Periodic Migration and Lowland Forest Refugia in a "Sedentary" Neotropical Bird, Wetmore's Bush-Tanager

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Abstract: *Although the concept of tropical birds as sedentary is pervasive, evidence suggests many are not. Our grasp of movement status in tropical birds is decidedly poor, but the successful long-term conservation of these birds depends on such information. Sedentariness will likely doom much tropical avian diversity, but increased vagility is a two-edged sword: beneficial in promoting immigration, but detrimental in that more than one habitat may be required. Birds requiring more than one habitat may be unable to locate a particular type as landscape modifications increase. Our long-term data set from the Sierra de Los Tuxtlas in southern Veracruz, México, reveals infrequent, large-scale movements in a local highland endemic. Wetmore's Bush-Tanager (*Chlorospingus ophthalmicus wetmorei*) seems occasionally dependent upon lowland forests (now greatly diminished) as a refugium from temporarily unsuitable highlands. Our data and observations lead us to three conclusions: 1) assumptions of sedentariness in tropical birds should be made with extreme caution; 2) normal, but periodic phenomena may be easily overlooked, even in relatively long-term studies; and 3) missing such phenomena jeopardizes the success of any conservation plan because over the long term a population may be dependent upon refugia only occasionally occupied.*

Migración Esporádica y Refugios en Bosques de Llanuras en una Especie Sedentaria de Ave Neotropical, el Chinchinero Común

Resumen: *Aunque la idea de que las aves tropicales son sedentarias es muy extendida, las evidencias sugieren que muchas de ellas no lo son. Nuestro entendimiento acerca de los movimientos de las aves tropicales es sin duda muy escaso, sin embargo, la próspera conservación a largo plazo depende de este tipo de información. El hábito sedentario seguramente perjudicaría gran parte de la diversidad aviaria tropical, pero un aumento en su vagilidad es un arma de dos filos: benéfica por permitir la inmigración, pero detrimente, pues mas de un hábitat puede ser requerido para su conservación. Las aves que requieren más de un hábitat pueden ser incapaces de localizar un tipo particular si las modificaciones en el paisaje se incrementan. Nuestro conjunto de datos de muchos años en la sierra de los tuxtlas, en el sur de Veracrŭz, México, nos revela movimientos de mayor escala, poco frecuentes en un ave endémica local de las tierras altas. El chinchinero común (*Chlorospingus ophthalmicus wetmorei*) parece ser dependiente ocasional de los bosques de las lla-*

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nura, (actualmente muy disminuídos) como un refugio temporal de las condiciones adversas de las tierras altas. Nuestros datos y observaciones nos llevan a tres conclusiones: 1) las suposiciones sobre el hábito sedentario de las aves tropicales deben hacerse con extrema precaución, 2) fenómenos normales pero periódicos pueden no tomarse en cuenta fácilmente, aún en estudios de relativo largo plazo, y 3) el no tomar en cuenta estos fenómenos obstaculiza el éxito de cualquier programa de conservación porque la población en el largo plazo puede depender de refugios ocupados solo ocasionalmente.

Introduction

The concept of tropical forest birds as sedentary, occupying a relatively small area in one habitat type throughout their lifetime, is pervasive in the ornithological literature. Although knowledge is gradually accumulating on the movement status of many species (e.g., Wetmore 1927, 1943; Zimmer 1938; McClure 1974; Pearson 1980; Stiles 1980; Willis 1976, 1988; Ramos 1983; Binford 1989; Remsen & Parker 1990; Levey & Stiles 1992; Sick 1993; Powell & Bjork 1995; Chesser 1994), our grasp of movements in the majority of tropical bird species is rudimentary. As remaining natural habitats become more fragmented and isolated, the long term existence of remnant populations will be dependent upon continued habitat availability, population size, and, if population size is low, an effective immigration rate to maintain genetic diversity (Charlesworth 1993; Vrijenhoek 1994). Even if some habitat preservation is assured, tropical birds often occur at low densities, guaranteeing that many will persist only as small, isolated populations. This situation jeopardizes long term population genetic diversity and increases the probability of local extinction.

From a conservation perspective, sedentariness is an affliction that will likely doom a substantial proportion of tropical avian diversity (though it is the source of much of that diversity). Departure from sedentariness (increased vagility) is, however, a two-edged sword: it is beneficial in promoting immigration into an area (decreasing the likelihood of local extinctions and increasing genetic diversity), but detrimental in that more than one habitat type may be required to sustain individuals through an annual cycle (or in the longer term if movements are less regular). As landscape modifications increase, birds requiring more than one habitat may be unable to locate a particular type when it is needed.

During a 22-year period of avifaunal study in the Sierra de Los Tuxtlas in southern Veracruz, México, we have conducted large-scale sampling efforts in 10 nonbreeding seasons. This paper examines our long-term data set on the lowland presence of the endemic Wetmore's Bush-Tanager (*Chlorospingus ophthalmicus wetmorei*; Aves: Emberizidae: Thraupinae), a highland bird usually considered sedentary (i.e., "restricted to isolated, mid-elevation patches of cloud forest," Peterson et al. 1992: 245) or as showing limited elevational movements (Wetmore 1943; Ramos 1983; Binford 1989). Our long-term data bring a new perspective to the habitat requirements, evolution, and conservation of this local endemic.

Study Area and Methods

The Sierra de Los Tuxtlas is a rugged, isolated volcanic range on the northwestern edge of the Isthmus of Tehuantepec. Los Tuxtlas, approximately 4200 km^2, ranges in elevation from sea level to 1660 m and contains the northernmost Neotropical rainforest (Andrle 1964; Pennington & Sarukhan 1968). More than 400 species of birds have been recorded from the area (Winker et al. 1992). Los Tuxtlas is host to at least one endemic bird species and at least five endemic subspecies (Winker 1996). Wetmore's Bush-Tanager is among the latter.

As in many tropical lowland areas today, Los Tuxtlas consists of a mosaic of habitats, varying from rapidly diminishing mature rainforest to pastures, with much agricultural and second-growth habitat. Lowland, second growth habitats range from sparse, low shrubs to dense, tall *Cecropia-Ochroma* woodlands. Andrle (1966) estimated that half of Los Tuxtlas was still forested in 1962. Using Landsat images and air photographs, we estimated that only 15% was still forested in 1986 (Winker et al. 1990; cf. Dirzo & Garcia 1992) and that approximately 7–10% remained forested in 1994 (Winker 1996). The majority of remaining forest is in the highlands; forest below 500 m elevation is now quite scarce (Rappole et al. 1994).

Our research in Los Tuxtlas began in 1973 and has continued in three major bouts through 1994. In each of these efforts our chief investigative methodology has been the intensive mist netting of lowland habitats. The habitats studied were primarily lowland rainforest and second growth forest of varying ages from ca. 5–40 years. During the first effort, 1973–1975, 70,488 net hours were accumulated between 7 August and 29 May. In the second major effort, 1982–1987, 54,774 net hours were accumulated between 2 October and 2 June. During the third major effort, 1992–1994, 76,256 net hours were obtained between 16 August and 20 May. Over the 22-year span, these efforts encompassed 10 nonbreeding seasons, and our lowland sample effort totals 201,517 net hours, or 46 net *years* if one bases these years on 12

Table 1. Sample effort and captures of *Chlorospingus ophthalmicus wetmorei* during 10 nonbreeding seasons in Los Tuxtlas, Veracruz.

Nonbreeding season	*Net hours*	*Captures*	*Capture rate**
1973–74	33,976	0	0.000
1974–75	36,512	2	0.055
1982–83	7,907	6	0.759
1983–84	9,311	2	0.215
1984–85	25,613	0	0.000
1985–86	7,632	2	0.262
1986–87	4,310	1	0.232
1992–93	12,605	80	6.347
1993–94	41,142	1	0.024
1994–95	22,509	5	0.222
Totals	201,517	99	0.491

**Captures per 1000 net hours.*

hours of sampling each day. Our efforts were conducted primarily during the nonbreeding season, and all netting occurred between 7 August and 2 June.

Within each major effort, varying degrees of between-year change in sampling occurred, from some change to none. In most cases the same net lanes were used between years. Knowing our sampling in great detail, it is highly unlikely that the small changes in sampling affected the results reported here (unpublished data). It is important to note that during the final effort (1992–1994) habitat sampling remained constant: the same net lanes were used in each season. All results reported here were obtained from sites below 180 m elevation. For detailed descriptions of the habitats and areas studied see Ramos and Warner (1980), Rappole and Warner (1980), Ramos (1983, and references therein), Winker et al. (1990), and Winker (1995).

Results

During our long-term study, 99 *Chlorospingus ophthalmicus wetmorei* were captured (Table 1). Captures occurred in lowland primary rainforest and in lowland second-growth forest and occurred regardless of whether a site was connected by a forested corridor to highland habitats. Captures occurred only in the nonbreeding season, with dates ranging from 25 August to 28 February. There was a dramatic difference in captures among years; just over 80% of total captures occurred in the 1992 season (Table 1).

Prior to 1992, from the occasional captures occurring during the 1970s and 1980s (Table 1, Fig. 1), we viewed this species as an infrequent visitor to the lowlands from the local highlands during periods of inclement weather (locally called *nortes*). *Nortes* are cold, wet weather systems from the north, generally last 2–6 days, and several usually occur each month from November–March (Ramos 1983; Winker et al. 1990). Nortes occurred frequently in all of the years of our study (e.g., Winker et al. 1990). It has been well established that many highland species in Los Tuxtlas occur in the lowlands largely or exclusively during nortes (e.g., *Empidonax flavescens*, *Turdus assimilis, Catharus mexicanus*, *Myadestes unicolor*, *Myioborus miniatus*, and *Piranga leucoptera*; Ramos 1983). Until 1992 *Chlorospingus ophthalmicus wetmorei* also fit this pattern. Nortes seem to produce similar movements in some wintering Nearctic-Neotropic migrants (Ramos 1989; Winker et al. 1990). Wetmore (1943) also noted the tendency of *Chlorospingus ophthalmicus* to visit the lowlands in Los Tuxtlas during cold weather. Our latest capture date of 28 February coincides roughly with the end of the norte season.

During relatively brief visits to highland sites, we have found this species to be locally fairly common above 500 m elevation. Wetmore (1943) and Andrle (1964) also found the species fairly common at higher elevations; Andrle (1964) noted that individuals occurred from 500–1600 m.

The relatively large numbers of captures occurring during the 1992 season began on the second day following a major storm (not a norte, but rather a system of tropical origin), whose heavy winds lashed the area for 5 days (27 September–1 October). This storm had considerable force, but the U.S. National Hurricane Center (Miami, Florida) registered neither a hurricane nor a tropical storm in this region during this period. Captures

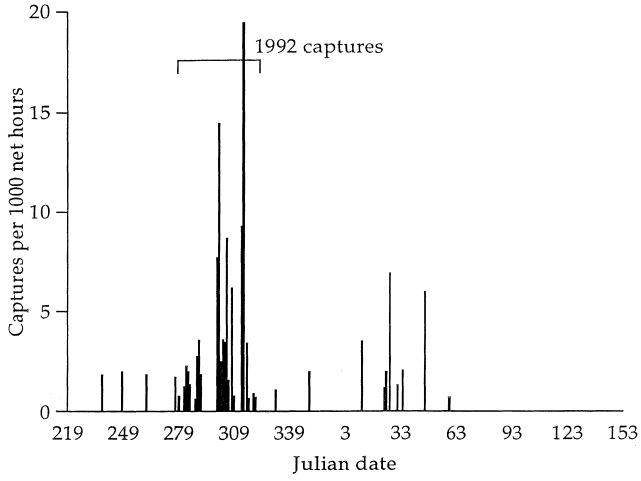

Figure 1. Within-year temporal distribution of 10 years of capture rate data for Chlorospingus ophthalmicus wetmorei *in the lowlands of Los Tuxtlas, Veracruz during the nonbreeding season. The horizontal axis encompasses the extent of our sampling dates from 7 August (Day 219 in nonleap years) through 2 June (Day 153 in nonleap years). Captures in 1992 occurred between 3 October (Day 277) and 13 November (Day 318) and are responsible for the capture pattern exhibited between those dates.*

during the 1992 season increased gradually from the first captures on 3 October (none occurred on 2 October, the first day of netting following the storm), to peaks on 28 October and 10 November (Fig. 1). Observations in forest up to 380 m elevation after the storm showed that vegetation had been affected by the heavy winds. Not only were recent tree- and branch-falls evident, but evergreen trees shed a considerable number of leaves during the weeks following the storm (presumably a response to wind-related stress). Highland forest on ridges seemed to have been hit particularly hard, with a higher rate of treefalls and limb damage evident. Many of the captures occurring after 3 October during 1992 were not associated with nortes (including the peak occurring on 28 October), but the largest capture peak occurring on 10 November was associated with a rather strong norte that lasted several days. Thus, although some captures in 1992 were norte-associated, unlike previous years most captures in 1992 did not occur in conjunction with nortes, but rather were spread over periods of very tranquil weather.

The occupancy of lowland habitats by this species seems mostly to be brief. Sightings are irregular, but birds return to the same lowland site periodically. Recaptures and resightings of color-banded birds showed that individuals remained on occasion for at least 5 days, and several returned to the same site during nortes between years (e.g., La Peninsula #1247, first captured 25 January 1984, recaptured at the same site, 150 m elevation, on 11 January 1986). Most captured birds were never recaptured, however, suggesting a substantial movement rate. Lowland occupancy thus seems to vary from brief transience to between-year temporary site fidelity.

Discussion

Except in 1992, captures of Wetmore's Bush-Tanager were usually associated with nortes, when individuals seemed to be using lowland habitats only occasionally as a refugium from temporarily unsuitable highland habitats. In 1992 we observed a dramatic change from this pattern. Not only were capture rates much higher than those of other seasons, but the lowland presence of the species was not as strongly tied to nortes as it was in other years. The species' occurrence in the lowlands during and shortly after nortes demonstrates a predisposition (or preadaptation) for elevational migratory movement when necessary (see Levey & Stiles [1992] and Ramos & Rappole [1994] for evidence that this predisposition also exists in many other Neotropical birds). It became clear in 1992 that this predisposition occasionally serves a vast number of individuals seeking refuge in lowland habitats. We categorize this type of movement as periodic irruptive elevational migration and consider that it was due to temporary habitat changes in the local highlands that rendered them largely unsuitable (due to storm-related habitat alterations). This species eats both insects and fruits (Isler & Isler 1987; unpublished data). The movements we observed may have been stimulated by a severe decline in food availability in the highlands.

Interhabitat movements of this nature have been documented for some species in Jamaica following Hurricane Gilbert, where highland species were particularly affected (Wunderle et al. 1992). The duration of highland habitat unsuitability following such storms will vary, depending on the extent of the damage. Thus, alternate habitat refugia may be needed for unknown periods. Our 1992 netting ended on 15 November, so we do not know when large numbers of Wetmore's Bush-Tanager ceased occupying the lowlands in Los Tuxtlas. This period was less than 1 year, however; capture rates of this species at the same lowland site in autumn 1993 had returned to low levels (Table 1).

The endemic Los Tuxtlas population of *Chlorospingus ophthalmicus* is not the only population of this species in which individuals occasionally occur in lowland habitats during the nonbreeding season. Binford (1989) documented the "very uncommon" lowland presence of the species in the Mexican state of Oaxaca (and the association of these movements with nortes), and Monroe (1968) noted that individuals occasionally wander into lowland habitats during the nonbreeding season in Honduras. Although it seems likely that the birds we captured in Los Tuxtlas in 1992 came from the local highlands (all adults were characteristic *wetmorei*), it is possible that individuals from other populations occurred in the region at this time.

At the species level the evolutionary consequences of movements like those observed in 1992 in a species ordinarily considered sedentary are twofold. First, movements of this nature—widespread transient occupancy of ordinarily uninhabited areas—would promote the original colonization of isolated habitat islands like the Sierra de Los Tuxtlas. Second, although the species' tendency toward sedentariness would promote the post-colonization divergence of isolated populations (e.g., Los Tuxtlas' endemic *wetmorei*) from other populations, periodic migrations would promote gene flow. That these movements are infrequent is suggested both by our data and by the genetic data of Peterson et al. (1992), who found that the Los Tuxtlas population showed substantial levels of genetic divergence from neighboring Mexican populations (including fixed allelic differences). Nevertheless, isolation-by-distance models did not seem to explain the patterns of divergence observed; divergence levels were not correlated with distances between sampled populations. This situation would be predicted if weather-related irruptive migrations among Mexican populations of the species showed a geographic pattern (as weather events often do), or some directionality (as migrations often do). Peterson et

al. (1992) estimated that effective dispersal among these populations was only 0.303 individuals per generation, a very low level of genetic exchange.

Edwards (1993), examining an island population of the presumed sedentary Grey-crowned Babbler (*Pomatostomus temporalis*) in Australia, found genetic evidence of interpopulation movement and concluded that birds were either being blown out to the island from the mainland or that they were actively migrating across the intervening open water (ca. 30 km).

Intratropical migrations are not as apparent as Nearctic-Neotropic or Palearctic-Paleotropic migrations because (1) individuals of a species may be present throughout the year, although population shifting has occurred; (2) we generally lack observer records throughout the year for most tropical locales; and (3) the records that exist have generally not been adequately synthesized to examine temporal as well as geographic distributions (however, see Parkes 1982; Binford 1989; Remsen & Parker 1990; Levey & Stiles 1992; Chesser 1994).

The conservation implications of the movements we observed in 1992 are probably applicable to many highland bird populations in the Neotropics. If lowland forest is no longer available as a temporary refugium, survival rates among birds needing such habitat will be lower during the periods of need. This becomes particularly worrisome in areas like Los Tuxtlas, where overall forest cover has declined by more than 80% since 1962, and lowland forest below 500 m elevation is now scarce.

Depending on the severity and frequency of highland climatic stress, in conjunction with lowland refugium capacity, temporarily lowered survival rates could lead to declining highland populations, lowered genetic diversity, and perhaps even local extinction. Raffaele (1977) and Wunderle et al. (1992) suggested that a situation of this sort led to the extinction of the Puerto Rican Bullfinch (*Loxigilla portoricensis grandis*), endemic to St. Kitts Island in the Lesser Antilles.

The use of lowland forest as a temporary refugium for tropical highland birds may be much more common than we realize (e.g., Willis 1976; O'Neill & Parker 1978; Wunderle et al. 1992). Additionally, although we have dwelt upon short-term, climate-driven periodic movements, factors such as seasonal changes in climate and shifts in resource abundance further increase the use of lowlands by highland birds (Loiselle & Blake 1991; Levey & Stiles 1994). Binford (1989) suggested that elevational migrations occur in 25% of Oaxacan cloud forest avifauna, and Nocedal (1994) found that over 50% of highland-breeding species in southern Durango wintered in the Pacific lowlands.

Given our long-term data set and observations, we conclude the following: (1) assumptions of sedentariness in tropical birds should be made with extreme caution; (2) normal, but periodic phenomena may be easily overlooked, even in relatively long-term studies; and (3) missing such phenomena jeopardizes the success of any conservation plan because over the long term a population may be dependent upon refugia only occasionally occupied.

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