ENSO SIGNALS CONTRIBUTE TO VARIATIONS IN BREEDING BIRD DENSITIES IN GRAND TETON NATIONAL PARK

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+ INTRODUCTION

We have monitored breeding bird densities over a variety of sites and habitats in GTNP since the early 1990s, utilizing fixed-area census sites of around 5 ha in size. The sites are located throughout the park in all habitat types and over a wide range of elevations, and number 30 in all. At some of these monitoring sites we have accumulated data in successive breeding seasons for almost two decades; the power of these census data in interpreting variation in bird species composition and breeding densities, species to species, site to site, and especially year to year, clearly increases with the span of the data set. Some of the measured variation in breeding densities is presumably attributable to conditions encountered by resident birds during the preceding winter, on-site in GTNP. Some may be attributable to conditions evaluated by migrant birds returning to GTNP after wintering elsewhere, also an on-site contribution. However, a further potential source of variation is off-site, and may be ascribed to conditions endured by the migrants on their wintering grounds. It is the source and extent of such variation in the winter habitats of GTNP migrants that is the subject of the ensuing discussion.

Wintering Grounds for GTNP Migrants

Just under 40% of the park's 150 or so breeding bird species are year-round residents, and pass the winters in situ; these include the familiar corvids, titmice, nuthatches and woodpeckers (and their predators) that are the core species of the forest winter flocks. Yet a substantial majority of the birds breeding in GTNP are migrants rather than year-

round residents, and these migrants overwinter in a wide range of habitats over a vast geographical area, from central U.S., south through Mexico and Central America, and beyond. While some reach the South American continent in winter (e.g. Yellow Warbler Dendroica petechia, Swainson's Thrush Catharus Wood-pewee Western Contopus ustulatus. sordidulus), others cross the Isthmus of Tehuantepec but remain within the tropical latitudes of Central America (e.g. Gray Catbird Dumetella carolinensis, Least and Willow Flycatchers Empidonax minimus, E. traillii). At the other end of the spectrum, some birds leave their GTNP breeding habitats to descend in winter to more benign elevations (e.g. Rosy Finch Leucosticte arctoa), and others winter locally or at least in state when weather permits (e.g. Song Sparrow Melospiza melodia, American Robin Turdus migratorius, Dark-eyed Junco Junco hyemalis). A number of short-distance migrants spend their winters in the southern plains or move coastwards in the SW U.S., but still remain within the country. Numerically, however, a greater proportion of GTNP breeding bird species that are summer visitors spend the winter in western Mexico, i.e. north of the Isthmus of Tehuantepec up to the border region. There they can be found in a wide range of habitats from coastal mangroves and tropical evergreen forest to Sonoran desert and thorn scrub, from tropical deciduous ("short-tree") woodland to oak, pine-oak and higher-elevation pine-fir forests (Cody 2005).

Breeding Density Variation and Overwinter Strategy.

Given the wide range of overwintering possibilities for GTNP breeding birds, we can first

ask whether wintering strategies—residency, local, short-distance or long-distance migration—appear to affect the year-to-year variability in breeding season densities. One possible test uses the coefficient of variation (CV: ratio of standard deviation to mean) of breeding season densities, computed from many years of census data. Since GTNP habitats themselves might vary and contribute variation to species' CV values, the CVs are likely site- as well as species-specific. In Figure 1A (upper pane) I plot CV from common breeding birds (>0.1 pr/ha) in two sites, Site #11 (Oxbow Willow-aspen) and Site #19 (AMK Lodgepole Pine) against overwintering strategy.



Figure 1A and B. A. Bird densities against overwintering strategy. B. Variation of Figure 1A, breeding density not site specific.

There is no statistically significant relation between CV (ordinate) and the categories (abscissa) that represent overwinter strategy. In Figure 1B (lower pane) I plot a variation of this test. Some of the common species represented in the upper pane are likely not in their most preferred habitat, and we might expect greater year-to-year variation in breeding density in suboptimal habitat relative to prime habitat. Thus, in the lower pane data are not site specific, but rather data for each species (represented by CV and overwintering strategy) are taken from the site where that species reaches maximum density. A reasonable inference is that, at sites of maximum density, species are least likely to vary in breeding density owing to the vagaries of overwinter survival, as sites of prime habitat will fill up first.

Data in the lower pane of Figure 1, 80% of which are different from the data in the upper pane, again support the notion that breeding season density variations are independent of overwintering The standard ANOVA and regression strategies. analyses reveal that there is no significant variation in CV, in the statistical sense, associated with the winter distributions along the abscissa. A lack of such a relationship might have been advanced a priori on purely logical grounds. If one overwintering strategy were consistently more productive and predictable than another, then more and more bird species would, under natural selection, move to adopt the safer option. It seems that the relative equality amongst different wintering strategies is an example of ecotypic selection, wherein different wintering syndromes return, on average, similar dividends in terms of off-season survival.

Is West Mexico a Risky Wintering Option?

Although ANOVA tests are non-significant (p = 0.12), the data in Figure 1 suggest that both residents and long-distance migrants are somewhat lower (more stable) in breeding density CV values than migrants that move intermediate distances. Thus species that winter either in West Mexico or Central America lie, as a group, above the overall mean CV value, whereas the first and last categories are both below that overall mean. There is, then, a tendency for the data in Figure 1 to show a "hump," with the largest CV values over the middle strategies. We ask, therefore, if there is any reason to suspect that, over the last 20 years at least, West Mexico and adjacent areas to the south may have been less than hospitable to wintering migrants from the north?

Many of the habitats in West Mexico utilized by the North American wintering birds are more or less arid: desert and semi-desert, dry scrub and thorny shrublands, open and dry woodlands of oak and pine-oak. Such habitats might be susceptible to variations in rainfall, and dry years might mean reduced survival for the migrants. Since precipitation in West Mexico south from Sinaloa through Nayarit, Jalisco, Colima to Guerrero is nearly all late summer rainfall lasting into the fall, it is variation in these late-summer/fall rains that might potentially affect overwintering success in migrants there. Along the Pacific Ocean coast the average annual precipitation increases steadily from around 700 mm/y at Mazatlán (SIN) to around 1400 mm/y at Acapulco (GUE). Rainfall increases slightly inland from the coast, but inland cities such as Tepíc and Guadalajara (NAY) still receive little more than 1000 mm/y. A typical seasonal rainfall pattern from near the middle of our

geographic zone of interest is illustrated by Manzanillo (COL), with an average 1013 mm/y precipitation. Rains begin in June, and about 70% of the annual total falls from July to September; rains tail off October-November, and December-May precipitation constitutes only about 6% of the annual total.

Rainfall along the western coast of México is greatly influenced by the adjacent Pacific Ocean and relatively little by the Gulf of México, where the highly destructive hurricanes are generated that customarily make landfall on the eastern seaboard of the country. The dominant source of variability at low latitudes in the Pacific Ocean is the well known El Niño or ENSO weather pattern (the El Niño-Southern Oscillation system). This is an irregularly periodic phenomenon that is first signaled by elevated sea-surface temperatures in the eastern tropical Pacific (the El Niño part); these are matched by and coupled to an increased incidence of high pressure in the western Pacific (the southern oscillation part). When the opposite conditions are well developed, a "La Niña" event is said to be underway. Normally cold currents like the southern Humboldt and the northern California currents become slowed, warmed, or reversed, cold water upwellings off the eastern Pacific coasts are precluded, and altered precipitation patterns are a widespread consequence. Meteorological data are closely monitored in order to predict El Niño years and prepare for their consequences, the more dramatic of which are to precipitation norms (although there are economic and other climate consequences world-wide). An impressive animation of the equatorial Pacific's sea-surface temperatures during the present (2010) El Niño event can be on the U.S. government viewed website: http://www.elnino.noaa.gov/ where the extent and duration of the anomaly are updated and it can be easily tracked. During El Niño events, eastern and northern Australia suffer drought conditions, the northwestern coastal areas of South America and of southern to central California experience extremely high winter rainfall (e.g. 3-4 times the long-term averages), and the northwest and northern parts of North America are unusually mild and dry.

An upcoming El Niño event is usually detected in midsummer before the northern hemisphere winter. The Oceanic Niño Index (ONI) is a standard indicator, a running 3-month mean seasurface temperature (SST) for the central eastern equatorial Pacific (Region 3.4: 5° N to S latitude; 120-170° W longitude); SSTs 0.5-0.9 °C over normal signify a Weak ENSO, +1-1.4 °C a Moderate and

≥1.5 °C a Strong ENSO event. The corresponding deviations below normal denote Weak, Moderate or Strong La Niña events. In Fig. 2 (upper pane) the ONI from -3 to +3 is depicted on the abscissa, and (June-November) the Summer-Fall rainfall deviations, averaged over 7 West Mexico cities, are represented on the ordinate as proportions of the long-term average precipitation. [The cities are Juan Carrasco and Mazatlán, SIN; Tepic and Guadalajara, NAY; Guanajuato, GTO; Manzanillo, COL; Acapulco, GUE; rainfall correlations are overall strongly positively correlated amongst them; climate data come from the period 1986-present]. The figure shows that West Mexico is generally a dry region in ENSO years; the regression is significant, with p= 0.013 and $R^2 = 0.39$.



Figure 2. Wilson Warbler 2A. Rainfall in West Meixco as compared with Oceanic Nino Index (ONI). Fibure 2B, Wilson Warbler densities in Grand Teton National Park as compared to Oceanic Nino Index

Wilson's Warbler *Wilsonia pusilla* is a common breeding species in GTNP, and reaches its highest densities in Site #10: JLJ Wet Willows, where it has been censused since 1966 and in consecutive years since 1991. Over that time period, breeding densities of this warbler in Site #10 have varied considerably; it has been present in every census year, but densities have varied 13-fold over the census years. The total number of breeding pairs at the site is shown as the ordinate in the lower pane

of Figure 2, where its relation to the ONI is represented. The regression bears a striking resemblance to the one shown above it (p = 0.031, $R^2 = 0.23$); the conclusion that variation in Wilson's Warbler breeding density in GTNP is closely related to rainfall in the West Mexico regions where it overwinters (see Milá et al. 2005) is difficult to avoid. Further, Wilson's Warbler densities in GTNP are statistically unrelated to winter (December-May) rainfall variations in West Mexico, and unrelated also to precipitation within GTNP during the 12 months preceding the breeding season (as recorded below Jackson Lake dam by L. Robinson and reported in NCDC files as "Moran 5 WNW").

At the same census site, #10, Yellow Warbler Dendroica petechia and Common Yellowthroat Geothlypis trichas are the commoner of the 4-5 species of breeding warbler. Most Yellow Warblers in the D. p. aestiva group winter much further south than the West Mexico region we have been considering so far. Although some winter in Mexico, the majority is distributed in winter throughout Central America and into South America as far as Peru, Bolivia and Amazonian Brasil (Lowther et al. 1999). In contrast, Common Yellowthroat is a widely distributed breeding species across most of North America and has many described but poorly differentiated subspecies (Guzy and Ritchison 1999). The morphological variations amongst populations or subspecies nevertheless help to distinguish where the different breeding populations tend to spend the winter. Both Wyoming breeding subspecies, G. t. campicola and G. t. occidentalis, are known to overwinter in the southwestern and southern United States south into northern Mexico, i.e. more northerly and easterly of the region of West Mexico we have been considering thus far.

In Figure 3A, B the CVs of breeding densities of these two additional warbler species, measured over exactly the same census-years interval as in Wilson's Warbler (Figure 2B), are plotted against ONI, the ENSO signal. In neither case are these warblers' CVs related to ONI, p>0.5 in both cases; it would appear that rainfall variations in West Mexico, in particular the droughts during ENSO years, have no influence on their breeding densities in GTNP; their wintering distributions suggest that this is precisely what we would have expected.

Recent History of ENSO Events

Published data (see for example <u>http://ggweather.com/enso/oni.htm</u>)on the incidence

of El Niño and La Niña events show that, since 1950, there have been 14 years with El Niño signals and 13 with La Niña signals (i.e. proportion 0.273 of the last 59 years show the former, 0.220 show the latter). Now divide the 59 year interval into two sections, the 40 years 1950-89 inclusive and the last 19 years of the record, 1990-2009, the period for which continuous census data are available from many of the GTNP monitoring sites. The expected numbers of La Niña events in the first 40 and the last 19 years of the period of record are 8.81 and 4.19, figures that do not differ significantly from the observed La Niña events: 10 and 3. In contrast, I compute the expected numbers of El Niño events in the earlier and later periods to be 9.49 (first 40 y) and 4.51 (last 19 y). The corresponding observed numbers are 6 ENSO years 1950-1989 and 8 ENSO years 1990-2009; by Chi-squared analysis (χ^2 = 3.98, p<0.05) there has been a significantly higher incidence of El Niño years in the last 19 than there were in the 40 y following 1950. Therefore it seems a reasonable possibility that the "hump" in the CV vs. Migration Strategy graphs (Figure 1) is attributable to the exceptionally high frequency of El Niño years during the post-1990 period during which breeding bird censuses have been assessed annually in GTNP.



Figure 3. In Figure 3A,B the CVs of breeding densities of these two additional warbler species, measured over exactly the same census-years interval as in Wilson's Warbler (Figure 2B), are plotted against ONI, the ENSO signal.

✦ ACKNOWLEDGEMENTS

Partially supported by NSF Award #016554.

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