

MECHANISMS OF *EN ROUTE* HABITAT SELECTION: HOW DO MIGRANTS MAKE HABITAT DECISIONS DURING STOPOVER?

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Abstract. Evidence reveals that habitat selection occurs during migration, but little is known about how migrants made decisions about habitat use during stopover. Although most nocturnally migrating birds end their migratory flight well before dawn, selection of habitat probably occurs during daylight hours. Possibly "morning flights" represent efforts to explore suitable habitats in which to rest and forage. Choice of habitat probably consists of a sequence of hierarchically ordered decisions that depend on different criteria. When migrants arrive they may settle in response to gross habitat features such as vegetation density, then search for resources based on more subtle habitat features or the behavior of other migrants. We used radio-telemetry to study the movement pattern of Summer Tanagers (*Piranga rubra*) during stopover. Use of habitat and pattern of movement differed between fat and lean individuals. Lean birds were more active, displayed a pattern of movement more consistent with exploration, and visited more habitat types than did fatter birds.

Key Words: exploration, habitat selection, landbird migrants, migration, stopover.

"The crucial first step to survival in all organisms is habitat selection. If you get to the right place, everything else is likely to be easier."—E. O. Wilson. *Biophilia*. 1984

Habitat is an area possessing resources and other environmental attributes that promote occupancy and survival of individuals (Morrison et al. 1992). Habitat selection may be defined (Block and Brennan 1993) as "innate and learned behavioral responses of birds that allow them to distinguish among various components of the environment resulting in disproportional use of environmental conditions to influence survival and ultimate fitness of individuals." This definition identifies habitat selection as a process with fitness consequences (Hildén 1965, Klopfer and Hailman 1965; see also Hutto 1985b).

When a migratory bird stops *en route*, it almost invariably finds itself in unfamiliar surroundings when energy demands are likely to be high (e.g., Loria and Moore 1990, Martin and Karr 1990, Moore 1991a). It may also face conflicting demands between predator avoidance and food acquisition (e.g., Metcalfe and Furness 1984, Lindström 1990b, Moore 1994) and competition with other migrants and resident birds for limited resources (e.g., Hutto 1985a, Moore and Yong 1991). How well migratory birds satisfy energetic requirements and meet contingencies that arise during passage depends largely on their ability to locate resources and avoid sources of stress (*sensu* Jander 1975).

If selection of one habitat over another during stopover has consequences for a migrant's survival and subsequent reproduction, then migrants should display a preference for certain habitats and select among alternatives during stopover (Hutto 1985b; Moore et al. 1990, 1995). Three lines of evidence reveal that habitat selection occurs during migration (Petit *this volume*): (1) year-to-year constancy in species-spe-

cific patterns of distribution among different habitats (Bairlein 1983); (2) seasonal shifts in habitat types (Winker et al. 1992a, Weisbrod et al. 1993, Moore and Woodrey 1993), sometimes correlated with changes in food availability (Hutto 1985a, Martin 1985, Martin and Karr 1986); and (3) use of habitat out of proportion to its availability (Johnson 1980; e.g., Moore et al. 1990, Bruderer and Jenni 1990, Mabey et al. 1993). Migrants that assess habitat quality should gain an advantage relative to individuals that fail to assess habitat options *vis-a-vis* choice of habitat (see Hutto 1985b, Moore et al. 1995).

Study of habitat selection in migratory birds has focused largely on describing habitat use during stopover (e.g., Bairlein 1983, Moore et al. 1990, Winker et al. 1992a) rather than examination of the underlying proximate mechanisms that mediate selection. How do migrants distinguish one habitat from another? How is habitat quality assessed? What cues do migrants use when deciding to settle in a particular habitat? These are proximate questions about the mechanisms of habitat selection, rather than questions about the functional consequences of habitat choice (Hutto 1985b).

How birds assess habitat is less clear than their decision-making about individual resources, and the mechanisms used to make habitat choices are best known for decisions made outside the migratory season (Hildén 1965, Klopfer and Hailman 1965, Morse 1985, Morton 1990). We are only beginning to understand migrant-habitat relations during migration (see Hutto 1985b; Moore et al. 1990, 1995), much less appreciate the mechanisms migrants use to identify habitat attributes on which habitat

choices are made during passage. Our objective is to explore how migrants might select habitat during stopover and to suggest ways to test predictions regarding habitat assessment.

To understand how migrants assess habitat during passage, it must be realized that birds make decisions at different spatial scales and that different factors, some extrinsic to habitat per se, operate at these different scales (see Hutto 1985b, Moore et al. 1995). Intrinsic constraints on habitat use are those factors thought to determine habitat quality and upon which migrants made decisions about habitat use. As the spatial scale broadens, factors intrinsic to habitat give way to factors largely unrelated to habitat, such as synoptic weather patterns. Yet, extrinsic factors may constrain opportunities to select habitat, not to mention the process of assessment itself.

Migration in relation to the Gulf of Mexico illustrates how an extrinsic factor such as prevailing winds constrains habitat use at different spatial scales. The likelihood of a successful flight across the Gulf of Mexico is tied to the occurrence of favorable flight conditions (Buskirk 1980). In spring, the peak of trans-Gulf migration, which occurs over the latter half of April through early May, corresponds to a period of predictable southerly airflow. Should migrants encounter unfavorable weather, flight is prolonged and energy stores depleted. Habitat assessment is likely to vary with energetic condition upon arrival (see Moore and Simons 1992a). Although migrants are observed crossing the Gulf of Mexico in fall, prevailing weather conditions during the peak of fall migration along the northern coast of the Gulf of Mexico facilitate movements parallel to the coast rather than across this barrier (Able 1972, Buskirk 1980; see Sandberg and Moore 1996). As a consequence, migrants are likely to encounter habitats during fall passage that differ from the habitats experienced during the return passage in spring.

WHEN DO MIGRANTS SELECT HABITAT?

Most nocturnally migrating songbirds end their migratory flight well before dawn (Kerlinger and Moore 1989), although exceptions occur, especially when night migrants must cross water barriers (see Gauthreaux 1971, 1972; Moore and Kerlinger 1991) or deserts (Moreau 1972; but see Biebach 1985, Bairlein 1987b). When crossing bodies of water, migrants have little choice but to continue migration until "suitable" habitat is found.

When migrants end their flight at night, selection of habitat probably occurs during daylight hours, most likely early in the morning, and not

at night when landfall occurs. Although the behavior of nocturnally migrating birds is influenced by gross topographical features such as rivers (Bingman et al. 1982), mountains and valleys (Bruderer and Jenni 1990), and coastlines (Able 1972), migrants probably do not possess the sensory capability to evaluate subtle habitat differences at night (cf. Martin 1990). If visual capacity constrains decisions about habitat upon nighttime landfall, we would expect the distribution of migrants among habitats and the amount of movement to vary in relation to night-time light levels (e.g., moonlit versus overcast night). We would also expect to observe age related differences in the interpretation of habitat when making landfall at night (see Gauthreaux 1982a). Little is known about habitat decisions immediately upon landfall, even when arrival takes place during daylight hours (but see Gauthreaux 1972, Moore et al. 1990).

Nocturnal migrants have been observed making "morning flights" at several locations in North America (Bingman 1980, Hall and Bell 1981, Wiedner et al. 1992; D. Cimprich, unpubl. data) and Europe (Alerstam 1978, Lindström and Alerstam 1986, Spina and Bezzi 1990). These morning flights appear to differ from normal nocturnal migration in that (1) they occur during daylight usually within the first two hours after dawn, (2) they occur at low altitudes (sometimes from treetop to treetop), (3) flights are of short duration, and (4) migrants are often in flocks. Moreover, the direction of "morning flight" is not necessarily the same as the previous night's migration (e.g., Wiedner et al. 1992; but see Bingman 1980), although there is no a priori reason why migrants would not bias their daytime movement in the migratory direction. For example, trapping data for fall migrating Sedge Warblers (*Acrocephalus schoenobaenus*) in northern Italy reveal movement concentrated in early morning (Spina and Bezzi 1990), which suggested that newly arrived birds were moving away from the landing area. When juvenile and adult Sedge Warblers were tested in orientation cages at dawn, juveniles showed more intense but less directional activity, whereas adults were oriented along the migratory direction (Spina and Bezzi 1990). Other observations suggest that birds may engage in "morning flight" to compensate for drift experienced during nocturnal migration (Moore 1990a).

These morning flights may represent a period of exploration as migrants seek more suitable habitat in which to rest and forage (see Lindström and Alerstam 1986, Wiedner et al. 1992). If so, the distribution of migrants among habitats should change between the time of arrival and subsequent settlement (i.e., migrants should dis-

tribute themselves according to variation in habitat quality during morning flight). Although this expectation has not been tested, some observations are consistent with an "exploratory" function for these morning flights. On the Cape May peninsula, New Jersey, thousands of fall migrants can be observed in "morning flight" to the north, away from the end of the peninsula, toward the forested areas up the Delaware Bay-shore (Wiedner et al. 1992). At other sites in the New Jersey coastal plain, "morning flight" is to the west or northwest, again toward forested areas (S. Gauthreaux, pers. comm.). Once the birds reach forested areas they diffuse, presumably settling in preferred habitats. When migrants stopover in alpine areas while crossing the Alps, juveniles are more likely to land in unfavorable habitats than adults (Bruderer and Jenni 1988). Finally, landbirds seem to be "attracted" to riparian areas following a night's migration in the southwestern United States (Terrill and Ohmart 1984). Within a riparian system consisting of different habitat types that presumably vary in suitability (Finch and Yong *this volume*), migrant abundance could be estimated relative to habitat availability and body condition assessed through mist-netting activity (J. Kelly et al., unpubl. data).

INFORMATION USED TO ASSESS HABITAT

Choice of habitat during passage probably consists of a sequence of hierarchically ordered choices (Johnson 1980; see also Orians and Wittenberger 1991), and different criteria may assume importance at different stages. Upon arrival, a migrant might settle on basis of gross habitat features (e.g., vegetation density), possibly choosing (or avoiding) area that bears some resemblance to previously experienced habitat. The decision to actually search for resources within a circumscribed area or to continue local movement may depend on more specific habitat features or the behavior of other migrants. During exploration a migrant might sample resources to make a more refined assessment of habitat.

Actually, the information migratory birds use to select among alternative habitats during stopover and the manner in which they do so is poorly understood. Migrating birds use habitat *en route* in different ways for different reasons: some birds try to deposit fat stores, others use the site as a molting ground (e.g., Winker et al. 1992a), while other birds simply rest until nightfall (e.g., Biebach 1990). Moreover, a hungry, fat-depleted individual undoubtedly has a different perspective on habitat than a migrant that is simply looking for a safe place to rest, and con-

sequently may react to different habitat features when selecting habitat.

Because food is critically important *vis-a-vis* energetic requirements, we consider habitat cues from the perspective of a migrant searching for food resources. What are the environmental stimuli that evoke a settling response in relation to habitat during stopover? Although the proximate factors that serve as "cues" in habitat selection are probably linked to the ecological factors that determine suitability (see Hutto 1985b, Moore et al. 1995), they are not necessarily those that directly affect the migrant's survival in a given habitat (Lack 1933, Klopfer and Hailman 1965).

VEGETATION STRUCTURE

The "niche-gestalt" model of habitat selection (James 1971, James et al. 1984) would predict that migratory birds respond to gross structural features (e.g., vegetation density or height), presumably because those features are correlated with feeding demands. Structural features of breeding habitat (Sherry and Holmes 1985, Morse 1989), including microhabitat structural components such as needle architecture (Parrish 1995a), do influence dispersion of birds in forest habitats. Results of a foliage discrimination experiment (Greenberg 1985) showed that migrant wood warblers (*Dendroica castanea* and *D. pennsylvanica*) rapidly learn to distinguish between leaf-types, which may explain why foliage-gleaning birds develop preferences for particular plant species.

If foraging success varies with vegetation structure (e.g., Robinson and Holmes 1984), energetically constrained migrants should attend to structural features as cues when selecting habitat during stopover. When Hutto (1985a) examined the distribution and abundance of migratory species over an elevational habitat gradient in the Chiricahua Mountains, the pattern of habitat used differed between spring and fall, yet few vegetation variables changed seasonally within habitats. Hutto (1985a) concluded that these habitat variables are unlikely to be the proximate cues used by the birds for a settling response. This expectation could be tested more directly by presenting migrants with alternative "habitats" that varied in some structural feature thought to be important in habitat assessment. Although it would be possible to arrange such an experiment in the field (e.g., Gwinner et al. 1985), the more manageable, albeit contrived, approach would be examine habitat preference in an aviary setting where greater control can be achieved (e.g., Hebrard 1978, Partridge 1979, Roberts and Weigl 1984, Morton 1990). We would not be surprised if migrants responded to

simple structural features, such as verticality (e.g., Morton 1990), which would provide flexibility when selecting habitat during migration.

SOCIAL ATTRACTION

Migrants may respond to the presence of other migrants, especially conspecifics, rather than habitat per se, when assessing habitat during stopover. Presumably a more suitable habitat would attract more individuals (sensu Fretwell and Lucas 1970; see Moore and Simons 1992a), although more migrants would more rapidly deplete resources and increase the likelihood of competition (Lindström et al. 1990, Moore and Yong 1991). In any case, responding to the behavior of other migrants as a mechanism to assess habitat quality would be especially useful if an area could not be thoroughly searched because of time constraints.

Imitation and observational learning are known to influence food preferences (e.g., Murton 1971, Tramer and Kemp 1979) and the effect is amplified when birds are food deprived (Mason and Reidinger 1981). When migrants stopover they often find themselves in the presence of other migrants, many of whom are trying to re-gain depleted nutritional stores. Circumstantial evidence leads us to believe that social facilitation may be involved in habitat selection during stopover. During "fallouts," when large numbers of migrants land at a stopover location over a short period of time, we have observed migrants to move quickly from tree-top to tree-top or shrub to shrub among habitats, often in loose mixed-species flocks, giving the impression that they were assessing habitats. Once migrants "settled" in a habitat, which appeared to take place within one or two hours after fallout, they often foraged alone or in small homospecific flocks (Moore et al. 1990).

If migrants "cue" on one another when selecting habitat, we would expect migrants to respond to playback of conspecific vocalizations (D. Cimprich, unpubl. data) or to the presence of model birds (cf. Gotmark and Unger 1994). Whether a migrant is attracted or repulsed by the presence of other migrants may depend on the bird's foraging strategy and the economics of resource defense during stopover. For example, Gray Catbirds (*Dumetella carolinensis*) rely heavily on patchily distributed fruits during fall passage (C. Dwyer, pers. comm.) and may attempt to exclude other migrants from those resources. Moreover, migrants that "cue" on the number of other migrants present in a habitat may also attend to the level of activity (e.g., feeding behavior) of other individuals as an indication of habitat use.

PREDATION RISK

Predation constitutes a significant hazard to migrating birds (e.g., Rudebeck 1950, 1951; Walter 1979, Kerlinger 1989, Lindström 1989, Moore et al. 1990). Consequently, the decision to use a particular habitat is influenced by the migrant's perception of predation risk (Lindström 1990b). Moreover, the need to avoid predators must be balanced against the need to acquire food to meet the energetic demands of migration. Balancing conflicting demands is not easily achieved during stopover for several reasons (Cimprich and Moore, in press): risk of predation varies widely in time and space (Aborn 1994); migrants are probably unfamiliar with foraging opportunities and predation risk; and they are under pressure to travel quickly. The reaction to predation and resolution of a conflict between food acquisition and predator avoidance surely varies with habitat (e.g., Lindström 1990b) and behavior of the predator (cf. Curio 1993), as well as the migrant's condition (Moore 1994) and age (Metcalfe and Furness 1984; D. Cimprich, unpubl. data).

Given time and energy constraints, we expect migrants to be especially sensitive to the threat of predation during stopover; time devoted to anti-predator behavior when there is little threat of predation is time not spent satisfying energy demand. Because the threat of predation is highly context dependent during stopover, we expect migrants to use various mechanisms of risk assessment; that is, a migrant behaves as if it were monitoring the degree of threat to itself or to other migrants (see Curio 1993).

SAMPLING RESOURCES DIRECTLY

A migrant might respond to resources independent of habitat structure or social factors. Information could be gathered about habitat by sampling resources directly, which might include the number of food items consumed, the time spent in a habitat, or the time since the last food item was consumed. A direct, accurate assessment of resources or sources of stress may be especially important to migrants because of the unpredictable nature of passage.

Because migrants find themselves in unfamiliar surroundings during stopover, particularly hatching-year migrants on their first passage, how they respond to novel circumstance will affect their use of habitat. Habitat decisions predicated on sampling could be constrained by a migrant's readiness to approach and feed on new food sources or in novel situations (sensu Greenberg 1984b, 1990). Although neophobia varies among species (Greenberg 1984b), the degree of neophobia does not decrease with increased hun-

TABLE 1. AVERAGE (± 1 SD) MEASURES OF MOVEMENT FOR FAT AND LEAN SUMMER TANAGERS ON HORN ISLAND, MISSISSIPPI, 1992-1994

Movement variable	Fat (N = 11)	Lean (N = 8)	t-value	P
Linear distance (m)	229.2 \pm 130.6	491.5 \pm 380.4	2.11	< 0.05
Total distance (m)	1,003.8 \pm 740.2	1,513.9 \pm 831.3	1.16	> 0.05
Time between moves (min)	28.5 \pm 25.1	18.0 \pm 16.9	2.75	< 0.05
Length of move (m)	68.9 \pm 24.8	89.2 \pm 63.4	3.03	< 0.05
Rate of movement (m/min)	6.5 \pm 3.1	12.1 \pm 9.6	2.87	< 0.05

ger (Greenberg 1987b), which suggest that responsiveness to novel circumstances may not change with heightened energy demand during migration (but see Loria and Moore 1990). Likewise, social enhancement does not reduce feeding neophobia in Chestnut-sided Warblers (*Dendroica pensylvanica*; Greenberg 1987b; but see Coleman and Mellgren 1994).

PRIOR INFORMATION

The disadvantage of sampling habitats is that it takes time, a commodity presumably in short supply for most migrants (Alerstam and Lindström 1990). Pressure to arrive at a destination in a timely manner probably explains why most migrants depart the night of their arrival day, if not sooner (Winker et al. 1992b,c), although length of stopover does vary with the migrant's energetic condition (Moore and Kerlinger 1987, Kuenzi et al. 1991, Morris et al. 1994). Sampling may also expose migrants to increased risk of predation. Nevertheless, previous experience in different locations is known to influence later choices (Partridge 1979), so migrants might arrive at a stopover site with prior information of the distribution of resources (or sources of stress) in the environment, which would increase efficiency with which they use habitat (cf. Valone 1992).

Prior information would include any information about habitats gathered prior to arrival at a given stopover site, including experience with habitats on the breeding grounds, wintering areas, and previous stopover locations. Black-chinned Hummingbirds (*Archilochus alexandri*) rely on prior information when making foraging decisions during stopover, although the extent to which they do so depends on environmental variability (Valone 1992). High fluctuations in resource abundance and availability makes the use of prior information impractical.

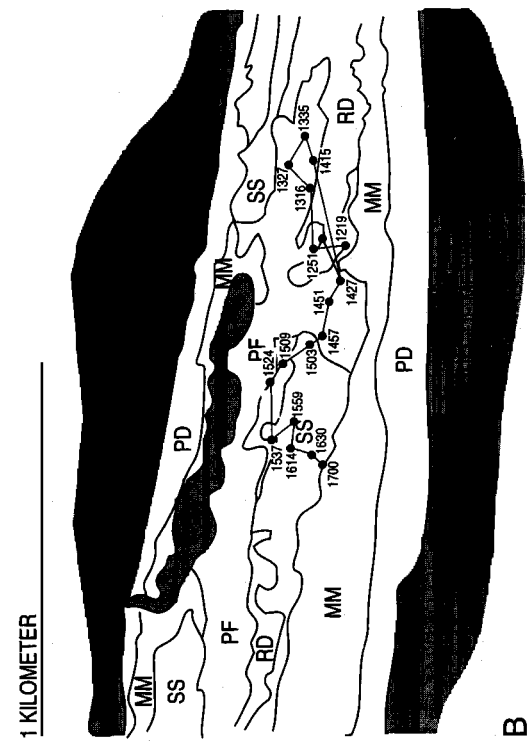
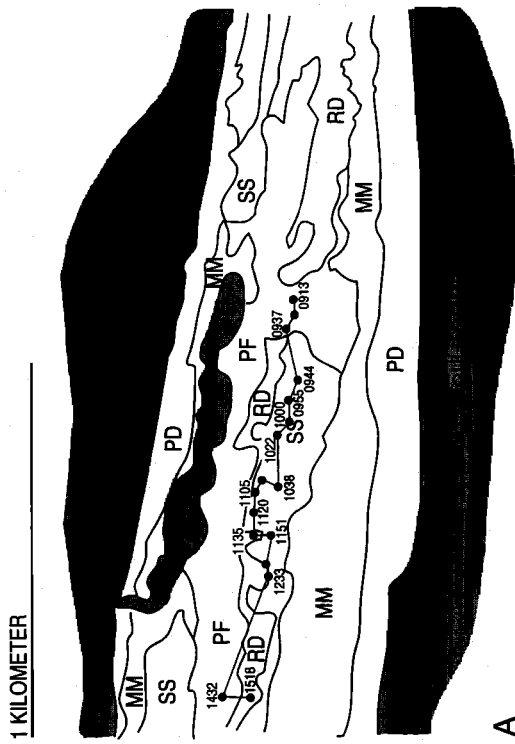
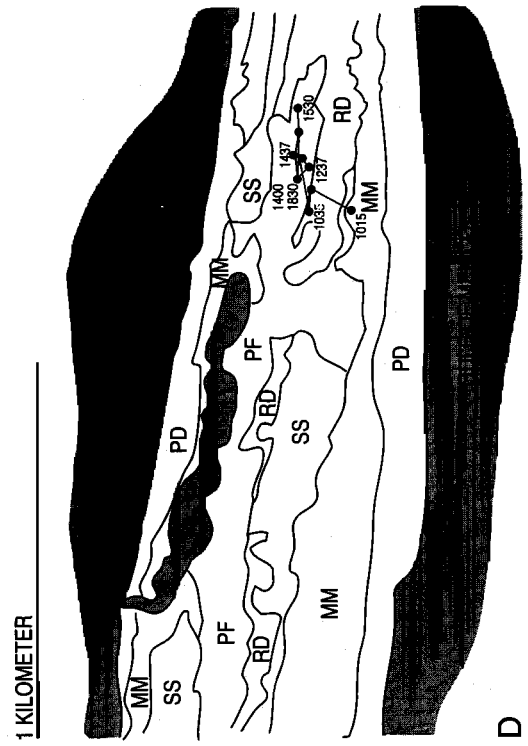
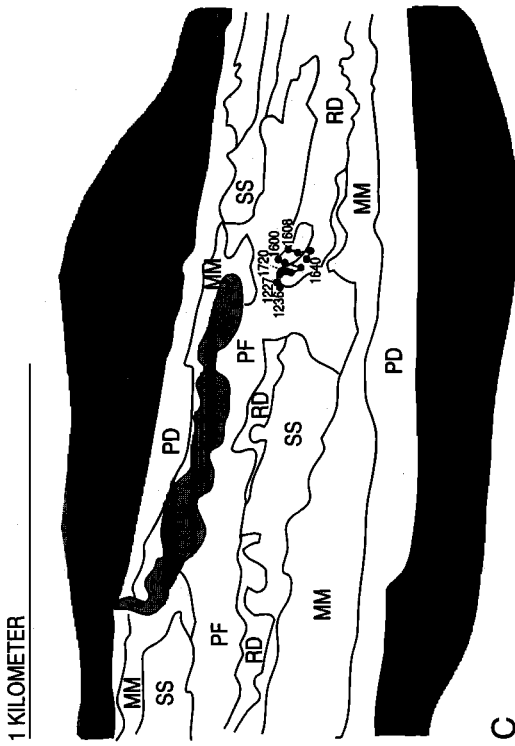
The difficulty with using prior information

gathered during migration is confounded by the fact that migrant landbirds seldom stop over at the same location. Suppose a migrant's settling response is influenced by previous experience, and the nature of that experience influenced by extrinsic factors (e.g., synoptic weather). As a consequence of extrinsic constraints, a migrant finds itself searching for food in a "strange" habitat, yet that experience influences subsequent decisions about habitat use.

INNATE PREFERENCES

Some habitat decisions made during passage are probably affected by innate (programmed) preferences (Hildén 1965, Klopfer and Hailman 1965), yet little, if any, attention has focused on the importance of such preferences during migration. Although it is unlikely that migrant landbirds would possess programmed habitat preferences specific to the migratory period, they may reference innate information about breeding habitat when making habitat decisions during passage. It is not unusual for migrants to occupy habitat during the nonbreeding season that resembles their breeding habitat (e.g., Parnell 1969, Power 1971, Lack and Lack 1973). Such behavior, which is consistent with the existence of innate preferences, may be especially beneficial for hatching-year birds given their lack of experience with different habitat types. Bairlein (1983) found species-specific habitat use among passage migrants that stopover at the west end of Lake Constance, Germany, and interpreted the year-to-year consistency in habitat distribution among adult and young birds without knowledge of the stopover area as evidence of innate preferences. If migrants do display innate habitat preferences during passage, we would expect *en route* experiences to shape those preferences in the face of variability encountered during passage.

FIGURE 1. Radio locations and movement tracks of lean (a, b) and fat (c, d) Summer Tanagers radio-tracked on Horn Island, Mississippi, following migration across the Gulf of Mexico. Two letter acronyms refer to habitat types: MM (marsh/meadow), PF (pine forest), RD (relic dune), SS (scrub/shrub).



EXPLORATION AND ENERGETIC CONDITION—AN EXAMPLE

The energetic status of a migrating bird is known to affect the likelihood of stopover (Moore and Kerlinger 1987, Kuenzi et al. 1991), length of stay (Rappole and Warner 1976, Yong and Moore 1993), foraging behavior during stopover (Loria and Moore 1991), and the response to the threat of predation (Moore 1994; D. Cimprich, unpubl. data). A migrant arriving at a stopover site in a fat-depleted condition is faced with the dilemma of needing to find quickly suitable habitat where it can deposit fat, while possibly not having the energy stores to adequately search among habitats. If high quality habitats are few in number or widely dispersed, fat-depleted migrants may be compelled to settle in a lower quality habitat, resulting in a longer stopover and delayed arrival on the breeding or wintering quarters.

Observations of neotropical landbird migrants that arrived along the northern coast of the Gulf of Mexico following a trans-Gulf flight suggest that birds may assess habitat during an initial exploratory phase (Moore et al. 1990, Aborn and Moore 1997). We used radio-telemetry to study the movement pattern of Summer Tanagers (*Piranga rubra*) during stopover following migration across the Gulf of Mexico (Moore and Aborn 1996, Aborn and Moore 1997).

Research was conducted on Horn Island (30° 14' N, 88° 40' W), a barrier island located approximately 20 km off the Mississippi coast. Vegetation on the island consists of a mosaic of five habitat types: pine forest, scrub/shrub, marsh/meadow, relic dune, and primary dune (see Moore et al. [1990a] for habitat descriptions). Birds were caught in mist-nets, fitted with radio transmitters (Custom Telemetry and Consulting, Inc., Watkinsville, GA; 1.3–1.4 g, 1-km range, 7-day life span), and tracked continuously until they left the island or the transmitter failed. We recorded the bird's location, habitat, and activity status (perched, active, or flying).

We calculated linear distance (distance between the point where bird was released to place it roosted at dusk), total distance moved, average distance per move, average time elapsed between each move, and average rate of movement. We also computed the angle of each turn and turn bias (i.e., whether the turn was left or right). An equal degree of left and right turns will result in an angular turn bias of 0°, whereas circling movement yields a larger turn bias, as if moving in a defined area or turning back on its previous move. Total distance divided by linear distance yields a "meander ratio" (Williamson and Gray 1975), which reflects area-restrict-

ed movement. We used vector analysis (Zar 1996) to determine whether a bird's sequence of moves were concentrated in a particular direction (r -statistic). Values close to zero indicate a high degree of variability in the directions (little directionality), whereas values that approach 1 suggest that birds tended to orient their movements in the same direction (high directionality). If Summer Tanagers move in a circular pattern or turn back on their previous movement the r -value should be small and statistically insignificant according to a Rayleigh test (Zar 1996).

Pattern of movement differed among individual Summer Tanagers that stopped over on Horn Island following trans-Gulf migration (Aborn and Moore 1997). Several factors undoubtedly contributed to observed variability, including the migrant's nutritional condition. Among the 24 Summer Tanagers tracked during spring migrations 1992 through 1994, 15 birds were classified as "fat" (body mass $\geq 15\%$ above fat-free mass) and nine birds were "lean" ($< 15\%$ above fat-free mass). Fat-free body mass equals 24.7 g for Summer Tanagers (Odum 1993). If we assume that the difference in body mass is fat and translate that difference into migratory flight range estimates (Pennycuick 1992), birds classified "fat" could fly on average 513 km flight distance, whereas lean birds could fly only 162 km.

Lean tanagers moved a longer linear distance, covered greater total distance, and moved at a faster rate than did fatter birds (Table 1; Fig. 1a,b). Fat tanagers were often perched for periods of an hour or more, whereas lean tanagers were rarely perched for extended periods (Table 1). Although the ratio of linear-to-total distance (meander ratio), which reflects the degree to which birds circumscribe their movements, did not differ between lean (ratio = 4.5) and fat (ratio = 5.0) birds, other measurements indicate that fat birds confined their movement to a smaller area than lean birds (Fig. 1c,d). Fat birds showed greater angular dispersion ($r = 0.248$) than lean birds ($r = 0.477$), which suggests that they did not concentrate their movements in a particular direction. Likewise, fat birds displayed a stronger turn bias (11.2) than lean birds (6.4), which is indicative of circling movement.

Habitat use also differed between the two groups (Fig. 2). Fat birds were located in pine forest twice as often as lean birds, whereas three-fourths of the radio locations for lean birds were in scrub/shrub habitat. Not only did habitat use differ between the two groups, but the tanagers used habitats out of proportion to habitat availability in different ways (Fig. 3), which suggests that they were actively selecting different habitats.

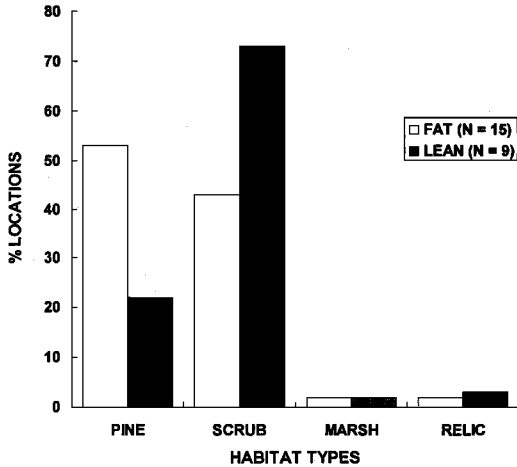


FIGURE 2. Habitat use by fat and lean Summer Tanagers radio-tracked on Horn Island, Mississippi, following migration across the Gulf of Mexico.

What might account for the observed differences between fat and lean birds? Replenishment of depleted fat stores is probably a higher priority for lean than fat tanagers (see Loria and Moore 1990), and scrub/shrub habitat appears to be the most suitable place for doing so (F. R. Moore, unpubl. data). Previous work on Horn Island (Moore et al. 1990) showed a high degree of selectivity for scrub habitat by most migrants, despite its low availability, and many migrants that stop over on Horn Island have catabolized much of their fat stores while flying across the Gulf of Mexico.

In contrast, conservation of remaining fat stores and avoidance of predation are probably priorities for fat tanagers, which would explain less movement and a preference for pine forest. Observations of migrant landbird behavior in the presence of raptors suggest that pine habitat may offer greater concealment (D. A. Aborn and F. R. Moore, pers. obs.).

We would not be surprised if tanagers used different cues to assess habitat depending on their nutritional condition. Moreover, the value of information about habitat gained during stop-over probably varies with the birds' internal state such that lean birds may be more likely to pay costs associated with acquiring habitat information.

CONSTRAINTS ON *EN ROUTE* HABITAT SELECTION

Upon arriving at a stopover site, a migrant is faced with a mosaic of unfamiliar habitats. When animals find themselves in such settings, we would expect them to familiarize themselves with the kinds, distribution, and abundance of

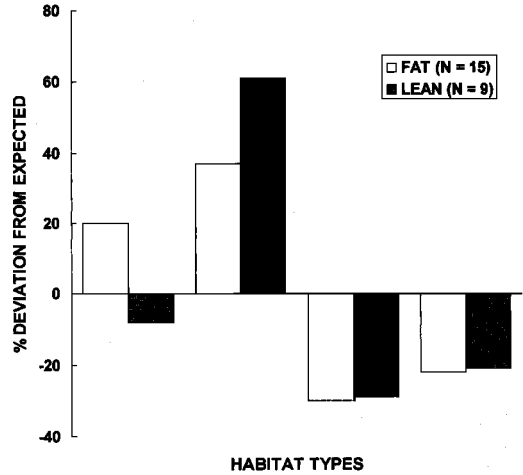


FIGURE 3. Deviation from expected use of habitat by fat and lean Summer Tanagers radio-tracked on Horn Island, Mississippi, following migration across the Gulf of Mexico. Expected habitat used is based on availability of habitat on the island.

available resources and places safe from predators, to exploit resources efficiently, and to replenish energy stores quickly (cf. Orians and Wittenberger 1991; see Hutto 1985b). Yet, time available for searching is an important component of any habitat selection process (Ward 1987), and migrants are probably time-constrained during passage (*sensu* Alerstam and Lindström 1990). The time constraints imposed on a migrating bird probably intensify the conflict between the value of information gained through exploration and pressure to minimize time spend *en route*.

How might the constraint of time affect the process of habitat selection? The threshold for acceptance of habitat during migration depends on the migrant's time program (*sensu* Berthold 1990; Gwinner 1986) and internal state (e.g., fat stores), which may be modified by external factors (e.g., competitors, weather). It may be that observed distributions of migrants among habitats reflect a lowered threshold of acceptance or errors in habitat assessment. When time for habitat assessment is brief, we expect migrants to obtain information on the quality of different habitats using cues that are virtually instantly assessable. We also expect migrants to use simple proximate cues for habitat choice, because a simple cue is more likely to occur in a variety of habitats (cf. Morton 1990). Moreover, we would expect migrants to be selective at first, but as time passes, to select less suitable habitats (Ward 1987), which means that the threshold for acceptance decreases over time.

Whereas evidence leads us to expect more exploration as circumstances become less familiar (Bell 1991), not to mention more exploration as the area becomes less suitable, time-constrained migrants may not have the time nor the energy for extensive search, especially if the area is of poor quality. Rapid exploration that yields incomplete information about the distribution of resources and sources of stress would not be surprising during stopover. The few studies that have examined the distributions of captured migrants among different habitats during stopover (Bairlein 1983, Moore et al. 1990, Winker 1995) suggest that exploration prior to settlement takes place quickly, probably within an hour of arrival, if at all. It may simply be best for birds that can not gain access to suitable habitats or experience difficulty distinguishing habitats, to continue migration (Rappole and Warner 1976, Terrill 1988).

Searching efficiency is an important component of the habitat selection process, which leads us to expect age and migratory experience to influence *en route* habitat selection. Distribution of migrants among habitats in the Alps (Bruderer and Jenni 1988) and along riparian corridors of the Rio Grande River (Yong et al. 1998) suggests that juveniles are more likely to land in unfavorable habitats than adults. Bairlein (1983) attributed age-specific differences in habitat use among European migrants to inaccuracies in habitat preference in young birds. *En route* "problems" are undoubtedly magnified for hatching-year birds on their first migration (Ralph 1978, Alerstam 1978, Gauthreaux 1982a, DeSante 1983, Moore 1984, Lindström and Alerstam 1986, Terrill 1988, Woodrey and Moore 1997, Woodrey *this volume*), and individuals with different levels of migratory experience can be expected to respond differently to the exigencies of migration. Hatching-year birds may be more likely to land in unfavorable habitats than adults and once landed, they may lack the experience to efficiently search an area. Hatching-

year migrants are also often behaviorally subordinate to adults (Terrill 1988), which could affect their reaction to other migrants *vis-a-vis* habitat assessment. In addition, experience is likely to effect assessment of habitat in relation to conflicting demands between energetics and other environmental factors (Yong et al. 1998). Choice of feeding location *vis-a-vis* predation risk and energetic requirements, for example, may be age-dependent (Cresswell 1994).

Mechanisms of habitat selection may also vary with the migrant's sex to the extent that habitat use is sex-specific during passage (e.g., Yong et al. 1998). Outside of the migratory period, males and females may settle in different habitats (cf. Lynch et al. 1985, Parrish and Sherry 1994) or use the same habitat differently (Morse 1989), and Morton (1990) found that male and female Hooded Warblers (*Wilsonia citrina*) use different structural cues to chose winter habitat. Laboratory experiments designed to study habitat segregation between sexes in Hooded Warblers found sex-specific preferences tied to vegetation structure consistent with differential habitat use on the wintering grounds (Morton 1990; see also Ornat and Greenberg 1990). That females and males might use different habitats or the same habitat differently warrants attention. For example, nutritional demands in relation to breeding performance differ between sexes. If efforts to satisfy differential demands take place during passage, sex-specific use of habitat may occur. Furthermore, if social dominance (Carpenter et al. 1993a,b; Parrish and Sherry 1994, Marra et al. 1993) manifests itself during passage, females may occupy different habitats by virtue of their status.

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