Seasonal Bird Traffic Between Grand Teton National Park and Western Mexico[1]

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Abstract

This paper presents data on variations in the breeding densities of birds in Grand Teton National Park, Wyoming, and evaluates these variations among years, habitats, and as functions of the migratory status of the breeding birds. Breeding opportunities certainly vary with the extremely variable weather conditions in the park year-to-year, and part of the variation in breeding density must be attributable to unpredictable on-site resources. A minority of the breeding birds is resident, but many species are long-distance migrants, and others make more limited winter movements of various distances. Most but not all of the migrants overwinter in habitats that are very dissimilar to those in which they breed. In some migrants the habitat range appears greater in wintering than in breeding habitats, and in others not. Some migrants winter syntopically with close relatives and others occupy winter habitats that lack resident relatives. I bring some perspective to these variations using winter and early spring observations of the same species (though not necessarily members of the same Teton populations) in western Mexico. In some instances in which Mexican wintering habitat similar to northern breeding habitat is available, wintering birds may be relegated to different habitats because of prior occupancy by resident species, often related species such as congenerics or even conspecifics.

Overwintering habitats are almost certainly at least as variable in survival opportunities as are the breeding habitats for reproduction. They also vary year-to-year in weather conditions that affect food supplies, and are co-occupied by resident species, some of which are close relatives to the winter visitors and have similar ecologies. The vagaries of overwinter survivorship and the transitions of the birds between breeding and wintering grounds constitute a broad and poorly understood category of off-site factors for conservationists and resource managers whose chief source of information is the breeding populations. A much closer integration of research on breeding and wintering populations will be required before useful conservation strategies for migrant bird populations can be devised. This integration, through organizations like Partners in Flight, must become a research priority in the future.

Introduction

Resource managers in parks and reserves at northern latitudes are faced with the daunting task of conserving populations of migratory birds that are within their jurisdictions only part of the year. The status of the breeding birds may be evaluated through monitoring programs, which can assess relative abundance or density of breeding birds as functions of habitat on-site, document changes in breeding abundance or density between years, and detect trends in relative abundance or breeding density over the longer term. However, interpreting changes in breeding density is difficult at best, as usually both off-site and on-site factors will be involved.

A brief evaluation of these factors illustrates the difficulties and the unknowns. At the breeding site, recent weather conditions may affect breeding densities in the current year. For example, precipitation from winter through spring as well as spring temperatures both affect different breeding resources in different ways, generally both species- and habitat-specific. Breeding densities also may be a function of recruitment and breeding success in the previous year, and therefore of the on-site conditions during earlier periods. The overwinter survival of resident birds may vary according to winter conditions on site, whereas the survival of migrants in the off-season depends on wintering conditions elsewhere. For breeding birds at middle latitudes in the United States, wintering sites are distributed as far south as northern South America, and encompass a wide range of non-breeding habitats. Wintering conditions for the migrants, and thence their over-winter survival, are likely to vary in species-, habitat-, and latitude-specific ways. The vagaries of the migration itself, the cues, timing, stopover resources, and so forth, comprise additional variables affecting a safe passage. And further, habitat perceived as offering good breeding opportunities to spring migrants might

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intercept birds that would otherwise continue north to breed in or near their natal habitats. Thus the range of factors contributing variation to breeding densities is indeed diverse.

Consideration of the broader aspects of nearctic-neotropical bird populations not only helps to identify gaps in our present knowledge, but also highlights a potential to gain a better understanding of the larger system through wider geographical and cooperative studies. While there are formidable challenges inherent in such studies, there are also causes for optimism. The large and enthusiastic attendance at this Partners in Flight conference attests to the broad perception that the challenges are appealing and perhaps tractable, and an extensive literature includes many excellent overviews of migration systems and confirms the widespread interest (e.g. Keast and Morton 1980, Berthold, 1988, Hagan and Johnson 1992, Finch and Stangel 1993, DeGraaf and Rappole 1995, Martin and Finch 1995, Rappole 1995, Marzluff and Sallabanks 1998, Bauer 2001, Faaborg 2003). The new technique of stable isotopes (Kelly et al. 2002, Rubenstein et al. 2002) promises to yield a more rapid understanding of some aspects of migration patterns than banding studies have produced, and interest in the "stopover ecology" of migrant birds is expanding (e.g. Hutto 1998, Wang et al. 1998, Warnock and Bishop 1998).

This paper makes no attempt to review or synthesize the growing literature, but presents a personal view of migrants that breed in Wyoming and winter south as far as northern South America. The data are generally sketchy, often incomplete, and obviously constrained in time and space; their use is intended to be more illustrative of themes and potential research avenues than supportive of specific facts or theories, and note that truly definitive data are elusive even in the best of cases. I discuss results of monitoring summer bird populations in Grand Teton National Park, Wyoming, and patterns of year-to-year variation in breeding densities measured at fixed and mapped sites. I then take a long stride to where and how these same birds may spend the non-breeding season in western Mexico, where they are often found in contrasting habitats and with different constellations of coexisting species. The northern and southern endpoints are those for which I have some familiarity, but presumably my data could be paralleled broadly by those of many other ornithologists, each with personal favorite summering and wintering birding locales.

Breeding Birds in Jackson Hole, Wyoming

Climate, Weather, and Habitats

Grand Teton National Park (GTNP) encompasses the larger part of Jackson Hole, a north-south rift valley between 1800-2000m elevation at around 44° N latitude, 111° W longitude, and flanked on the west by the Teton Range (elevation <2000 to >4000 m). The landscape is spectacular (Love and Reed 1968, Knight 1994), and supports a wide range of habitats from Great Basin sagebrush (*Artemisia* spp.) desert on the valley floor through wetlands and marshy willow (*Salix* spp.) scrub to broad-leafed woodlands (cottonwoods, aspen-*Populus* spp.), coniferous forest, and alpine tundra. In the mid-1990's, the National Park Service supported a proposal to instigate a series of breeding bird monitoring sites that span the complete habitat range, some 30 sites in all. At these sites, standardized census protocols yield breeding bird densities spot-mapped in sites mostly around 6 ha in size (Cody 1996, 1999; Cody and Cain 1997). The monitoring sites differ from one another in vegetation structure, as illustrated in *Figure 1*, though clearly this quantification of habitat provides at least a crude indication of the resources available to breeding birds. At several sites we now have around a decade of continuous coverage, but two have a more extended coverage, and were first censused in the 1960's (Cody 1974). In all, around 150 bird species breed or have bred at the monitoring sites.

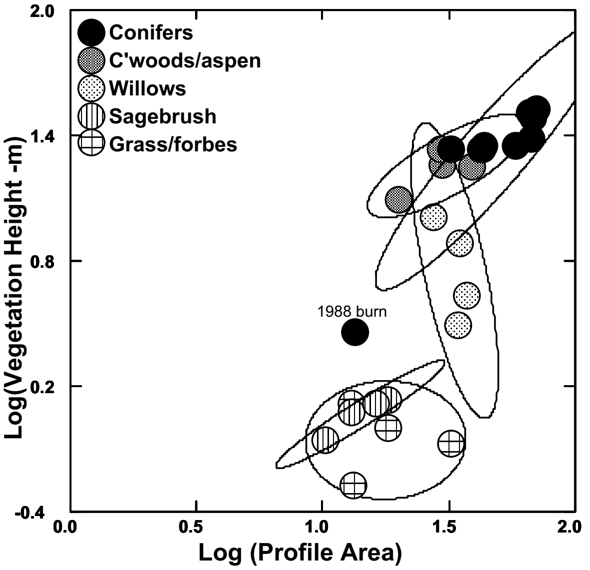

Figure 1—Monitoring sites for breeding bird densities in Grand Teton National Park, Wyoming, classified by vegetation structure. The ordinate reflects vegetation height, the abscissa the total amount of vegetation under the foliage profile, or total vegetation density. Waterfowl, aerial foragers, and tundra survey sites are not represented on the graph.

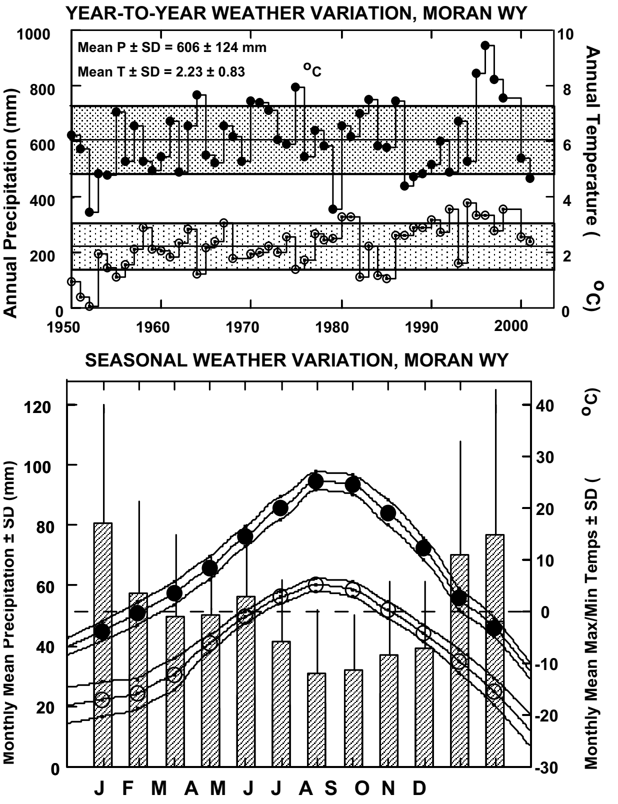

Figure 2—Year-to year (upper) and seasonal (lower) weather variations at Moran, Grand Teton National Park, Wyoming, over a 50-year period. Note both the inter-year variation and the extreme seasonality of the site. Upper graph: solid symbols, precipitation; open symbols, temperature; stippled regions: ±1SD of the mean. Lower graph: hatched histogram, monthly precipitation; solid symbols, mean maximum monthly temperature; open symbols, mean minimum monthly temperature; each with ±1SD as indicated.

The climate in Jackson Hole is typical of its mid-continental location and higher elevation (*fig. 2*). There is considerable year-to-year variation (*fig. 2*, *upper*), with around one-third of the annual temperature and precipitation means lying beyond the 50-year standard deviation band. There is no strong ENSO ("El Niño") signal in the climate here; the four ENSO winters of the 1990's that brought average winter rainfalls of 1330 mm to Topanga, in southern California (3.3 times the non-ENSO average), are barely detectable in GTNP, where ENSO winters are about 10 percent drier and 2° C warmer. The last 50 years also show a significant warming trend in mean temperature maxima of spring and summer months. Season temperature variations are extreme (*fig. 2*, *lower*), and the lowest precipitation occurs in the warmest months. Note that mean monthly temperature maxima are below 0° C for three winter months, and that mean monthly temperature minima are likewise above zero for three summer months only. The severe climate makes GTNP habitats particularly conducive to seasonal use by birds, and the great majority are migratory species. Further, returning migrant species face considerable uncertainty in local conditions, in terms of both the timing of the turn of the seasons and the absolute temperature and precipitation values they encounter.

Variations in Breeding Bird Densities

In most years passerine birds are established on-site in GTNP and breeding is underway by late May or early June, and breeding densities are high in many habitats (see e.g. Johnsgard 1986 for general distributional information). Some species are rather cosmopolitan in habitat use, as exemplified by Chipping Sparrow (*Spizella passerina*). This species winters chiefly in Sonoran Desert habitats of SW North America. It breeds in most of the GTNP monitoring sites (*fig. 3*, *upper left*; densities averaged over years), with a preference for drier habitats open at ground levels, and peaking in density in lodgepole pine (*Pinus contorta*) forest. Breeding densities, averaged over habitat, vary among years as well (*fig. 3*, *upper right*). Density variations are synchronized over years among some habitats, yet differ among others; a strong correspondence exists in density variation between some paired sites, but less correspondence between others (*fig. 3, lower*). Both on-site and off-site variation apparently contribute to these patterns.

About 17 passerine species breed each year at GTNP in a Wet Willows habitat (site #10). Variation in breeding density for four species of emberizine sparrows and five species of paruline warblers, over a discontinuous 35-year period, suggest that both on-site and off-site factors influence density in any given year (*fig. 4*). Inter-year variations in precipitation on-site are further influenced by beaver (*Castor canadensis*) activities, which raise or lower the water table. Wetter conditions (requiring hip-wader work) tend to favor species such as Virginia Rail (*Rallus limicola*), Marsh Wren (*Cistothorus palustris*), Northern Waterthrush (*Seiurus noveboracensis*), and Song Sparrow (*Melospiza melodia*), and disfavor species that are ground-foragers in drier sites such as Swainson's Thrush (*Catharus ustulatus*), White-crowned Sparrow (*Zonotrichia leucophrys*) and Fox Sparrow (*Passerella iliaca*). But the importance of off-site factors is suggested by the precipitous decline of Wilson's Warbler (*Wilsonia pusilla*) between 1991 and 1992 and its steady recovery since then, in apparent independence of factors operating at or within the site. This bird utilizes insect resources similar to those used by Yellow Warbler (*Dendroica petechia*) and Common Yellowthroat (*Geothlypis trichas*), though it forages higher in the vegetation (Cody 1999). Both of these latter species increased in density between 1991

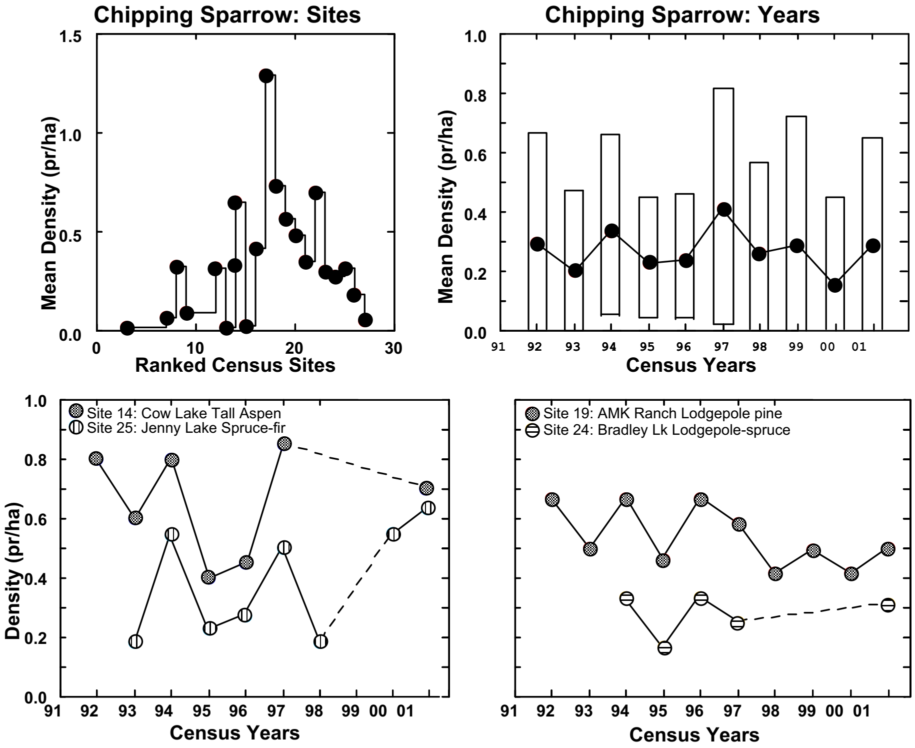

Figure 3—Variation in breeding density of Chipping Sparrow in Grand Teton National Park. Breeding densities vary over habitat (upper left) and among years (upper right; n.b. years 1999-2001 are averaged over a slightly reduced subset of monitoring sites). Variation in density is shown at four monitoring sites in the two lower parts of the figure.

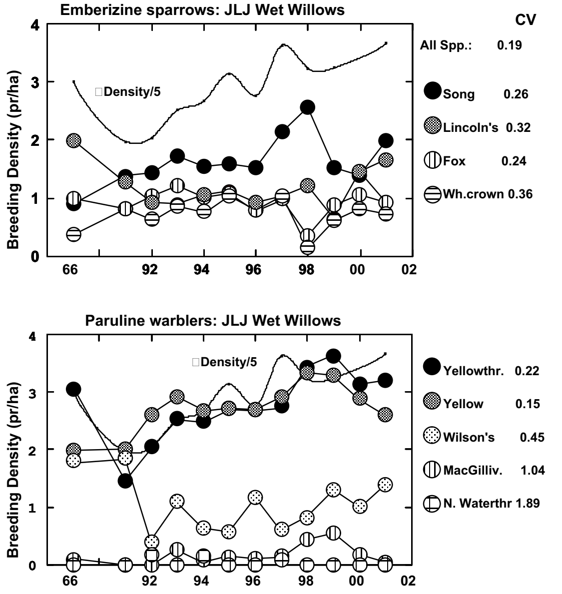

Figure 4—Variations in breeding densities of emberizine sparrows (above) and paruline warblers (below) at a Wet Willows monitoring site. Note the discontinuity between 1966 and later censuses. Total breeding bird density at the site is represented by the smoothed curve, with total density values divided by 5 to utilize to the same scale on the ordinate. The coefficient of variation (CV) is shown at the right; uppermost CV value is that for the total breeding density (all species) at the site.

and 1992, as did the overall breeding bird density at the site. Given the similarity of diet and foraging ecology between Wilson's Warbler and these other two warbler species that maintained steady or increasing populations at the census site, off-site factors seem the more reasonable cause of its breeding density variations.

Of the Wet Willows birds discussed, only Song Sparrow remains to winter locally. However, in a Lodgepole Pine forest (site #19), which harbors an average of 22 breeding passerine species, about half of the breeding community is resident or winters locally. Density variations in several resident species and migrant foliage insectivores and thrushes in the lodgepole forest also suggest the operation of both on-site and off-site factors (*fig. 5*). The resident species (*fig. 5, upper*) vary in density over the years in a notably synchronous way, presumably density variations result from variations in on-site factors to which all three residents respond in a similar fashion. The same is not true for the migrants (*fig. 5, lower two graphs*), in which density variations are generally unsynchronized over years. The Yellow-rumped Warbler (*Dendroica coronata*) winters farther north than nearly all other warblers, and no obvious on-site effects account for its striking peak in breeding density in 1999. However, this species was at 63 percent higher densities in 1999 at two other GTNP monitoring sites relative to densities in 1998 and 2000, which suggests that the cause was not extremely localized. Note also that the two congeneric thrushes, Swainson's Thrush and Hermit Thrush (*C. guttatus*), tend to vary in density among years in the opposite way (Spearman r = -0.35). This observation has at least three interpretations: density varies due to on-site competition for Catharus resources, varies with on-site factors that affect the two species in opposite ways, or varies with factors on their respective wintering grounds that happen to be negatively correlated.

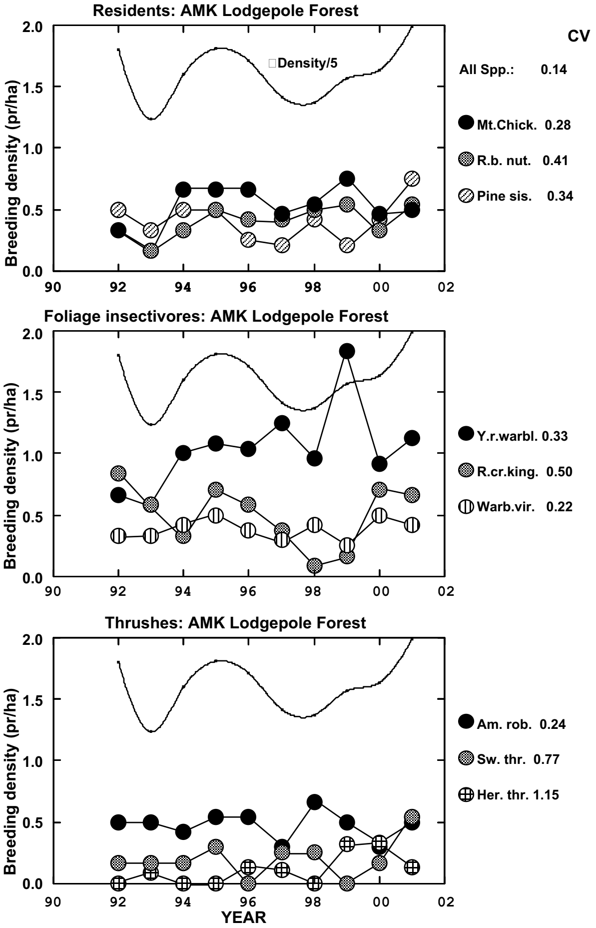

Figure 5—Variation in breeding densities of species in a Lodgepole Pine monitoring site in Grand Teton National Park. Abbreviations denote Mountain Chickadee (*Parus gambeli*), Red-breasted Nuthatch (*Sitta canadensis*), Pine Siskin (*Carduelis pinus*), Ruby-crowned Kinglet (*Regulus calendula*) and Warbling Vireo (*Vireo gilvus*). See caption for *fig. 4*, and text for discussion.

Variations in Wintering Areas for GTNP Breeding Birds

Most of the bird species that are found together in summer breeding habitats in GTNP are widely dispersed over southerly latitudes in the winter, and overwinter in a wide range of habitats, from desert to rainforest. Such information comes from limited personal observations in Mexico and Nicaragua, and from general sources (e.g. field guides) and the published literature for wintering birds in other Central American and South American areas. An indication of this variety of wintering strategies within taxonomic groups is shown for thrushes, sparrows, and warblers (*fig. 6*). Each of these three broad taxa has one or two species that winter in or close to GTNP, but the remainder are spread far and wide. Note, however, that the thick-billed sparrows, which make use of seeds rather than fruit or insects in winter habitats, have more northerly winter distributions in general. Two patterns are especially noteworthy in the figure. First, within each broad taxon the latitudinal range of a given species is much narrower than the range of the whole species group, and second, characteristic wintering habitats are very different among species, even though they may, and often do, breed together in the same GTNP sites. Differences among closely related species are particularly conspicuous, as among the *Catharus* thrushes, the grassland and scrub sparrows, and the *Dendroica* warblers. Thus, species that breed together in GTNP habitats, such as Wet Willows or Lodgepole Pine, winter over a wide range of latitudes in a diverse array of habitat types. Presumably, their relative overwintering success is determined correspondingly by a wide range of factors that are largely independent of each other.

Is it the case that species undertaking longer migrations and wintering further south show greater variation in breeding densities in GTNP? If greater uncertainty in overwinter survival and thence spring breeding density were attendant on longer migrations, such a relation might be expected. *Figures 4* and *5* include the coefficient of variation (CV) of each species depicted, and in *Figure 7* these CV values are plotted against categories reflecting the varying extent of the winter migrations, from on-site (residents) at one extreme to species that reach South America at the other. Though the relation is not statistically significant and the data are limited, there is the suggestion that the lowest CV's of breeding density, rather than the highest, are associated with the long distance migrants. Certainly there is no support for the hypothesis that resident bird populations remain more stable in density over the years, though that might seem the more likely or expected relationship. I believe a more logical argument is that there should be no overall difference in surviving winter as a resident or as a long-distance migrant. Selection surely has modified overwintering strategies such that survival in the non-breeding season is maximized, and must operate within species via cost-benefit trade-offs in the contest for off-season resources that will not result in gross survivorship inequities among species. I suggest that, amongst a plethora of viable overwintering strategies, major variations in survival are not expected, and not likely to correspond systematically to one or another particular strategy. Thus, *a posteriori*, it is expected that breeding CV's will not

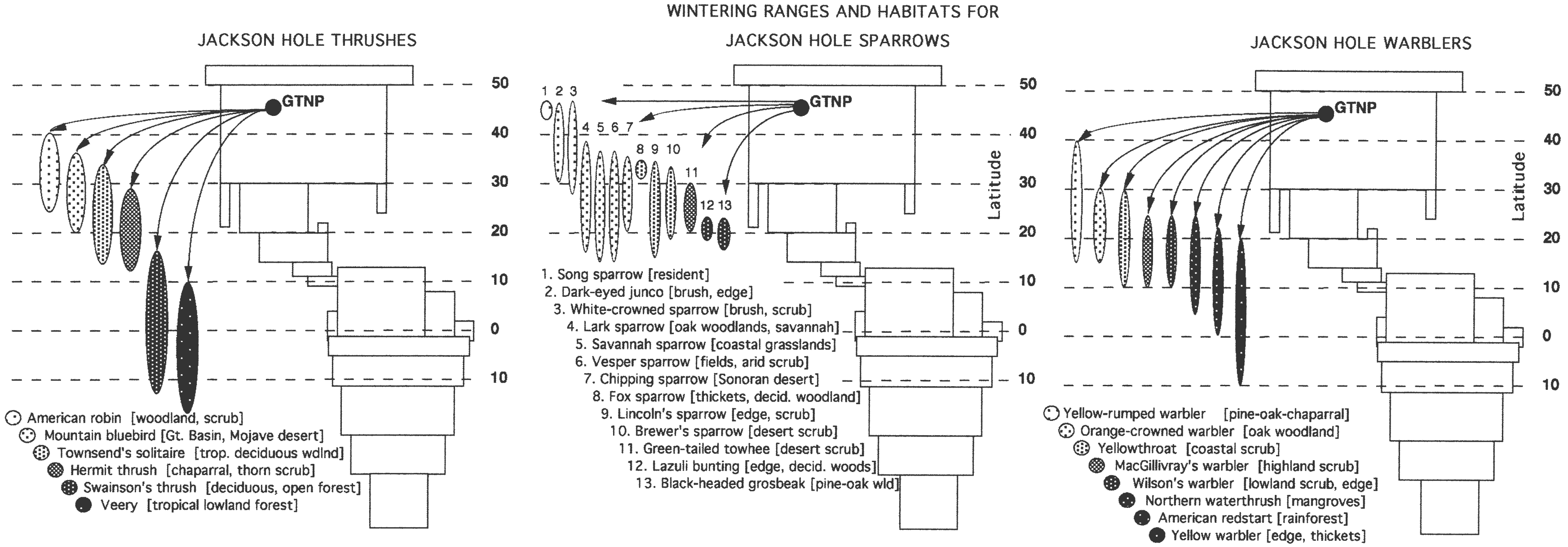

Figure 6—The range of approximate latitudes and of habitats used by wintering birds that breed in Grand Teton National Park, Wyoming. The figures display the wide variation in overwintering strategies found in these birds, which include residents to local, short- and long-distance migrants, and the use of winter habitats from desert to rainforest. Scientific names are given in the text, except for Veery (*Catharus fuscescens*), Dark-eyed Junco (*Junco hyemalis*), Savannah Sparrow (*Passerculus sandwichensis*), Vesper Sparrow (*Pooecetes gramineus*), Lazuli Bunting (*Passerina amoena*), and Black-headed Grosbeak (*Pheuticus melanocephalus*).

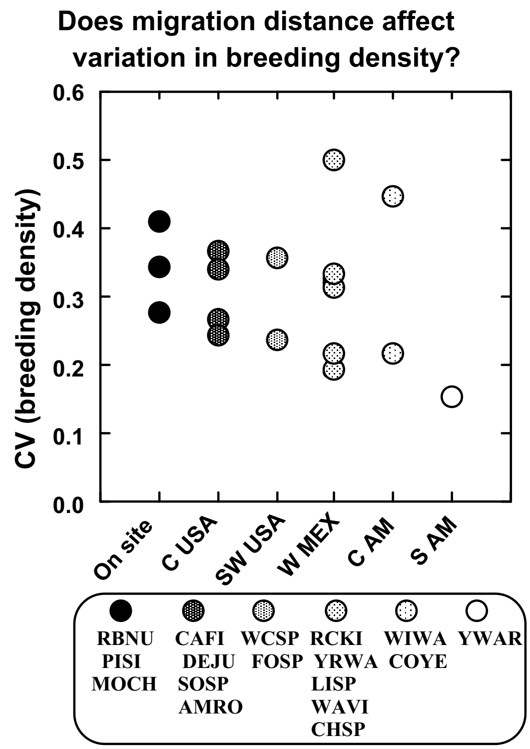

Figure 7—Coefficient of variation (CV) is plotted as a dependent variable with categories of distance to wintering sites on the abscissa. The species are those represented in Figs. 4 and 5, denoted by AOU codes, below. The relation is not statistically significant, but suggests, contrary to intuition, that long-distance migrants are not more variable in breeding density than are resident birds.

vary with migration distance or overwintering habitats, although it certainly is conceivable that overwintering strategies that entail more risk and cost might be offset by greater production in the breeding season.

Wintering Birds in Western Mexico

Winter Bird Habitats in West Mexico

Leapfrog migrations, in which the more polewards breeding populations overfly populations breeding to their south and winter at the lowest latitudes, are probably routine. Supportive data come from several sources: from species with well-defined (recognizable) subspecies (e.g. Fox Sparrow, Bell 1998), from banding studies (e.g. on Gray Catbird [*Dumatella carolinensis*], Cody 2003), and from recent stable isotope studies (e.g. Kelly et al. 2002 for Wilson's Warbler). Thus, it seems reasonable to conclude that species at mid-latitude sites in their breeding ranges will winter at mid-latitude sites in their winter ranges. I use this to justify associating species of breeding birds in GTNP with wintering populations in West Mexico, although the precise wintering grounds of the GTNP populations are not known (but this ignorance is not really critical to the points I wish to make). It is to be expected, given the recent enhancement of both interest and technology (*op. cit.*), that over the next decade or so the wintering areas of specific northerly breeding populations eventually will become known with much greater precision.

Over a long series of late winter and early spring visits to sites in western Mexico, I have seen many of the GTNP breeding bird species, recorded their winter habitats, and noted the species with which they are associated. Some of my observations undoubtedly refer to migrant birds in transit, but the habitat preferences of birds in transit, relative to those of breeding or resident birds, are relevant too. Far more comprehensive studies of wintering birds in this region have been conducted, e.g. by Hutto (1992); my observations, while anecdotal, are hopefully representative of the wintering ecology of GTNP breeders.

A view of the structural characteristics of the West Mexican habitats and their geographic locations is given in *Figure 8* (which includes a few sites in SE Arizona). The lower desert and thorn scrub habitats are much more open and sparsely vegetated than are the breeding habitats in the Tetons, but there is some concordance between tropical deciduous woodland and aspen/cottonwoods, and between the higher elevation Mexican pine forests and structurally similar GTNP conifers.

Emberizine Sparrows

Many emberizid sparrows breeding at northern latitudes winter no farther south than the Sonoran Desert and its scrubby fringes. Emberizines wintering on islands in the Sea of Cortés may escape the competitive influences of relatives that are locally present year-round, as most islands have only Black-throated Sparrows (*Amphispiza bilineata*) as residents. Incidence functions (proportions of islands occupied over island size classes) for seven of the commoner species, all GTNP breeders, vary widely among species (*fig. 9*, upper; from Cody and Velarde 2002). Incidence is highest in the Green-tailed Towhee (*Pipilo chlorurus*); notably Brown Towhees (*P. fuscus*), which are common mainland residents, are absent from nearly all islands). The figure shows that congeneric Chipping and Brewer's Sparrows (*Spizella passerina* and *S. breweri*), both common Tetons breeding birds, have very different island incidences. Wintering birds appear to use the islands in an "ideal free" fashion, in that they occur in higher species numbers on larger islands and in constant proportion to the number of island residents (same slope of Species-Area curve; *fig. 9*, *lower*).

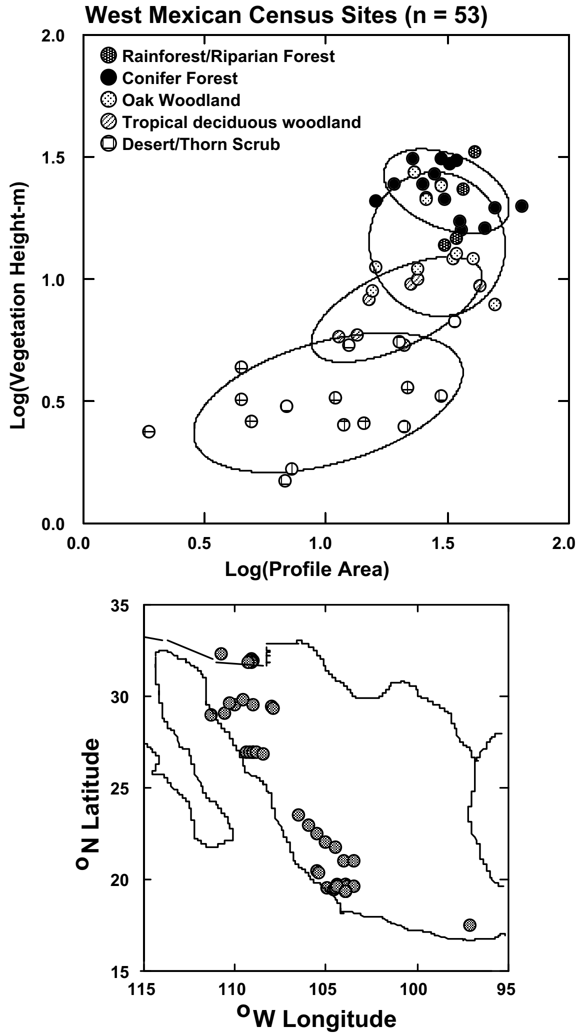

Figure 8—Locations of sites in West Mexico where observations on overwintering species that breed in Grand Teton National Park have been accumulated. Sites are depicted by vegetation structure and grouped into habitat categories (above; cf. *fig. 1*), and set by geographic location (below).

Some GTNP breeding species also breed in western Mexico. Chipping Sparrow breeds in pine-oak and pine woodlands in the Sierra Madre Occidental, in habitats that are the closest structural equivalents of its GTNP breeding habitats (*fig. 10*, *upper right);* no wintering Chipping Sparrows were encountered on the West Mexican transects. Lincoln's Sparrow (*Melospiza lincolnii*) and Brewer's Sparrow are common breeding species in GTNP, and Lark Sparrow (*Chondestes grammacus*) is an uncommon breeding species there. These three sparrows winter in western Mexico, but only Lincoln's Sparrow winters in habitats similar in structure to some of those in GTNP in which it breeds (*fig. 10, lower left*). The other two species are found in winter in low thorn scrub and desert habitats that are much different from their breeding grounds. Note that "similarities" in vegetation structure are assessed with respect to vegetation height and density only; there may well be other aspects of habitat that are more pertinent to certain, even many, bird species, than those summarized by the habitat variables that I measured. There are many breeding emberizines in western Mexico, besides the Chipping Sparrow of the woodlands and Black-throated Sparrow of the deserts already mentioned (*fig. 10*, *upper right*). The residents include species of the large genus *Aimophila*, some five species of which are shown in breeding habitats in *fig. 10* (*lower right*); these include Stripe-headed Sparrow (*A. ruficauda*), Rufous-crowned Sparrow (*A. ruficeps*), Rusty Sparrow (*A. rufescens*), Rufous-winged Sparrow (*A. carpalis*), and Black-chested Sparrow (*A. humeralis*). The presence of these breeding species might well influence the habitat options for wintering emberizines.

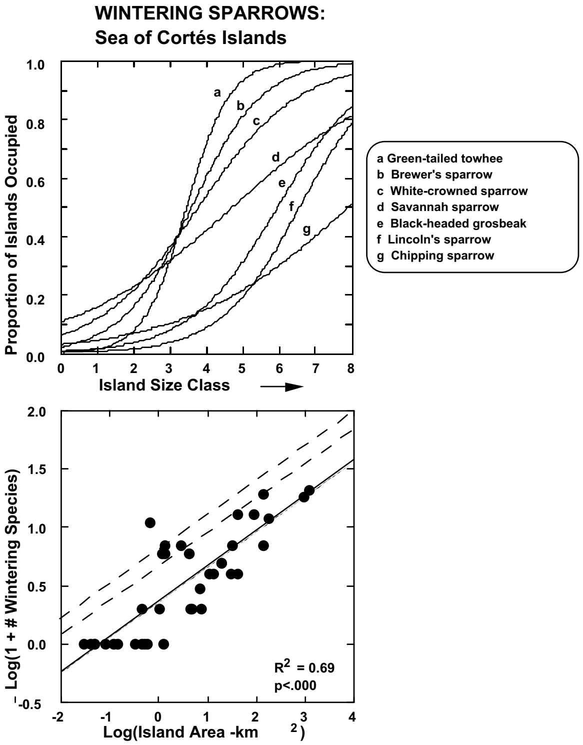

Figure 9—Many of the emberizine sparrows that breed in Grand Teton National Park winter in desert and near-desert habitats, and occur on islands in the Sea of Cortés. They differ in their incidences over island size (upper), but islands are occupied by numbers of wintering species in proportion to the numbers of resident species on the island, suggesting an "ideal free" distribution of the wintering birds. From Cody and Velarde, 2002.

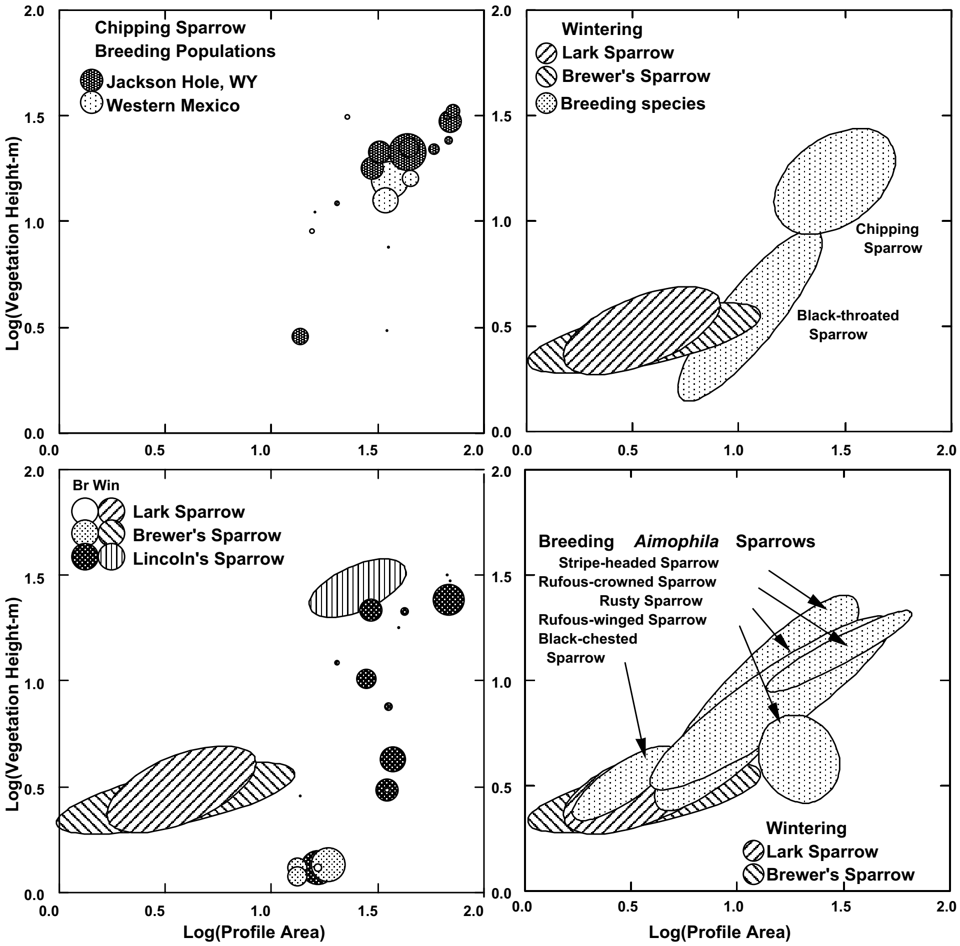

Figure 10—Chipping Sparrow breeds in similar habitats in GTNP and in western Mexico (upper left). Lark, Brewer's, and Lincoln's Sparrows winter in western Mexico, in habitats relatively dissimilar (first two species) or similar (last species) to their breeding habitats (lower left). The wintering sparrows encounter a wide range of resident species in western Mexico, the breeding ranges of which are shown (stippled, upper and lower right). Generally the wintering sparrows winter in lower and more open habitats than those used by the breeding birds.

Turdine Thrushes

Another common GTNP breeding species that, like the Chipping Sparrow, also breeds in western Mexico is American Robin (*Turdus migratorius*), where it is common in woodlands and forest in the upper Sierra. GTNP robins almost certainly winter within the U.S., many likely close to their GTNP breeding habitats, and thus they would not encounter their western Mexican conspecifics. Two GTNP breeding thrushes that do occur this far south are Hermit and Swainson's Thrushes, where they winter in pine- and pine-oak woodlands similar to their breeding habitats. The latter can be found at somewhat lower elevations in deciduous woodland, a difference that parallels the differences between the two species in GTNP where Hermit Thrush, but not Swainson's Thrush, is restricted to conifers. Here again there are resident breeding species, including two congenerics of the wintering birds, Russet and Orange-billed Nightingale- thrushes (*Catharus occidentalis* and *C. aurantiirostris*, respectively). These and other residents, including three *Turdus* species (White-throated Robin [*T. assimilis*], Rufous-backed Robin [*T. rufopalliatus*] along with American Robin), the Eastern Bluebird (*Sialia sialis*), Brown-backed Solitaire (*Myadestes obscurus*), and the Aztec Thrush (*Zoothera pinicola*), all breed in habitats similar to those in which the wintering thrushes occur (*fig. 11*, *right, upper and lower*). These local residents must constitute a survivorship challenge to the migrants in tough years. Note that migrant GTNP Mountain Bluebirds (*Sialia currucoides*) winter in open desert habitat, typically farther north in the Mojave, and migrant Townsend's Solitaires (*Myadestes townsendi*) are encountered chiefly in tropical deciduous woodland; both are too rare in my surveys to be shown in the figure. Both migrants therefore avoid their congenerics in the pine-oak and pine forests at higher elevations.

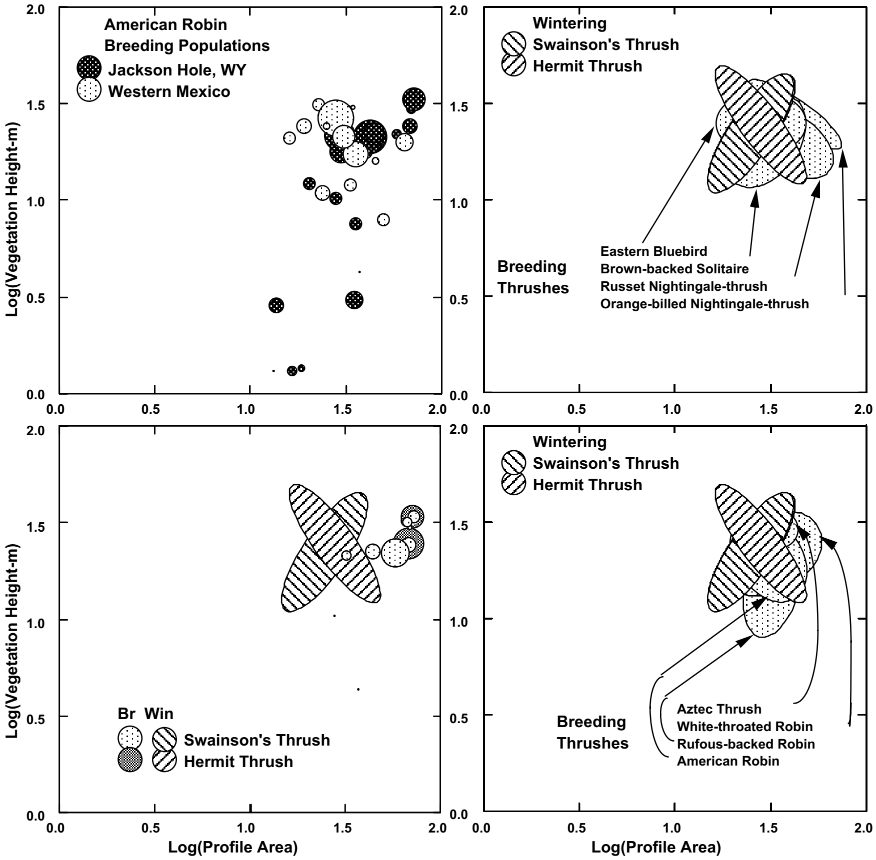

Figure 11—American Robin (upper left) breeds in similar habitats in western Mexico do Grand Teton National Park birds, which winter further north. Hermit and Swainson's Thrush winter in Mexican habitats most similar to their breeding habitats (lower left), even though these habitats support breeding and resident populations of numerous other thrushes, including two conspecific nightingale-thrushes (upper right) and others (lower right).

Paruline Warblers

Lastly I discuss the paruline warblers, which are common both as GTNP breeders and as wintering species in western Mexico. Two species, Yellow-rumped Warbler and MacGillivray's Warbler (*Oporornis tolmei*), winter in habitats relatively similar to their breeding habitats (*fig. 12*, *upper*), but in winter they occupy a much wider habitat range, being found in lower and more open vegetation. Two other species, Orange-crowned Warbler (*Vermivora celata*) and Wilson's Warbler, breed characteristically in tall willows and low aspens in GTNP (*fig. 12*, *lower*), but in winter, by contrast, are found in much taller vegetation, ranging from deciduous woodland to oaks and pine-oak.

The wintering warblers are faced with a diverse array of resident warblers in western Mexico, where my surveys recorded 11 species of migrants and 16 species of residents or locally breeding species (*Figure 13*). In *Dendroica* warblers (*fig. 13*, *upper left*), four migrant species (Yellow-rumped Warbler, Hermit Warbler [*D. occidentalis*], Townsend's Warbler [*D. townsendi*] and Black-throated Gray Warbler [*D. nigrescens*]) encounter resident Grace's Warbler (*D. graciae*) in the pines and pine-oak woodland. Note that the migrants are largely separated by geographic range in the breeding season (three are members of the same "superspecies"), and secondarily by habitat (with e.g. Black-throated Gray Warbler largely an oak woodland, rather than conifer, species in its breeding range). Thus they would seem to have the potential for far more congeneric competition in winter than they do at their breeding sites. In *Vermivora* warblers, three migrants and two breeding species occur over the Mexican habitats. The residents segregate by habitat, with Crescent-chested Warbler (*V. superciliosa*) typical of oak woods and Lucy's Warbler (*V. luciae*) breeding in tall thorn scrub and open deciduous woodland. The migrants tend to occur in more open habitats, with differences amongst them in habitat use that mirror the differences in their breeding habitats: Virginia's Warbler (*V. virginiae*) in lower scrubby habitats, Orange-crowned warbler (*V. celata*) in lower, more open, woodland and Nashville Warbler (*V. ruficapilla*) in taller, denser woodlands.

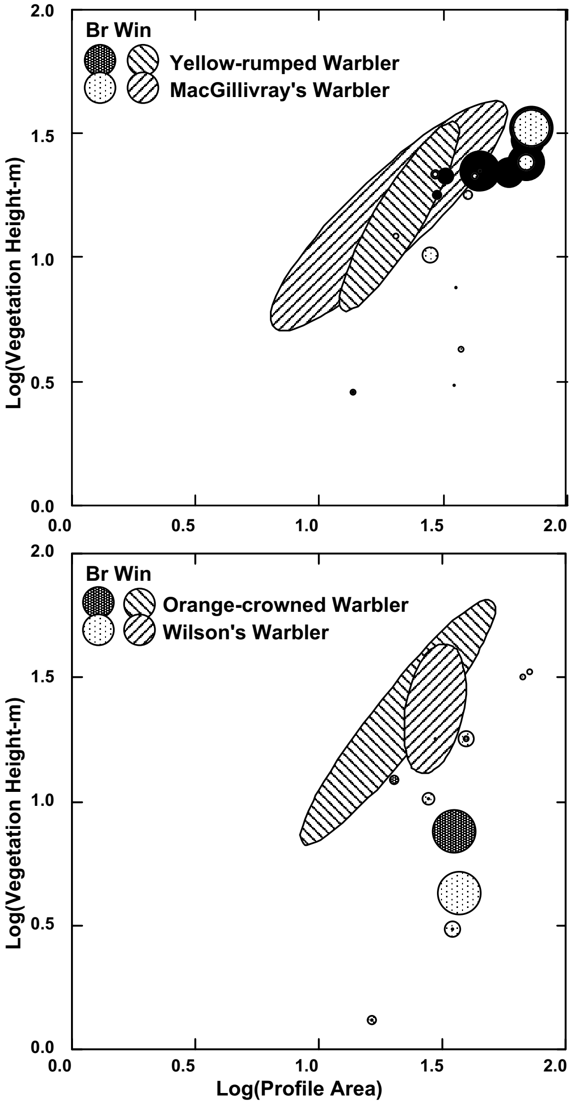

Figure 12—The winter habitats of common Grand Teton National Park breeding warblers in western Mexico may be similar (upper two species) or quite different (lower two species) from their breeding habitats.

Four other migrant species are depicted in the lower parts of *fig. 13*, where the habitat usage of additional breeding species is shown. The Central American endemic *Basileuterus* breed in the dense understory vegetation of the higher woodlands and forests; three species are represented here (Golden-crowned Warbler [*B. culicivorus*], Golden-browed Warbler [*B. belli*], and Rufous-capped Warbler [*B. rufifrons*]), in habitats co-occupied by wintering MacGillivray's and Wilson's Warblers. Of particular interest is the American Redstart (*Setophaga ruticilla*), which I found wintering exclusively in the coastal rainforest patches in western Mexico. Its closest ecological counterparts among the breeding birds are the *Myioborus* redstarts (a chiefly South American genus), Slate-throated (*M. miniatus*) and Painted (*M. pictus*). However, these residents are exclusively pine-oak and pine forest species, and have no contact with the wintering American Redstart.

Weather and West Mexican Winters

It is possible that variations in winter conditions in western Mexico are responsible for some of the variation in breeding bird densities of GTNP migrants. ENSO events, which have little impact on the Jackson Hole weather, apparently have decreasing effects to the south along the Pacific Ocean coast. However, it appears that western Mexico is unusually dry in these years; major cities from Sinaloa and La Paz (Baja California) south to Acapulco, with one exception in one year, recorded well below average rainfall in the winter months January-March of the ENSO years 1988, 1991, 1992, 1995, and 1998. Presumably drier winters in a generally arid region could impair the survival of wintering birds. Looking back at *Figure 3*, Chipping Sparrow breeding densities dipped in 1993, 1995, and 1998, all years immediately following ENSO winters. The Wilson's Warbler crash in the Wet Willows (*fig. 4*) followed two consecutive ENSO winters, 1991-92 and 1992-93. These associations suggest that variation in breeding densities may be dominated by phenomena occurring far from the breeding habitats.

Coda

The observations and figures discussed above present only a cursory overview of where migrants occur and which breeding or resident relatives they might encounter. It does not elucidate the many other ways in which migrants and residents may differ in their ecologies at tropical and subtropical latitudes (e.g. in foraging height, behavior, spatial disposition, sociality, diet, etc.), on which a good deal of information has been forthcoming in recent years. The emerging picture, supported by many of the references I have cited but still hazy, is that contrary to earlier views migrant birds fill rather precise ecological roles on their wintering grounds. These roles appear in some cases to be at least as circumscribed as those they fill on their breeding grounds. Some species are philopatric to the same wintering sites, some remain localized while others may be itinerant; some species integrate into mixed-species flocks, while others forage independently in edge, gap, or tree-top territories. Indeed, if breeding birds at high latitudes capitalize on seasonal flushes of temporarily abundant resources, there is a potential for even more fine-tuning of foraging ecologies, relative to resources and the constellation of consumers that vie for them, in wintering than in breeding grounds.

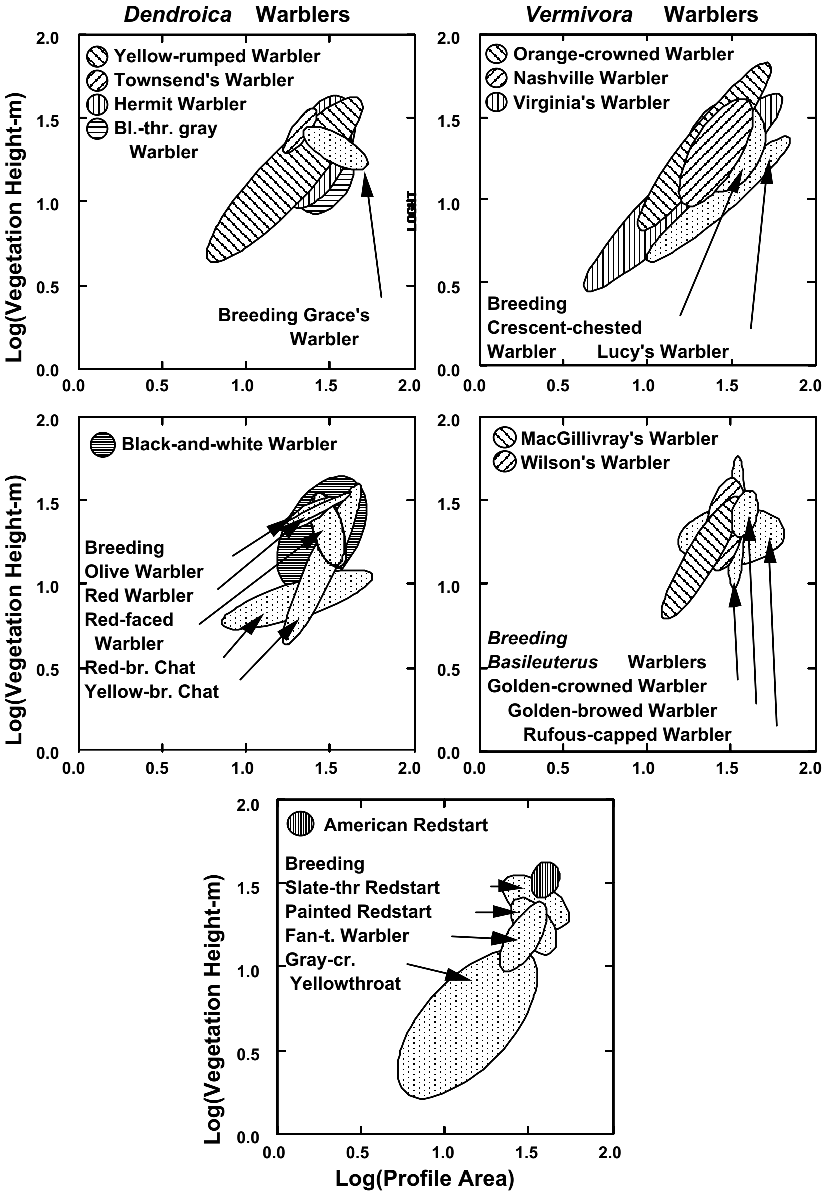

Figure 13—Wintering warblers in western Mexico encounter a wide range or breeding or resident species there. Migrant *Dendroica* warblers tend to occupy similar pine and pine-oak habitats as the resident Grace's Warbler (upper left), but migrant *Vermivora* warblers tend to occur in more open habitats than the two resident species (upper right). The winter habitat use of four other migrants are shown, including American Redstart (lower), which is marginal in Grand Teton National Park, and Black-and-White Warbler (*Mniotilta varia*), a species of eastern hardwood forests. Scientific names of species not mentioned in the text include Olive Warbler (*Peucedramus taeniatus*), Red Warbler (*Ergaticus ruber*), Red-faced Warbler (*Cardellina rubrifrons*), Fan-tailed Warbler (*Euthlypis lacrimosa*), Gray-crowned Yellowthroat (*Geothlypis poliocephala*), Red-breasted Chat (*Granatellus venustus*) and Yellow-breasted Chat (*Icteria virens*). See text for discussion.

Clearly our understanding of the details of migrant bird ecology is at best imperfect and the generation of a holistic perspective that incorporates both breeding and wintering aspects is not yet close at hand. Facile yet true, even the most accurate and comprehensive of monitoring efforts of breeding populations will be extremely limited in their explanatory power if the birds spend half the year elsewhere facing completely different challenges—more than half in the case of birds on the Neotropical wintering grounds! And even the "northern" half of the equation seems in jeopardy, with limited material input, and apparently limited interest, from governmental and regulatory agencies in precise, definitive, and coordinated monitoring programs. Technology is certainly a boon, but cannot begin to replace an essential commitment to competent, well-funded and -managed basic field research. It does not cost much to keep able and eager young researchers in the field watching birds, but we seem particularly slow in developing programs that harness this talent. Surely studies that closely integrate the ecologies of breeding with non-breeding populations will prove to be a tremendously attractive and rewarding arena for future research.

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Literature Cited

Bauer, H.-G. 2001. **Bird migration: A general survey**. Oxford, NY: Oxford University Press.

Bell, C. P. 1998. **Leap-frog migration in the Fox Sparrow: minimizing the cost of spring migration**. Condor 100: 470-478.

Berthold, P. 1988. **Bird migration**. Oxford, NY: Oxford University Press.

Cody, M. L. 1974. **Competition and the structure of bird communities.** Monographs in Populations Biology #7. Princeton, NJ: Princeton University Press; 318 p.

Cody, M. L. 1996. **Bird communities in the central Rocky Mountains** In: M. L. Cody and J. A. Smallwood, editors. Long-term Studies of Vertebrate Communities; 291-342. Orlando, FL: Academic Press.

Cody, M. L. 1999. **Assembly rules in plant and bird communities**. In: P. Keddy and E. Wieher, editors. Assembly Rules in Communities. New York: Cambridge University Press.

Cody, M. L. 2003. **The Mimidae.** In: J. del Hoyo and A. Elliot, editors. Birds of the World**.** Barcelona, Spain: Lynx Ediciones.

Cody, M. L. and S. Cain. 1997. **Monitoring breeding bird populations in Grand Teton National Park: 1995-1997**. Unpublished Report by the National Park Service, U. S. Department of the Interior.

Cody, M. L. and E. Velarde. 2002. **The birds. In a new biogeography of islands in the Sea of Cortés.** In: T. Case, M. L. Cody and E. Ezcurra, editors. Oxford, NY: Oxford University Press.

DeGraaf, R. M., and J. H. Rappole. 1995. **Neotropical migratory birds: Natural history, distribution, and population change.** Ithaca, NY: Cornell University Press.

Faaborg, J. R. 2003. **Saving migrant birds: Developing strategies for the future**. University of Texas Press, Austin, TX.

Finch, D. M. and P. W. Stangel, editors. 1993. **Status and management of neotropical migratory birds**. Gen. Tech. Rep. RM-229. Fort Collins, CO: Rocky Mountain Forest and Range Experimental Station, Forest Service, U. S. Department of Agriculture.

Hagen, J. M. and D. W. Johnson, editors. 1992. **Ecology and conservation of neotropical migrant birds**. Washington, DC: Smithsonian Institution Press.

Hutto, R. L. 1992. **Habitat distributions of migratory landbird species in western Mexico**. In: J. M. Hagen and D. W. Johnson, editors. Ecology and Conservation of Neotropical Migrant Birds. Washington, DC: Smithsonian Institution Press.

Hutto, R. L. 1998. **On the importance of stopover sites to migrating birds**. Auk 115: 823-825.

Johnsgard, P. A. 1986. **Birds of the Rocky Mountains**. Lincoln, NE: University of Nebraska Press.

Keast, A. and E. S. Morton. 1980. **Migrant birds in the Neotropics: Ecology, behavior, distribution and conservation**. Washington, DC: Smithsonian Institution Press.

Kelly, J. F., V. Atudorei, Z. D. Sharp, and D. M. Finch. 2002. **Insights into Wilson's Warbler migration from analyses of hydrogen stable-isotope ratios**. Oecologia 130: 216-221.

Knight, D.H. 1994. Mountains and Plains: **The Ecology of Wyoming landscapes**. New Haven, CT: Yale University Press; 372 p.

Love, J. D. and J. C. Reed Jr. 1968. **Creation of the Teton Landscape** Moose, WY:. Grand Teton Natural History Association; 120 p.

Martin, T. E. and D. M. Finch, editors. 1995. **Ecology and management of neotropical migratory birds.** Oxford, NY: Oxford University Press.

Marzluff, J. M. and R. Sallabanks, eds. 1998. **Avian conservation: Research and management**. Washington, DC: Island Press.

Rappole, J. H. 1995. **The ecology of migrant birds: A neotropical perspective**. Smithsonian Inst. Press, Washington, DC.

Rubenstein, D. R., C. P. Chamberlain, R. T. Holmes, M. P. Ayres, J. R. Waldbauer, G. R. Graves, and N. C. Tuross. 2002. **Linking breeding and wintering ranges of a**

migratory songbird using stable isotopes. Science 295: 1062-1065.

Wang, Y., D. M. Finch, F. R. Moore, and J. F. Kelly. 1998. **Stopover ecology and habitat use of migratory Wilson's Warblers**. Auk 115: 829-842.

Warnock, N., and M. A. Bishop. 1998. **Spring stopover ecology of migrant Western Sandpipers**. Condor 100: 456-467.