstrate that patch orientation, alone or in combination with patch area, is correlated with species richness and nest abundances for migrant birds. The most parsimonious explanation for this seems not to be a simple 'sampling' effect, in which directional movement is irrelevant. Instead, an 'interception' model, in which patches 'capture' individuals during their northward progress across the landscape, seems appropriate. If patches were just 'sampling' individuals in proportion to their area, patch orientation should not have been detected as a significant influence. Patch area, however, may influence both 'interception' rates and 'sampling' rates. Thus a 'sampling-interception' effect due to AREA seems most plausible. Patch area also appears to influence community structure in nonrandom biological ways (e.g., Ambuel and Temple 1983, Gutzwiller and Anderson 1987a). We suspect stochastic interception due to patch area and orientation occurs in combination with deterministic influences of habitat structure (cf. Haila 1986); the latter effects were apparent at three spatial scales within and adjacent to patches (Gutzwiller and Anderson 1987a).

In an interception model, it is not necessary to assume that organisms will become established in the first patch that intercepts them, although in plants and in other relatively immobile organisms this may be true generally. One needs only to postulate that on the average, large intercepts will interfere with the flow of more dispersing or migrating species and individuals (or disseminules), all else being equal. Some of these will remain and flourish, some will not. In the present analysis, nest abundance probably does not reflect the total number of interceptions that occurred, but the relations that emerged suggest nest abundance is proportional to the probability of interception. In the northern hemisphere, northward movement during the breeding season is expected for migrant organisms that winter south of an area. But for the permanent residents of an area, patch orientation relative to a northerly path of travel should not be important because organisms disperse from natal areas in various directions. Patch area alone should influence nest abundance of resident species because larger intercepts would by chance intercept more organisms during multidirectional dispersal. For most of the residents we were able to study individually (downy woodpeckers, European starlings, and American kestrels), AREA (but not orientation) was indeed a significant influence (Gutzwiller and Anderson 1987a).

In the system analyzed here, it is logical to expect interception to have occurred not only during the two breeding seasons studied, but also in previous years. Each year a few 'new' individuals may be intercepted, but most of the 'old' individuals (i.e., those that nested previously) return because of site fidelity. Yearly interception may amount to only a few individuals for most patches, but the cumulative effect at any point in time (e.g., this study), due to overlapping generations, may be two or three times this number. Indeed, cumulative effects may have enhanced the detection of the patterns observed. Interception, regardless of whether migrating or dispersing organisms are involved, should influence the persistence of patch populations,

Interception effects should be evident in various mobile taxa; the extent of this within species may vary with the mobility of particular stages of the life cycle. Interception effects should occur at different temporal and spatial scales, depending on dispersal and migration rates and distances. And there is no reason to believe that they do not occur in both terrestrial and aquatic systems. Interaction effects often underlie ecological patterns. Thus, when studying variables suspected to affect interception, researchers should consider interaction effects, not just additive influences. Past emphasis by insular ecologists on additive effects may explain the present paucity of evidence for interception. Simulations and field experiments are necessary to determine how the shapes, sizes, and orientations of sink patches affect populations and communities. Tagged or telemetered individuals, or marked propagules (real or mimics), should be followed across landscapes.

Landscape planners and conservation biologists stand to profit from such studies (see Golley [1989] and Turner [1989: 186, 189] too) because the interception of moving organisms has important ramifications for species preservation. The interception of dispersing or migrating organisms by sink or source patches can affect such patch population properties as age structure, social structure, population growth rates, sex ratio, and genetic features (cf. Lidicker 1982: 126; see Lidicker and Caldwell 1982: 200–202; Stamps *et al.* 1987; Levin 1988; and Pulliam 1988). And unless patches that strongly favor settlement, survival, and reproduction also are effective intercepts, emigrant fitness is likely to be poor (cf. Anderson 1989: 28). Through these influences, patch community structure and preservation could also be affected. Patch shape, size, and orientation could conceivably be manipulated to maximize interception (or minimize it if the consequences were undesirable, as in the case of exotic invaders). Contrary to arguments for circular patches (e.g., Wilcove *et al.* 1986: 255–256), if patches are large enough to contain true interior habitat and interior species and detrimental edge effects are minimal, oblong patches oriented perpendicular to the flow of organisms may be beneficial (cf. Game 1980). Even interception that occurs over short distances, tens or hundreds of meters for example, may have important influences on extinction for some organisms (see Burkey 1989). Autecological data, including dispersal distances and patch-detection abilities (Fahrig and Paloheimo 1988), will be essential to ensure planned interceptions are realized.

We believe interception effects on populations and communities are more widespread than their absence in the literature implies, and that our results do not simply reflect idiosyncrasies of the system we studied. But additional work is needed to substantiate our hypotheses. If interception proves to be important across ecosystems, taxa, and various temporal and spatial scales, land-use planners will have a powerful landscape-management tool for preserving biodiversity.

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