Chapter 16

Habitat Selection by Nonbreeding, Migratory Land Birds

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I. HABITAT SELECTION: SOME DEFINITIONS AND CONCEPTS

A. A Working Definition of Habitat

I offer a working definition of the term "habitat" so that we begin from a common point concerning what it is that a bird selects for or against (see Par-
tride, 1978, for a similar perspective). For the purposes of this report, a habitat will be defined as a spatially contiguous vegetation type that appears more or less homogeneous throughout and is physiognomically distinctive from other such types. Granted, large groups of animal or plant species have not been shown to have entirely coincident distributions in space (Whittaker, 1975), as the superorganism concept would have it, so the point at which one habitat type ends and another begins is sometimes quite arbitrary. Nonetheless, there is a tendency for the physically dominant plant species to alter the environment to such an extent that important subsets of species are coincident in their distributions, and, in general, habitat types can be said to correspond well with biome types (Whittaker, 1975) or plant community types (Ricklefs, 1979). These might include categories such as grassland, pine-oak woodland, desert, deciduous forest, and so forth. More refined categories are possible if they are spatially and physiognomically distinct (e.g., shortgrass prairie, tallgrass prairie, desert bajada, desert riparian, etc.). Birds that differ in, say, the height at which they forage within an oak woodland illustrate within-habitat (microhabitat) differences in foraging locations, rather than habitat differences, according to this definition.

B. Habitat Selection: Proximate versus Ultimate Causation

Questions regarding habitat selection in birds can generally be thought of as belonging to one of two types: (1) Why does a species occur in the range of habitats that it does? and (2) What cues do individuals use as indications that they are in an appropriate habitat or not? The two really represent a division of the concept into ultimate and proximate causation. The former asks what are the evolutionary costs and benefits of using each of a possible range of habitat types, and the latter asks what is the mechanism by which the "choice" of habitat is achieved. In this chapter, I wish to concentrate on the first question as it relates to habitat selection in nonbreeding migrants and will consider whether the mechanisms involve direct or indirect assessments of those evolutionarily important costs and benefits by individual birds.

C. Habitat Selection: Intrinsic and Extrinsic Factors Associated with Ultimate Causation

Although habitat selection, in the evolutionary sense, involves a weighing of the costs and benefits associated with use of each available habitat type, it must be made clear that the costs and benefits may be determined by different factors at different levels of organization. These include what I call intrinsic (within-habitat) evolutionary constraints on suitability (how much, say, food or predator protection is afforded by the habitat) and extrinsic (extra-habitat) evolutionary constraints on suitability (habitat accessibility or weather patterns that might
influence habitat use during migration, for example). The overall costs and benefits of using a given habitat will be the sum of those associated with the intrinsic and extrinsic constraints. Note that extrinsic factors could override a ranking of habitats determined solely from intrinsic criteria when the habitats become more greatly separated in space, because, at some point, the absolute costs and benefits associated with extrinsic factors become much greater than the costs and benefits associated with intrinsic factors (Table I). In the next section, I suggest how both intrinsic and extrinsic constraints might interact to determine the patterns of habitat use in nonbreeding migratory birds.

D. Mechanisms of Habitat Selection

The very phrase "habitat selection" carries with it the unfortunate connotation that organisms consciously choose among alternative habitats. In no instance do I mean to imply such here. Even though the chapter title includes the phrase "habitat selection," I prefer "habitat use" because it does not connote a conscious choice; it merely indicates the actual distribution of individuals, through whatever mechanism (see Morse, 1980, for a similar, but not identical, distinction).

Consciousness aside, the ultimate range of habitats used by a species is likely to be a combined result of the following processes, or mechanisms: (1) individuals may cue into a geographical area (Hildén, 1965, p. 65) and thereby select (or avoid) habitat types, simply as a geographical or historical consequence of the fact that they have not been given an equal opportunity to discover each of a variety of habitats; (2) the habitat types (or geographic locations) currently used or avoided by an individual may reflect innate instructions passed on by ancestors who made relatively successful evolutionary "choices" in the past; (3) individuals may actively choose among habitats based on their own previous experience; or (4) individuals may "explore" possibilities and settle according to a ranking based on such exploration.

The extent to which exploratory ranking is possible depends on the geographic
scale of resolution. Location decisions that are based on ultimate cost–benefit criteria, such as the economics of foraging or differential susceptibility to predation, are almost certainly important at local (microhabitat) scales but become less likely at levels that we feel comfortable calling the level of "habitat selection," i.e., choices among distinct vegetation types separated by several kilometers or more. In most of the latter cases, habitat use is believed to reflect innate responses to some proximate environmental cues that are themselves well correlated with the presence of ultimately important needs (Klopfer, 1976; Partridge, 1974), and the possibility of exploratory choice has been played down at this level. Habitat types separated by several hundred kilometers or more lie at the far end of the spectrum, where it seems certain that exploratory ranking of alternative locations is not possible and where habitat use undoubtedly reflects innate responses to proximate orientation cues that place the bird in an appropriate location (Emlen, 1975).

Since it is unlikely that the broad-scale cues alone will ensure that all necessary requisites for survival and reproduction are present, it is useful to think of the process of habitat selection as a hierarchical series of decisions that an animal must make (see also Hildén, 1965; Gass and Montgomerie, 1981; Tinbergen, 1981; Cody, 1981). At the most general level, a geographic location is chosen. Then a particular habitat is chosen. Finally, the precise location within the habitat (microhabitat) is chosen, based on cues that probably differ from those used at the more general levels. The proximate cues used at the microhabitat level will be close to the ultimate factors that determine a bird's success, if not the ultimate factors themselves. Cues at the broad-scale level may therefore be necessary but insufficient for habitat use to occur.

Using my own research on migratory wood warblers as a focus, I now review the evidence that local-scale nonbreeding microhabitat selection is based on some sort of exploratory comparison of intrinsic ultimate factors, and I discuss the implications in terms of more broad-scale patterns of habitat use. Next, I review the evidence that broad-scale habitat selection might also be based, in part, on an exploratory assessment of intrinsic ultimate factors. Finally, I discuss how extrinsic ultimate factors act to limit the range of possible choices and thus place constraints on a migratory species' overall pattern of habitat use during the nonbreeding season(s).

II. INTRINSIC FACTORS AND MICROHABITAT USE

A. Theoretical Expectations

The factors that contribute to a bird's choice about a precise location within which to feed, roost, nest, sing, etc., are characteristics that occur within a
habitat—intrinsic factors such as food type or abundance, perch characteristics, branch configurations, and so forth. For nonbreeding birds, food acquisition must figure prominently in decisions about use of space, since getting enough food to store fat, or merely survive, could be considered the single most important constraint during these periods. I have therefore chosen to illustrate the role of intrinsic factors by concentrating on the relationship between food availability and a bird’s use of space within a given habitat.

On a theoretical basis, we expect food availability to influence a bird’s use of space. In fact, a major subset of optimal foraging theory involves patch choice (Pyke et al., 1977), and habitat selection might be considered a logical extension of patch choice (Morse, 1980). So long as food is limited in supply there will be selective pressure on individuals to use space in the most profitable (Royama, 1970) manner possible. The key here is that this is true even if food is not limiting—it only need be limited in supply (Hespenheide 1973, p. 218). No matter how much food there is, as long as it is limited in supply, there will be better and worse (relatively good and bad) places to settle, and selection will favor discrimination among sites on that basis alone. Admittedly, selective pressure will vary directly with the degree to which food is limited, but there will always be some pressure related to the economics of foraging that will tend to lead toward a close match between resource production and its utilization (MacArthur, 1969, 1970). At the other extreme, it could be argued that foraging constraints (competition for food) are unimportant except under extreme conditions (ecological crunches) and that the positions of bird territories in space may very well be products of random, stochastic processes (checkerboard model described by Wiens and Dyer, 1975; Rotenberry and Wiens, 1980; and Wiens, 1981). The answer may very well depend on the scale of consideration (Wiens, 1981). For example, local-scale patterns might be influenced markedly by relative differences in food availability among sites, but large-scale (habitat) patterns may not be so influenced, because of an inability of individuals to track differences in food availability on broad, geographic scales.

B. Empirical Evidence

As an example of a close match between resource availability and use of space, consider the combined foraging-height profile of three wood warbler species that I observed in Grand Teton National Park during May 1975 (Fig. 1). The relative availability of food at each height was estimated from the product of relative insect density (as determined from daily counts of four sets of five sticky boards that were hung for 4 days at 0.5-m height intervals) times the vegetation density at each height interval (see Hutto, 1980, for further explanation). The insectivorous bird “impact” histogram was calculated as the product of each species’ height distribution times its relative abundance, summed over all spe-
cies. The most striking aspect of the birds' use of space in this instance was the atypically low foraging heights of both the Yellow Warbler (*Dendroica petechia*) and Yellow-rumped Warbler (*Dendroica coronata*); at other times of the year it is common to find either species foraging from 4–8 m, in the canopy of more forested habitats (see Fig. 3 in Hutto, 1981). The uncommon observation recorded here can only be explained, I believe, on the basis of food distribution at that time.

There is much stronger evidence that food is nonrandomly distributed in space on a local level and that the use of space by birds (microhabitat use) corresponds strikingly well with the distribution of available food. An especially clear example comes from the work of Tinbergen (1981), who demonstrated that female Starlings (*Sturnus vulgaris*) foraging within pastureland spent most of their time in areas that yielded the highest food intake rates, which coincided with locations of highest prey (leatherjacket) density. Tinbergen's study represents but one of a host of studies that have produced similar results (e.g., Goss-Custard, 1970; Smith and Dawkins, 1971; Smith and Sweatman, 1974; Cody and Walter, 1976; Gill and Wolf, 1977; Davies, 1977; Greenwood and Harvey, 1978; Zach and Falls, 1979; Gradwohl and Greenberg, 1980; Thomas, 1980; Holmes and Robinson, 1981). These references include breeding and nonbreeding season studies—situations in which absolute food densities and additional constraints on the birds' time are extremely varied. The results are even more remarkable when one
considers that attributes of food other than its density, such as patch distribution or degree of isolation from other patches, also influence the probability of patch use (Gradwohl and Greenberg, 1980). Moreover, additional intrinsic factors, such as predator avoidance (Pulliam and Mills, 1977; Grubb and Greenwald, 1982), territorial defense, or other constraints, may also influence the probability of patch use and should therefore decrease the predictability of a bird’s use of space that is based on food availability alone. For example, Tryon and MacLean (1980) found that Lapland Longspurs (Calcarius lapponicus) used the space immediately surrounding nest sites more than would be expected solely on the basis of food availability.

The point I wish to stress is that the evolutionarily important costs and benefits associated with use of an area are largely, if not exclusively, a result of intrinsic factors at this level, and the factors to which the birds appear to be responding are close to, if not identical with, the ultimate factors determining their evolutionary success. Food is one such factor, and its power of influence has been emphasized here.

The implications are profound. If birds choose locations based largely on food availability, then large-scale habitat distribution patterns may be determined to some extent by factors operating at this level. For example, it is possible that an individual of one species could influence the food distribution or abundance enough (as has been described by Davies and Houston, 1981; and Tinbergen, 1981) so that an individual of another species might not choose to settle nearby, thereby influencing community-level patterns, such as species diversity.

It is also possible that decisions to settle in a given habitat are made in response to more proximate cues and that the most these smaller-scale foraging decisions can do is rearrange territories or home ranges slightly or cause individual modifications in foraging behavior in response to differences in vegetation structure (Holmes et al., 1978) or to differences in food abundance among patches (Tinbergen, 1981). Whether the intrinsic factors (e.g., food availability) that are ultimately responsible for local-scale patterns of microhabitat use might also influence the patterns of space use on a broader scale (habitat use) is, as yet, unknown. The next section approaches this question.

III. INTRINSIC FACTORS AND CHOICE AMONG HABITAT TYPES

A. Theoretical Expectations

The idea that the breadth of habitat types occupied by a species is directly related to its population size was perhaps originally published by Mayr (1926) and further developed by Svärdson (1949) and Hildén (1965). A more thorough
theoretical treatment of this problem of how population size might affect the intrinsic quality of a habitat and thereby influence patterns of habitat use was presented by Fretwell and Lucas (1970) and Fretwell (1972). In their model, they described how habitats could be ranked on the basis of a suitability derived from intrinsic costs and benefits. The absolute suitability of a given habitat is then assumed to decrease with increasing bird population size, because of changes in costs and benefits due to changes in levels of competition or predation. The relevance to us here is that, according to the model, the final decision a bird makes about which habitat to settle in must be based on an exploratory mechanism whereby the individual assesses the costs and benefits of possible choices in some direct or indirect manner. The alternative extreme is that birds are innately programmed to settle in a particular habitat type and are inflexible in this behavior; intrinsic factors would, of course, still be involved in determining the evolutionary success of individuals in a given habitat, but the birds would merely be programmed to settle in the habitat that, on average, is the best place to settle.

In a compromising fashion, both processes could operate if an innate preference to settle in a particular habitat type were contingent upon additional micro-habitat needs being met or if the threshold of acceptance for a habitat changed with "motivation" level of the bird (Svärdsön, 1949). Here, I wish to explore the possibility that assessment of intrinsic factors influences habitat settlement patterns, just as the process apparently influences decisions about microhabitat selection (last section).

B. Empirical Evidence

A wealth of examples of flexibility in habitat use in relation to population size was provided by both Svärdsön (1949) and Hildén (1965). For example, Hildén described how the Northern Lapwing (Vanellus vanellus) occupied only the most productive coastal habitat at the end of the nineteenth century but then began to occupy suboptimal habitats (less productive, small patches of meadow and tilled land and peatlands of forest areas) as its population size increased. In all, Svärdsön and Hildén referenced more than two dozen examples of direct relationships between population density and habitat breadth. Such findings would be difficult to explain if birds were inflexibly programmed to "choose" a habitat on the basis of the absolute level of some cue(s). The most compelling argument against an inflexible mode of habitat selection, however, comes from examples of niche shifts in habitat use in the presence or absence of competitors (Lack, 1971; Diamond, 1978)—particularly from short-term removal experiments in which one species has been observed to invade a previously unoccupied habitat after removal of another species (Davis, 1973).

To what intrinsic factor(s) might birds be responding during such shifts in habitat use? Such a factor may reflect an important basis for habitat selection in
general. Cody (1978) has suggested, for example, that birds might use cues that are directly related to the presence or absence of competitors, such as vocalizations. In addition to such direct cues, field studies of a correlative nature suggest, once again, that food availability might also be a critically important variable. During the nonbreeding season in western Mexico, resident insectivorous birds of the lowland evergreen forests fail to exploit the edge and second-growth situations for reasons apparently associated with an innate "mental conservatism" (Willis, 1966; Terborgh and Weske, 1969; Lack, 1971), which may have evolved in response to high predation rates in edge situations (Gates and Gysel, 1978). Food availability is four times greater in edge than interior habitats, and migratory insectivorous bird density is, correspondingly, five times greater in edge than interior habitats (Hutto, 1980). In speculation, perhaps the migrants can afford the "luxury" of high food levels in edge situations because, for some reason, they are less susceptible to predation in edge habitats than are residents.

In a similar fashion, during the 1975 spring migration period in Grand Teton National Park, Wyoming, the combined density of three wood warbler species was 12 times greater in the grass willow (Salix spp.) habitat than in the adjacent Lodgepole Pine (Pinus contorta) habitat (Fig. 2). This corresponded with an estimate of food density which was 13 times greater in the grass willow habitat (Fig. 2). The preference for grass willow habitat was particularly interesting in

![Fig. 2. Correspondence between the average (±SD) combined density of three warbler species (Dendroica petechia, D. coronata, and Geothlypis trichas) (□) and adjusted insect density (■) in each of two habitat types in Grand Teton National Park, Wyoming.](image-url)
the case of the Yellow-rumped Warbler which, in midsummer, nests in the lodgepole habitat and is not seen in the grass willow habitat. Clearly, with nesting constraints removed, food availability appears to be an intrinsic factor of major importance in determining patterns of habitat use in this case.

Burger et al. (1977), Davies (1977), Connors et al., (1981), and Sabo and Holmes (1983) have also demonstrated a close relationship between food availability and switches in habitat use by birds. Presumably, birds spend time exploring various habitats to keep track of the relative profitability of each. Consistent with this hypothesis is the observation by Gass and Montgomerie (1981) that (exploration?) time away from a territory by nonbreeding hummingbirds (Amazilia rutila) is inversely related to food productivity on their territories at any given time (Fig. 3). Habitat selection based on exploratory assessment of food availability has also been hypothesized to be important in fishes (Werner et al., 1981) and mammals (Lewis, 1980).

As habitats become more widely separated from one another, we would expect single individuals to be unable to assess the relative costs and benefits of using each and that nonexploratory mechanisms of habitat selection would come into play exclusively. However, as long as individuals explore adjacent habitats, the logical consequence will be large-scale shifts in use to match food productivity (or the availability of some other intrinsic factor) over a wide range of habitats through a kind of domino effect.

![Graph](image)

**Fig. 3.** The proportion of time Amazilia rutila individuals spend on their territories is directly related to the availability of food therein ($r_s = 0.86$). Time away from their territories when food is scarce is possibly spent in exploratory activities (from Gass and Montgomerie, 1981, by permission of Garland Publishing, Inc., New York, New York).
Is there any evidence that birds collectively assess the relative suitability of a number of more widely spaced habitats and settle accordingly? Although the precise mechanism remains unknown, I have recorded strong correlations between a measure of food availability and bird density among widely distributed habitats on two occasions. Such correlations would not be expected if food were not at least ultimately involved in habitat settlement patterns. In winter, the density of west Mexican insectivorous birds belonging to the small, foliage-gleaning guild was significantly correlated ($r = 0.79, p < 0.05$) with a measure of food availability over eight habitat types that varied in elevation from sea level to almost 3000 m elevation (fig. 4). In contrast with the permanent resident species, the more eurytopic migratory species seem to have been largely responsible for the close match between food availability and bird density ($r = 0.93$ versus $r = -0.71$ for migrants and residents, respectively); migrants may be in a better position to explore alternative habitats and incorporate an assessment of food availability into their settling response.

Similarly, the small, insectivorous foliage-gleaning species that migrate through southeastern Arizona during the spring and fall seasons reveal a shift in their use of the available habitats from one season to the next (Hutto, 1985). During the northward migration, most species occupy the low elevation desert
habitats, while during the southward migration there is a dramatic increase in migratory bird density in the highest elevation pine-fir forests (Fig. 5). Within a season there is a good correlation between bird density and a measure of food availability such that the seasonal shifts in habitat occupancy correspond well with the seasonal shifts in food availability among habitats. Food availability thus appears, again, to be an important intrinsic factor that is ultimately responsible for the habitat distribution pattern of nonbreeding birds during migration (see Balda et al., 1975, and Graber and Graber, 1983, for similar conclusions). An alternative hypothesis that might be invoked to explain such a correlation is that populations of both the predators (birds) and their prey (arthropods) are independent but affected similarly by a third variable, such as weather. This is most improbable, however, because the birds are in southeastern Arizona for only a matter of days in comparison with the arthropods, which carry out their entire life cycles in that location.

The mechanism by which birds assess the relative food availability among habitats remains unknown as mentioned earlier but must be a result of their cuing in on either some proximate factor that is well correlated with food availability between seasons (such as vegetation density) or on food availability itself, as has been suggested on occasion in the past (Hildén, 1965; Root, 1967; Verner, 1975; Pearson, 1977; Cody, 1981; Meents et al., 1982). In either case, it is worth pointing out that whatever the cues, they are much closer to the ultimately important intrinsic factors that determine success than those that have been suggested to be important during the breeding season, such as percentage of canopy cover or tree density (James, 1971; Whitmore, 1975; Clark et al., 1983), because the latter cues simply do not change seasonally in this case, while the habitat distribution of birds does. In addition, shifts in habitat use from summer to winter, which are quite common among migratory land birds (Lack, 1971),

Fig. 5. The correspondence between insectivorous bird density and adjusted insect density (see text) over seven habitat types during two seasons in southeastern Arizona (spring season, open histograms; fall season, hatched histograms; insects, circles).
imply either a shift in proximate cues used by individual birds or use of cues that are much closer to those of ultimate importance than those implied as important through breeding season studies. This idea of a facultative settlement pattern which is conditional upon food availability has been expressed by several authors in the past (Serventy, 1971; Ward, 1971; Fretwell, 1972; Sinclair, 1978; Pulliam and Parker, 1979; Smith, 1982; Nudds, 1983) and, in my view, deserves more attention in the future.

IV. GEOGRAPHICAL AND HISTORICAL CONSTRAINTS ON PATTERNS OF NONBREEDING HABITAT USE

The overwhelming majority of northern temperate migratory land bird species move more or less directly northward and southward during migration (Cooke, 1904; Wallace and Mahan, 1975). Consequently, the longitudinal separation of species and populations that exists during the breeding season persists during the winter season (see also Barlow, 1980; Fitzpatrick, 1980, 1982, for examples involving the Vireonidae and Tyrannidae). In the case of New World wood warblers, let us define 40 "Eastern" and 15 "Western" species and subspecies as those whose entire geographic ranges [as determined from the AOU checklist (1959)] are restricted to one side of the Rocky Mountains or the other and for which the geographic centers of their ranges lie north of the Mexican border during the summer. Using this definition and the specific or subspecific identity of populations as a convenient marker, one can draw the summer and winter ranges of each "species" and calculate the geographic overlap between all possible pairs. During the breeding season, Western–Western species pairs share 23.7% \((SD = 23.9)\) of their combined geographic ranges, on average, and Eastern–Eastern species pairs share 24.1% \((SD = 25.5)\) of their combined geographic ranges, on average. Eastern–Western species pairs share no area in common, by definition. To illustrate the maintenance of an East–West separation in winter, note that during the nonbreeding season, Western–Western species pairs share 38.5% \((SD = 27.2)\) of their combined geographic ranges, on average, while Eastern–Eastern species pairs share 16.2% \((SD = 18.6)\) of their combined ranges, on average. The Eastern and Western species remain largely separate in winter, as only 4.4% \((SD = 7.1)\) of the combined ranges of Eastern–Western species pairs is held in common, on average. Each of the last three mean values is statistically distinct from the other two \((t\text{-}tests, p<0.001)\). Thus, the Eastern species and subspecies remain geographically distinct from the Western species and subspecies in both summer and winter; a more random migratory pattern to and from the wintering grounds would produce average proportions of joint overlap that are statistically indistinguishable for all three groupings. The Western warblers winter almost entirely within a narrow strip of west Mexican
Fig. 6. The geographic centers of distribution are illustrated for Western (circles) and Eastern (triangles) migratory wood warblers during the breeding (closed symbols) and nonbreeding (open symbols) seasons. Only those species whose breeding range is centered north of the Mexican border are illustrated. The Western species and subspecies include (from north to south, closed circles) *Dendroica townsendi*, *Seiurus noveboracensis*, *Wilsonia pusilla*, *Oporornis toulmiei*, *Vermivora celata*, *Geothlypis trichas*, *D. petechia*, *V. ruficapilla*, *D. occidentalis*, *D. coronata*, *D. nigrescens*, *V. virginiae*, *Icteria virens*, *V. luciae*, and *D. graciae*. The Eastern species and subspecies include (from north to south, closed triangles) *V. celata*, *D. striata*, *D. coronata*, *V. peregrina*, *W. pusilla*, *O. agilis*, *D. palmarum*, *S. noveboracensis*, *D. magnolia*, *D. castanea*, *D. tigrina*, *W. canadensis*, *O. philadelphia*, *D. virens*, *D. caerulescens*, *D. petechia*, *V. ruficapilla*, *D. fusca*, *D. pensylvanica*, *S. aurocapillus*, *D. kirtlandii*, *Setophaga ruticilla*, *Parula americana*, *V. chrysoptera*, *G. trichas*, *Mniotilta varia*, *V. pinus*, *D. pinus*, *D. cerulea*, *D. discolor*, *S. motacilla*, *Helmithos vermivorus*, *D. dominica*, *I. virens*, *Protonotaria citrea*, *O. formosa*, *W. citrina*, *V. bachmani*, *Limnothlypis swainsonii*, and *D. chrysoparia*. 
mainland from southern Sonora south to Guatemala, while the Eastern warblers generally winter in geographically separate areas in the Bahamas, West Indies, eastern Mexico, Central America, and northern South America (Fig. 6).

There are minor exceptions to this generalization. For example, the "Eastern" Black-and-White Warbler (Mniotilta varia) and American Redstart (Setophaga ruticilla) both winter, in part, in western Mexico (see Chapter 1, this volume); however, each represents a species whose breeding range bends westward across the Rocky Mountains in the north, and the individuals that winter in western Mexico may very well be "Western" individuals of these primarily Eastern species. On the other hand, there is at least one recorded case in which an Eastern individual [Nashville Warbler (Vermivora ruficapilla) banded in Oklahoma] was recovered in Nayarit, Mexico, in winter (Shackford, 1983), so the generalization is not without exception.

A further point of interest is suggested from the previous analysis. In the case of most migratory European passerines (Lack, 1971) and Eastern North American wood warblers (MacArthur, 1958; Chipley, 1980; Keast, 1980, this analysis) there is an increase in geographical isolation in winter compared with summer. In the case of sylviid warblers, the degree of geographic overlap among the various species is unchanged from summer to winter (M. Cody, personal communication). The situation is clearly different for Western North American wood warblers, and they may be unique among passerine bird species in this respect. The trend is unequivocally toward an increase in geographical overlap among species within the relatively tiny area in winter compared with summer. The relevance of all this to the question of habitat selection is that the range of habitats used during the nonbreeding season may be influenced, in part, by the geographic area occupied during the breeding season.

Why do the Western wood warblers "choose" not to occupy a greater geographic range in winter and thereby use a wider range of habitat types than they presently do? Before attempting to answer this question, I must address another issue that may be in the minds of some readers. Some might claim that the question of where to winter, or what geographic range to occupy, is entirely a product of a northern temperate bias, and if viewed from a more southerly perspective the question would be moot, because the species simply occur in those areas where they originated; the question should be "Why do they occupy the breeding range that they do?" However, even if the taxa in question were derived from tropical ancestors that were once permanent residents (Mengel, 1964), the eventual use of more seasonal and increasingly widespread northern habitats following glacial retreats would have allowed increased population sizes, which would have eventually placed pressure on individuals to expand into new geographic locations or habitats in winter. Hence, discussion of the influence of the geographic locations of breeding season habitats on the geographic
locations and variety of habitat types used during the winter by a species is quite valid.

Back to the question of why the Western wood warblers occupy such a restricted winter range relative to their Eastern counterparts—it could be that both intrinsic and extrinsic (distance) factors make the cost of using other habitats outweigh any potential benefits, such that ancestors that have tried other options have been selected against. Alternatively, it could be that extrinsic factors alone have played the important role here, i.e., historically, Eastern habitats have always been avoided by Western migrants because of geographic constraints associated with restricted migratory routes. Certainly, the latter would be the more likely explanation for why Western migrants do not use, say, African scrub habitats, and such extrinsic constraints may play an important role within the hemisphere as well.

In addition, many of the habitats in western Mexico (desert scrub, riparian, oak woodlands, pine-oak woodlands, pine forests, pine-fir forests) are nearly contiguous with the same types farther north into the western United States and Canada (Mengel, 1964; Szafer, 1975). Moreover, these more xeric west Mexican habitats differ vegetatively from the other west Mexican habitats more than the others differ among themselves (the other habitat types are primarily variations of tropical evergreen or tropical deciduous forest types) (Szafer, 1975). This similarity between, and contiguity of, breeding and wintering habitats of the western North American migrants is unmatched by Palaeartic or eastern North American migratory systems and may have allowed many of the Western migrant species to become specialized toward year-round use of the more xeric Western habitat types. For Western migrants to winter in geographic locations (and habitats) farther removed from their present wintering grounds in western Mexico would mean dealing with the additional costs associated with using habitat types that are very dissimilar to their breeding habitats and encountering additional ecologically similar species farther eastward. Those additional costs are apparently outweighed by the advantages of using similar habitat types year-round and avoiding ecologically similar Eastern species, despite the build up of relatively high migrant densities that occur in most west Mexican habitats in winter (Hutto, 1980). In contrast, Eastern North American migrants winter in forests that, although once extensive and coterminous with their breeding forests (Braun, 1950; Graham, 1973; Howard, 1973), are now disjunct and relatively dissimilar to the more northern forests. Restriction of close competitors to different wintering zones (allopatry) might be expected to have evolved in this case, because the habitat differences that have developed among disjunct zones have provided a more geographically varied environmental backdrop against which the competitive differences among species have been expressed, creating the geographic replacement patterns commonly observed among the Eastern migratory species. MacArthur (1958), for example, found only one of his five
warbler species (Dendroica virens) in Costa Rica when he traveled south to study the birds during winter; the other four species were wintering primarily in the West Indies (D. tigrina), southeastern United States and Mexico (D. coronata), South America (D. fusca), and Colombia (D. castanea).

Whether the above generalization is correct in detail, the example illustrates

Fig. 7. A diagrammatic illustration of the hierarchical decision-making process involved in "choice" of nonbreeding habitats by a migratory bird. The process at level (A) is probably inflexible and innate, while the process at levels (B) and (C) may very well involve exploratory assessment of intrinsic costs and benefits associated with each option.
how extrinsic factors might operate to constrain the patterns of habitat use during the nonbreeding season.

V. SUMMARY

Habitat selection in nonbreeding, migratory land birds is seen as a hierarchical decision-making process (Fig. 7). At the highest (broadest) level (Fig. 7A), most land birds are probably inflexibly programmed to head along a certain migratory route to a wintering area. Thus, even though the intrinsic factors that determine the suitability of a habitat for nonbreeding season use may have influenced the evolutionary choice of the currently used migratory routes and wintering areas, once established, some habitats that lie outside the major migratory route or wintering areas may be unused simply because of the high extrinsic costs associated with getting to them, rather than the high intrinsic costs associated with their use. Similarly, the use of some habitats (particularly while in route) may be largely determined by the extrinsic benefits of using a particular (wind-aided, more direct, etc.) route, rather than being a result of the habitat’s intrinsic quality.

The next level in the decision-making process occurs when the bird views the situation from a more restricted geographic perspective (Fig. 7B). At this level, where birds can actually explore alternatives, the intrinsic costs and benefits associated with the use of each habitat may be assessed directly or indirectly by the birds and each used accordingly. There is strong evidence that food availability is one intrinsic factor that plays an important role in the birds’ assessment of habitat quality during the nonbreeding season and that use of direct or indirect cues enables birds to settle such that their densities match food resource production quite well.

At the lowest (most local) level (Fig. 7C), the same process involving an assessment of intrinsic factors (especially food availability) also appears to influence the use of space within a habitat (microhabitat use). This implies that decisions involving use of space on a local level may be partly responsible for the patterns of space use that we observe at a higher level—the level of habitat selection. Thus, patterns of habitat use during the nonbreeding season are simultaneously based on extrinsic factors that predispose birds to use a given habitat or not and on the intrinsic quality of the habitat itself, which appears to be determined, in part, by food availability.

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