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The use of movement data as an assay of habitat quality

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Abstract Based on our observations and those of others from the literature, we construct a graphical model of habitat use in territorial species at high densities relative to optimal habitat availability. This model ignores differences in abundance among habitats, and, together with other models of habitat use, predicts that there should be greater stability (lower turnover rates) among individuals occupying optimal habitat than among those in suboptimal habitat(s). Future studies assessing quality among habitats might take advantage of this by comparing individual turnover rates among habitat types using standard mark-recapture methodology. As an illustrative example, we present a case in wintering wood thrushes (*Catharus mustelinus*; Muscicapidae: Turdinae) in which relative abundance and habitat quality were inversely related. Many individuals of this nearctic-neotropical migrant species hold nonbreeding territories in the seemingly crowded rainforest of southern Veracruz, Mexico.

Key words Habitat selection · Model · Nearctic-neotropical migrant · Rainforest · Territoriality

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Introduction

Although population densities or density estimates are often used to determine habitat quality, it has been demonstrated that in some cases density is not a good predictor of habitat suitability (following the definition of Fretwell 1972, pp. 82–83). Van Horne (1982) described higher densities of deer mice (*Peromyscus maniculatus*) in suboptimal habitats. The inhabitants of marginal areas were primarily juveniles, and were presumably forced into the lower-quality habitat. States (1976) found that subdominant yellow-pine chipmunks (*Tamias amoenus*) accumulated in suboptimal habitat, and that these areas seemed to be dispersal sinks. Occupants were largely immigrants, and survival probability was low. Other examples where density was a poor indicator of habitat quality were given by Van Horne (1983). Without knowledge of local population demography, assuming that abundance is directly related to suitability is unwarranted (see Wiens and Rotenberry 1981; Van Horne 1983).

In developing his theory of territoriality, Brown (1964, 1969) stated that competition for an economically defendable resource is the mechanism behind the evolution of this social system. Intraspecific competition for resources in populations at high densities has been suggested as the driving force behind suboptimal habitat use (Jenkins et al. 1963, 1967; Brown 1969; Christian 1970; Fretwell and Lucas 1970; Krebs 1971; Zimmerman 1971; Gauthreaux 1978). Individuals driven to less-than-optimal habitats through competition should not simply remain, however, but should attempt to find or create vacancies in more optimal patches, taking advantage of stochastic variables like mortality and more predictable factors like variation in competitive ability.

These considerations lead us to suggest a graphical model of how habitat use and the distribution of individuals might appear among territorial populations at

high densities relative to optimal habitat availability (Fig. 1). Territorial individuals exclude nonterritorials from optimal habitats, forcing them into less optimal areas (downward arrows; see references above). In high quality habitats, the aggression of territorial individuals probably keeps nonterritorial individuals moving; in less optimal habitats unsuitable conditions, environmental instability, and adequate mobility to seek better situations elsewhere would have the same effect (upward arrows and increasingly large proportions of nonterritorial individuals; Fig. 1). Patterson (1980) and Van Horne (1983) also stated that social interactions may cause variations in the densities within and between habitats, and implied that these interactions act in a way similar to the downward arrows in Fig. 1. In addition to our own observations (see below), Jenkins et al. (1963, p. 369) and Krebs (1971, p. 8) found movements suggestive of the upward arrows in Fig. 1. Further, McPeck and Holt (1992) showed that dispersal is theoretically favored under most conditions of habitat variability.

Because organismal densities (or relative abundances) do not always indicate a habitat's quality or importance to a species or population, it is useful to ask:

1. What might explain higher relative abundances of individuals in suboptimal habitat?
2. If apparent densities or abundances are not always accurate indicators, what cues can researchers use to assess habitat quality?

Possible reasons for density imbalances

Different movement rates among habitats (or differences in directionality of movements) might cause differences in encounter rates which do not reflect differences in actual density. We have not seen evidence from avian studies that this is particularly problematic, and correcting density indices (e.g., capture rates) for differences in movement rates is probably not practical. Relative abundance will likely continue to be the most commonly used index of organism density.

Temporary resource abundance in a habitat of ordinarily low basal suitability might cause density imbalances (see Fretwell 1972), but these should be temporary and individuals should redistribute themselves when normal suitabilities return. Differences in individual competitive ability, a factor not considered by Fretwell and Lucas (1970) or Fretwell (1972), can also cause density imbalances. Rosenzweig (1985) stated that "dominant" or "alpha" individuals could obtain and defend a disproportionately large percentage of the best patches, and that this might result in lower densities in the better patches. A modification of the Fretwell-Lucas model of ideal despotic distribution accounting for variability in individual competitive ability can be shown to cause density imbalances under various conditions

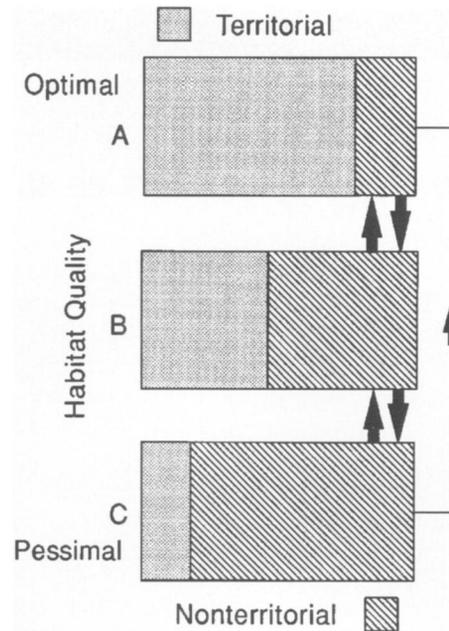


Fig. 1A–C Model depicting how intraspecific competition might force nonterritorials into lower-quality habitats (*downward arrows*), where they should reside only temporarily before attempting to find something better (*upward arrows*). Stability probably increases with optimality, due to the preponderance of territorials in quality habitat(s). Further, environmental unsuitability in lower quality habitat(s) may favor mobility, raising the rate of individual turnover in such habitat(s)

of habitat availability and distributions of relative competitive ability among the settling individuals.

Holt (1985) proposed that densities could become greater in suboptimal habitats when high densities cause a reversal in suitabilities. As Rosenzweig (1985) noted, this could occur if the standing crop of resources and the renewal rate of those resources were inversely related. It would seem, however, that in such a system the definition of the optimal habitat would change with density, because optimality is based on the actual suitabilities of the habitats.

Habitat quality assessment

Regardless of the reasons for density imbalances, it is clear that numbers alone are not always a good indicator of habitat quality, and that the success of individuals is ultimately the best gauge of habitat suitability. This parameter is difficult to determine, however, and assessments of habitat quality usually rely on other indicators (e.g., relative abundance). Krohn (1992) proposed one alternative: that density fluctuations and sequence of habitat abandonment might prove useful in evaluating habitats. This supposition is supported by habitat use theory, but the method requires substantial changes in population size to be effective. Hobbs and Hanley (1990) proposed that habitat quality evaluations be based on determining the

underlying relationships between individual resource acquisition and population dynamics. While a justified final goal, this approach will likely only be taken with populations and habitats warranting substantial concentrations of effort. We propose an alternative method of habitat quality assessment.

Our graphical model (Fig. 1) suggests a method of habitat suitability assessment that does not use relative abundance. This model (Fig. 1) and others of habitat use (e.g., Fretwell and Lucas 1970; Fretwell 1972; Lomnicki 1978; Adler and Wilson 1987; Pulliam 1988; McPeck and Holt 1992) all seem to predict that there will be greater stability (lower turnover rates) among individuals occupying optimal habitat than among those in suboptimal habitat(s). When assessing quality differences among habitats, future investigations might take advantage of this by comparing individual turnover rates among habitat types using standard mark-recapture methodology.

An illustrative example

We studied the population dynamics of wintering wood thrushes (*Catharus mustelinus*; Muscicapidae: Turdinae), a nearctic-neotropical migrant, in southern Veracruz, Mexico. The wood thrush, primarily a ground-level forager, is a common member of this rainforest bird community during the boreal winter, and many individuals hold nonbreeding territories throughout the winter months (Rappole and Warner 1980; Winker et al. 1990b). This study was part of a broader investigation of wintering wood thrushes. Radio telemetry was the main investigative tool, and many of the telemetry results have been reported elsewhere (Rappole et al. 1989; Winker et al. 1990b). During the full course of the study, radio telemetry revealed two distinct movement classes: sedentaries and wanderers (Rappole et al. 1989; Winker et al. 1990b). Although we were unable to determine the precise behavioral status of every transmitter-bearing bird, we concluded that most sedentary individuals were territorial and that most wanderers were not. Wanderers experienced higher mortality than sedentaries due to predation (Rappole et al. 1989), and made up approximately 50% of the wintering population. Our impression was that this system was similar to Fig. 1.

Here we examine capture records between two habitats where we had baseline data on individual movements. These data provide an example of imbalance in relative abundance between habitats differing in vegetative structure and apparent suitability.

Study area and methods

Our study area was located in southern Veracruz, Mexico, in the Sierra de Los Tuxtlas (elevation approximately 150 m). This iso-

lated volcanic range on the coast of the Gulf of Mexico contains the northernmost neotropical rainforest. The two sites discussed here were in the steep valley of the Rio de Coxcoapan, a small, rocky mountain river. The forest in the area was "selva alta perennifolia," or tropical evergreen forest (Miranda and Hernandez 1963; Pennington and Sarukhan 1968), and was characteristic of the plant community at this elevation.

The two sites were located only 150 m from each other, but differed in several respects. The La Peninsula site (350 × 250 m, 8.75 ha) was slightly above (c. 10–30 m in elevation) the Coxcoapan, and was lightly disturbed by selective logging in the mid-1970's (see Winker et al. 1990a). Topography on the La Peninsula site was varied, including minor valleys and ridges. The Riverine Disturbed site (550 × 50 m, 2.75 ha) was on a somewhat level, rocky floodplain on the river itself, and several streambeds ran through it. On one edge it was bordered by a steep bluff, while on the other it abutted the main river channel. During the boreal winter, storm systems from the north, called *nortes*, usually bring heavy rain and cool temperatures several times per month. During and after *nortes*, portions of this habitat were often flooded. The Riverine Disturbed site was heavily logged in the mid-1970s, and much of the habitat was approximately 10-year-old second growth. *Cecropia* trees, which colonize forest gaps, were common on this site.

Nylon mist nets of 30 mm and 36 mm mesh (12 m × 2.6 m) were set 50 m apart (on a grid) at ground level on both sites. During 6–28 February 1985 nets were open simultaneously on both sites for 11 days, for totals of 1,797 net hours on the La Peninsula site (48 nets) and 1,071 net hours on the Riverine Disturbed site (12 nets). In addition to this period, the La Peninsula site was netted for several months through the winter of 1984–1985, so net shyness in resident territorial birds was probably a factor on this site. Methods of telemetry were presented by Winker et al. (1990b). Vegetative structure was measured on both sites following the point-centered quarter method (Cottam and Curtis 1956; Barbour et al. 1987, pp. 203–204). On the La Peninsula site 100 points randomly selected from a 25-m grid system were measured; on the Riverine Disturbed site 50 points were similarly used.

Results

The Riverine Disturbed site was initially established as an auxiliary net plot to examine the area many transmitter-bearing wanderers used temporarily after leaving the La Peninsula site. The area seemed to be of marginal value for wood thrushes. Many parts of this habitat used by transmitter-bearing birds were not forest, but rather quite young second growth, a habitat where territorial birds are rare (personal observations). More importantly, portions of the site often became flooded during *nortes*, and were thereby made unusable to this primarily ground-level forager (pers. obs.). Wanderers showed two general types of movements: individuals moving relatively large distances (type 1), and those whose movements were largely constrained to the forested regions of the lower Coxcoapan valley (type 2; Winker et al. 1990b). Of seven birds in the latter category, six moved from the La Peninsula site to the Riverine Disturbed area and subsequently departed. The movements of these six birds while in the Riverine Disturbed area often appeared to be caused by *norte*-related flooding, and this flooding seemed directly responsible for the eventual departure of at

least three of these birds (see Winker et al. 1990b for a description of one individual).

Net shyness was eliminated as a complicating variable in a comparison of captures between the two sites by removing from each habitat sample those birds that seemed territorial (from telemetry, resighting, or recapture data). Four birds were removed from the Riverine Disturbed sample and three from the La Peninsula sample. We know of three more territorial birds that were present on the La Peninsula site but not captured during this period (unpublished data), probably because of net shyness. Although we had no evidence of their presence either during or after the 6–28 February sampling period, as many as four additional territorial birds may have been present on the La Peninsula site (evidence for territoriality in these individuals obtained prior to 25 January). Thus, there were possibly ten resident territorial birds on the La Peninsula site during this period. This figure fits well with our understanding of the distribution of territorial birds on this site through the entire winter period (estimated as nine to ten individuals; data from three winters). However, territorial individuals occasionally left the site for up to 15 days (see Winker et al. 1990b, p. 449). Thus, without net shyness we might not have captured ten territorial individuals on the La Peninsula site during 6–28 February 1985, but we probably would have captured at least six, instead of only three.

There was no overlap in individuals between the two sites. Excluding those birds removed from each sample, there were 8 captures and 3 recaptures on the La Peninsula site, and 19 captures and 5 recaptures on the Riverine Disturbed site (overall capture and recapture rates in Fig. 2). The difference in capture rates (birds per 1000 net hours by day) between the two sites is significant ($t = 2.56$, $df = 20$, $P < 0.01$; t -test for independent samples). This difference in relative abundance suggests that the density of wood thrushes was higher on the Riverine Disturbed site. The proportion of birds recaptured on each site did not differ between the two sites ($G_{adj} = 0.16$, $P > 0.5$, G -test with Williams' correction), but this comparison is not very informative because of net shyness and the consequent exclusion of territorial birds from the samples.

Comparing capture rates between the two sites shows significantly higher rates in the Riverine Disturbed site no matter how the data are examined, even when all known or possible territorial birds are included in the analysis (regardless of whether they had been captured during this period). However, because of net shyness, removing territorial individuals from the respective data sets results in a more realistic comparison of capture rates between the two sites. During the period of simultaneous netting we had direct evidence of six territorial birds on the La Peninsula site, and up to ten may have been present; eight additional birds (probably transients) were captured. On the

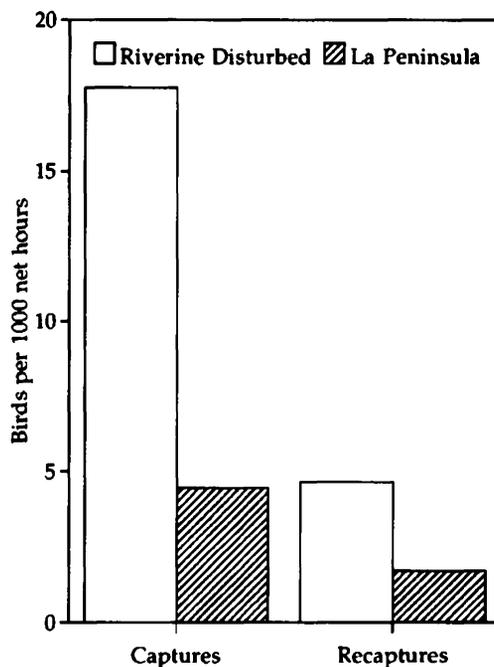


Fig. 2 Captures and recaptures per thousand net hours on the Riverine Disturbed (open bars) and La Peninsula (shaded bars) sites from 11 days of simultaneous netting. Territorial birds from both areas are not shown

Riverine Disturbed site four presumed territorial birds were captured in addition to 19 other birds. Given the relatively small size of the Riverine Disturbed site, together with the local topography (bounded by a river on one side and a steep bluff on the other), the majority of these 19 additional birds could not have been sedentary or territorial, and were therefore transients. At this time of year individuals cannot be reliably aged or sexed.

The wood thrush is partly frugivorous in winter (Winker et al. 1990b), and movements of birds could be affected by availability of temporarily abundant fruits. Wood thrushes take fruits from both trees and understory plants ("saplings"), but feeding observations suggest fruits are more frequently taken from saplings than from trees (K. Winker, unpublished data). During the course of the study 13 species of "sapling" produced fruits consumed by birds. In our vegetation analysis these species were noted when encountered at each point. On the La Peninsula site these species made up 11.25% of the total sapling population; on the Riverine Disturbed site they represented 10.5%. This difference is not significant [Wyatt and Bridges (1967) test for population proportions, $z = 0.28$, $P = 0.38$]; the component of the sapling population made up of potentially fruiting species was similar between the two sites. We did not record the fruiting times and avian activities at fruiting saplings or trees with equal intensity on both sites; our observations were restricted primarily to the La Peninsula site. Nevertheless, we did

not record a single fruiting tree on the Riverine Disturbed site during the netted period. Although two were noted on the site on 11 January 1985, they no longer had fruits available by 6 February 1985. During the period of simultaneous netting one fruiting tree and a few small fruiting saplings and "shrubs" were noted on the La Peninsula site. Although we did not make direct measures of fruit availability between the two sites, it was our distinct impression that this was not a factor promoting a higher relative abundance of wood thrushes on the Riverine Disturbed site.

Vegetation analysis showed significant structural differences between the sites in trees, saplings and seedlings per hectare, and in basal area (m^2/ha), canopy cover, and number of lianas per sample point on both trees and saplings. Values were higher for all characters on the La Peninsula site. Only ground cover did not differ between the two (summary data available from the senior author). Structural differences reflect the logging history of the two sites, but also the riverine, periodically flooded nature of the Riverine Disturbed site, where a lower canopy cover (54% Riverine Disturbed versus 73% La Peninsula) did not result in a correspondingly higher level of ground cover (54% versus 55%). Winker et al. (1990a) examined forest microhabitat preferences in wood thrushes in this area and found that vegetative characters were not good predictors of wood thrush distribution in forest. Home range sizes of sedentary birds were on average smaller in areas with heavier ground cover (Winker et al. 1990a), the only character that did not differ between the two sites.

Nonterritorial wanderers appeared on the La Peninsula site throughout the winter (Winker et al. 1990b), and we consider these movements to represent the upward arrows in Fig. 1. Also, three of the transmitter-bearing individuals that went to the Riverine Disturbed area returned briefly to the La Peninsula site, but again did not remain long. We do not know what caused their departure, but such departures would be predicted in a territorial system.

Discussion

On the La Peninsula site territorial individuals were present all winter long, several returned between seasons, and newcomers (wanderers) did not appear able to remain for more than a few days (Winker et al. 1990b). The Riverine Disturbed site, on the other hand, showed instability both in the structure of its population (a high proportion of probable transients) and in its physical nature (portions periodically flooded). Several transmitter-bearing wanderers spent time there after leaving the La Peninsula site, but were forced for some reason to move on. Most of these birds seemed to move with weather changes, suggesting that envi-

ronmental variability (probably flooding) played an important role in wanderer movement in this habitat (Winker et al. 1990b). Further, we know that being transient in this population increased the likelihood of predation (Rappole et al. 1989). These observations, together with the well-reasoned theory that densities in territorial organisms should be highest in optimal habitats [the ideal despotic model of Fretwell and Lucas (1970) and Fretwell (1972)] made the finding of a higher capture rate in the Riverine Disturbed habitat unexpected.

Despite apparently high densities in the Riverine Disturbed habitat, we believe it was similar to the pessimal habitat type depicted in Fig. 1. We consider it unlikely that movement rate differences caused our abundance index (captures per 1000 net hours) to be an inaccurate reflection of actual densities. We postulate that intraspecific competition drove nonterritorial birds into this habitat, but environmental variability (e.g., flooding) and the search for potentially defensible space in better habitats caused them to leave. The situation we observed in this habitat may occur commonly among other nearctic-neotropical migrants in the younger seral stages of second growth forest in southern Veracruz (e.g., Rappole and Morton 1985).

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