The Auk 122(3):938–948, 2005

EVIDENCE OF LATITUDINAL SEXUAL SEGREGATION AMONG MIGRATORY BIRDS WINTERING IN MEXICO

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Abstract.—Latitudinal sexual segregation during the nonbreeding season, in which males tend to winter farther north than females, is known to occur in many temperate-zone bird species. This pattern, however, has rarely been reported in species wintering in tropical regions. We investigated latitudinal sexual segregation in 45 Nearctic–Neotropical migratory bird species that winter in Mexico, using specimen records from 35 natural-history museums. We found significant latitudinal segregation in nine species: Yellow-bellied Sapsucker (*Sphyrapicus varius*), Swainson's Thrush (*Catharus ustulatus*), Orange-crowned Warbler (*Vermivora celata*), Yellow Warbler (*Dendroica petechia*; *aestiva* group), Yellow-rumped Warbler (*Dendroica coronata*; *coronata* group), Black-and-white Warbler (*Mniotilta varia*), Ovenbird (*Seiurus aurocapilla*), Wilson's Warbler (*Wilsonia pusilla*), and Indigo Bunting (*Passerina cyanea*). In most cases, males predominated in the northern part of species' winter ranges and females in the south, but the trend was reversed in Indigo Buntings. Discovering the frequency of latitudinal sexual segregation in Neotropical migratory birds will influence understanding of avian ecology and migration systems. *Received 28 January 2003, accepted 1 March 2005.*

Key words: differential migration, Nearctic–Neotropical migration, Neotropics, sexual segregation.

Evidencia de la Segregación Latitudinal Sexual en Aves Migratorias durante el Invierno en México

Resumen.—Se sabe que la segregación latitudinal de sexos durante la temporada no reproductiva ocurre en muchas especies de aves de la región templada, en las cuales los machos predominan en las zonas norteñas de las distribuciones de invierno. No obstante, este patrón raramente ha sido reportado en especies que invernan en las regiones tropicales. Analizamos 45 especies que invernan en México con base en especímenes alojados en 35 museos de historia natural, para investigar cuáles especies podrían mostrar segregación latitudinal entre sexos. Encontramos patrones significativos de segregación en 9 especies: *Sphyrapicus varius*, *Catharus ustulatus*, *Vermivora celata*, *Dendroica petechia* (grupo *aestiva*), *Dendroica coronata* (grupo *coronata*), *Mniotilta varia*, *Seiurus aurocapilla*, *Wilsonia pusilla* y *Passerina cyanea*. En general, los machos predominaron al norte de su distribución invernal, mientras que las hembras fueron relativamente más

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comunes al sur, pero el patrón fue el inverso para *P. cyanea*. El descubrimiento de la extensión de la segregación sexual latitudinal en aves migratorias neotropicales influenciará el entendimiento de la ecología de las aves y los sistemas migratorios.

The tendency for male and female birds to segregate during the nonbreeding season was first noted in partial migrants, in which males tend to occupy breeding ranges year-round but females migrate to areas with warmer temperatures (Laskey 1935, Nice 1937, Lack 1954). Gradually, researchers in Holarctic regions noted that many short- and medium-distance migrants also exhibit patterns of latitudinal (or geographic) sexual segregation on the wintering grounds, with males generally wintering farther north than females (Howell 1953, King et al. 1965, Ketterson and Nolan 1983). Now, distinct winter distribution patterns between sexes (and frequently age classes also) have been documented for more than 100 species (Cristol et al. 1999).

In spite of occasional reports of winter latitudinal sexual segregation in long-distance Nearctic-Neotropical migrants (Howell 1953, Johnston 1970, Pearson 1980, Russell 1981), segregation has been largely overlooked in this group and was assumed to be rare (Morton 1990). Indeed, only in the past decade was it reported from Neotropical wintering grounds of two parulid warblers (Vidal et al. 1994, Sherry and Holmes 1997). Cristol et al. (1999), reviewing differential migration, predicted that latitudinal segregation occurs more widely than has been reported. Discovering the extent of latitudinal segregation in Neotropical migratory birds on their wintering grounds is important for understanding migratory behavior and the ecology of migratory species in tropical bird communities. The existence of such segregation has far-reaching consequences: segregation could lead to different annual survival rates between sexes or evolution of different habitat preferences, either of which could influence conservation strategies for threatened species. Also, such patterns imply that selective forces may differ between males and females, because of differences in habitat, geography, and local components of ecosystems.

In most latitudinally segregated species, males winter farther north than females (Cristol et al. 1999), so explanations have focused on explaining why males winter farther north. One popular hypothesis is that the territorial sex (males) winters farther north to be able to return earlier to breeding grounds to claim territories (King et al. 1965; Ketterson and Nolan 1976, 1983). In temperate areas, another explanation for males wintering farther north is that the larger sex (males) can physiologically withstand colder temperatures (Ketterson and Nolan 1976). Alternatively, geographic segregation may result from intersexual competition: Lack (1954) suggested that the dominant sex may exclude the other from some areas. The hypothesis that sexes have evolved different foraging niches in response to intersexual competition (Selander 1966, Lynch et al. 1985, Morton 1990) can be extended to include geographic wintering areas, if those areas are interpreted as one element of the foraging niche.

Here, we ask the question: how common is latitudinal sexual segregation among a diverse set of medium to long-distance Nearctic–Neotropical migratory species on their wintering grounds? The group of species studied includes 3 hummingbirds, 1 woodpecker, 6 tyrannid flycatchers, 2 vireos, 1 kinglet, 2 thrushes, 1 catbird, 18 parulid warblers, 2 tanagers, 3 emberizid sparrows, 4 cardinalid buntings, and 2 icterid orioles (all common and scientific names given in Table 1).

Methods

We extracted records of migratory birds from a comprehensive database of bird specimens from Mexico (*Atlas of Mexican Bird Distributions* project; Peterson et al. 1998, Navarro S. et al. 2002, 2003; institutions listed in Appendix). We used only records for which precise locality data were available, and for which collecting date was within December–February, to minimize inclusion of transient individuals (Ketterson and Nolan 1976, Remsen 2001). We also excluded species that do not form winter home ranges and, in effect, are transients throughout the winter period (e.g. Cedar Waxwing [*Bombycilla cedrorum*]), and species that have permanent resident breeding populations in Mexico (e.g. Lesser Nighthawk [*Chordeiles acutipennis*], Broad-tailed Hummingbird [*Selasphorus*

Table 1. Samples of males and females of 45 migratory bird species collected in Mexico within December–February for which point locality data were available. The samples have been divided north and south of the median latitude calculated for each species from the distribution of point localities within Mexico.

Species		Winter-range geographic class	Males north	Males south	Females north	Females south	*n*	Barnard's exact *P*
Ruby-throated Hummingbird	*Archilochus colubris*	Mexico and south	11	11	20	20	62	1.000
Black-chinned Hummingbird	*A. alexandri*	Mexico	9	9	8	8	34	1.000
Rufous Hummingbird	*Selasphorus rufus*	Mexico	22	17	10	12	61	0.511
Yellow-bellied Sapsucker	*Sphyrapicus varius*	Mexico and north	27	19	39	48	133	0.134
Yellow-bellied Flycatcher	*Empidonax flaviventris*	Mexico and south	12	17	10	9	48	0.529
Least Flycatcher	*E. minimus*	Mexico and south	61	58	82	85	286	0.757
Hammond's Flycatcher	*E. hammondii*	Mexico	31	26	20	23	100	0.478
Gray Flycatcher	*E. wrightii*	Mexico	21	17	18	22	78	0.428
Dusky Flycatcher	*E. oberholseri*	Mexico	46	50	54	50	200	0.614
Pacific-slope Flycatcher	*E. difficilis*	Mexico	58	54	32	36	180	0.573
Bell's Vireo	*Vireo bellii*	Mexico	31	30	21	22	104	0.915
Blue-headed Vireo	*V. solitarius*	Mexico and north	55	45	39	49	188	0.158
Ruby-crowned Kinglet	*Regulus calendula*	Mexico and north	48	49	43	42	182	0.939
Swainson's Thrush	*Catharus ustulatus*	Mexico and south	34	32	13	15	94	0.741
Hermit Thrush	*C. guttatus*	Mexico and north	61	63	43	42	209	0.890
Gray Catbird	*Dumetella carolinensis*	Mexico and north	8	11	7	17	43	0.410
Orange-crowned Warbler	*Vermivora celata*	Mexico and north	65	47	48	63	223	0.028 [a]
Nashville Warbler	*V. ruficapilla*	Mexico	42	43	27	28	140	1.000
Yellow Warbler	*Dendroica petechia* (*aestiva* group)	Mexico and south	51	64	35	28	178	0.166
Magnolia Warbler	*D. magnolia*	Mexico and south	14	12	10	13	49	0.504
Yellow-rumped Warbler	*D. coronata* (*coronata* group)	Mexico and north	9	12	19	16	56	0.527
Black-throated Gray Warbler	*D. nigrescens*	Mexico	28	22	7	13	70	0.122
Black-throated Green Warbler	*D. virens*	Mexico and south	22	19	5	8	54	0.527
Townsend's Warbler	*D. townsendi*	Mexico	19	7	14	13	53	0.133
Hermit Warbler	*D. occidentalis*	Mexico	13	13	8	8	42	1.000
Black-and-white Warbler	*Mniotilta varia*	Mexico and south	28	16	13	25	82	0.009 [a]
Ovenbird	*Seiurus aurocapilla*	Mexico and south	17	22	11	6	56	0.161
Northern Waterthrush	*S. noveboracensis*	Mexico and south	8	8	9	9	34	1.000

Table 1. Continued.

Species		Winter-range geographic class	Males north	Males south	Females north	Females south	*n*	Barnard's exact *P*
Louisiana Waterthrush	*S. motacilla*	Mexico and south	14	10	6	7	37	0.587
Kentucky Warbler	*Oporornis formosus*	Mexico and south	14	12	3	8	37	0.165
MacGillivray's Warbler	*O. tolmiei*	Mexico and south	29	29	16	16	90	1.000
Hooded Warbler	*Wilsonia citrina*	Mexico and south	12	12	6	6	36	1.000
Wilson's Warbler	*W. pusilla*	Mexico and south	77	43	29	63	212	0.000 [a]
Yellow-breasted Chat	*Icteria virens*	Mexico and south	58	47	27	38	170	0.087
Summer Tanager	*Piranga rubra*	Mexico and south	46	48	34	32	160	0.800
Western Tanager	*P. ludoviciana*	Mexico	26	29	22	20	97	0.676
Clay-colored Sparrow	*Spizella pallida*	Mexico	26	26	24	24	100	1.000
Lincoln's Sparrow	*Melospiza lincolnii*	Mexico and north	68	82	59	45	254	0.078
White-crowned Sparrow	*Zonotrichia leucophrys*	Mexico and north	27	22	24	29	102	0.363
Rose-breasted Grosbeak	*Pheucticus ludovicianus*	Mexico and south	20	17	10	18	65	0.165
Lazuli Bunting	*Passerina amoena*	Mexico	16	17	4	3	40	0.786
Indigo Bunting	*P. cyanea*	Mexico and south	41	54	30	23	148	0.126
Painted Bunting	*P. ciris*	Mexico and south	56	57	33	43	189	0.415
Orchard Oriole	*Icterus spurius*	Mexico and south	27	26	16	15	84	1.000
Baltimore Oriole	*I. galbula*	Mexico and south	34	28	12	14	88	0.487

[a] Supports hypothesis of latitudinal segregation.

platycercus]), to ensure that all individuals in our analyses were medium- or long-distance migrants. We excluded specimens from one collector (M. del Toro Avilés) known for doubtful date and locality information (Binford 1989) and excluded all species for which <30 records were available.

For the 45 remaining species, we sorted records by latitude and tested for differences in numbers of each sex north and south of the median latitude in the Mexican data set. Individuals collected at exactly the median latitude were excluded, because they could not be assigned to either northern or southern groups. We used contingency-table analysis to compare frequencies of each sex, north versus south, with *P* values determined using Barnard's test (α = 0.05), which is an exact unconditional test of equality of two binomial proportions (STATXACT, Cytel Software, Cambridge, Massachusetts) and is appropriate for model I contingency tables (Sokal and Rohlf 1995). We did not correct alphas for multiple comparisons because (1) that would assume the universal null hypothesis (no geographic differences across sex classes in any and all species) to be relevant, obviating the biological significance of the tests and the *a priori* expectation that meaningful patterns might exist (Perneger 1998); and (2) it would increase Type II error rates.

Given that the expected pattern of sexual segregation across Mexico may be different for species that winter mostly to the north or mostly to the south, we classified each species into one of three geographic range classes: wintering (1) mainly in Mexico, (2) substantially to the north, or (3) substantially to the south of Mexico. We defined "substantial" as approximately 40% or more of the winter range, and based our classifications on published accounts and range maps of winter ranges (species accounts in *Birds of North America* series, and American Ornithologists' Union 1998).

For species with substantial winter ranges north or south of Mexico, we determined the probability (*P*) that the overall sex ratio in the Mexican sample was equal to unity, based on cumulative expected frequencies for the rarer sex generated from the binomial distribution. We doubled the expected frequencies to obtain *P*, because either sex could have been rarer than the other (we did not know *a priori* the direction of segregation patterns); hence, the statistical test was two-tailed. Given the tendency for most cases of documented sexual segregation to be in one direction (males predominating to the north and females to the south), a one-tailed test may have been appropriate, but the two-tailed test is more conservative.

For species in the northerly or southerly groups with significantly skewed sex ratios in Mexico, we further investigated sex ratios from other parts of their wintering ranges. We queried 10 museum collection databases (Academy of Natural Sciences, Philadelphia, Pennsylvania; Delaware Museum of Natural History, Wilmington; The Field Museum, Chicago [FMNH]; Louisiana State University Museum of Natural Science, Baton Rouge [LSU]; Museo Nacional de Costa Rica, San José; Museum of Vertebrate Zoology, Berkeley, California; Peabody Museum, Yale University, New Haven, Connecticut; Universidad de Panamá Museo de Vertebrados, Ciudad de Panamá; University of Kansas Natural History Museum, Lawrence; and U.S. National Museum of Natural History, Washington, D.C.) for non-Mexican wintering records. For species wintering north of Mexico, we counted all records of males and females collected in the United States, excluding Florida, during December, January, or February. For species wintering south of Mexico, we counted all records of males and females collected in Costa Rica or Panama to determine representative sex ratios from the southern part of the winter range. For two species that winter more broadly southward, we also checked collections (FMNH, LSU) from South America (mostly Colombia and Peru) to see whether sex ratios farther south differed.

For species wintering mostly within Mexico, we were interested in the possibility of clinal variation in sex ratios, which might not be detected by the above methods. We selected the 12 species with samples of ≥60 specimens for analysis, divided their locality records into latitudinal quartiles, and compared the sex ratios in the northernmost and southernmost quartiles by contingency-table analysis, using Barnard's exact tests. Data from localities that fell exactly on the limits between latitudinal quartiles were excluded.

RESULTS

Significant ($P < 0.05$) segregation of sexes was found in 9 of 45 species. Segregation around

TABLE 2. Samples of males and females of migratory bird species wintering mostly in Mexico, from northernmost and southernmost latitudinal quartiles for specimens collected in Mexico within December–February. The quartiles were derived independently for each species from the point localities of museum specimens collected in Mexico.

Species	Males north	Males south	Females north	Females south	*n*	Barnard's exact *P*
Selasphorus rufus	13	11	3	9	36	0.099
Empidonax hammondii	17	12	8	12	49	0.240
E. wrightii	12	8	7	11	38	0.256
E. oberholseri	21	25	22	24	92	0.872
E. difficilis	27	27	15	18	87	0.738
Vireo bellii	13	15	12	9	49	0.525
Vermivora ruficapilla	23	21	12	10	66	0.884
Dendroica nigrescens	12	12	4	5	33	0.817
D. townsendi	10	4	5	6	25	0.225
Piranga ludoviciana	15	12	8	8	43	0.756
Spizella pallida	8	12	15	13	48	0.528

the median latitude of Mexican distributional records (Table 1) occurred in Orange-crowned Warbler, Black-and-white Warbler, and Wilson's Warbler. In all three, males were more frequent than females in the northern part of the wintering distribution. For species wintering principally in Mexico, we compared sex ratios from the northernmost quartile to the southernmost quartile; none of the sex ratios differed significantly (Table 2).

Of species wintering extensively north of Mexico, three of nine showed significantly unequal sex proportions in Mexico, but only two of nine showed sex ratios in Mexico significantly different from sex ratios in the United States (Table 3). In both Yellow-bellied Sapsucker and Yellow-rumped ("Myrtle") Warbler, females outnumbered males in Mexico, but males outnumbered females in the United States, a pattern consistent with latitudinal sexual segregation.

Among species wintering extensively south of Mexico, 14 of 22 showed sex ratios in Mexico significantly different from unity, and 3 others had nearly significant ($0.05 < P < 0.10$) differences (Table 4). In most cases,

TABLE 3. Samples of males and females of northerly wintering bird species collected in Mexico and the United States (except Florida) within December–February. *P*–equity represents the probability that the Mexican sample was taken from a population with equal numbers of males and females. Barnard's exact *P* is the probability that the ratios in Mexico and the United States are the same; this statistic and United States sample sizes are provided only for species with significantly skewed sex ratios in Mexico and for *Dendroica coronata*.

	Mexico			United States		Barnard's
Species	Males	Females	*P*–equity	Males	Females	exact *P*
Sphyrapicus varius	46	87	0.0004	96	76	0.0002 [a]
Vireo solitarius	100	88	0.4220			
Regulus calendula	97	85	0.4150			
Catharus guttatus	124	85	0.0080	244	152	0.5890
Dumetella carolinensis	19	24	0.5420			
Vermivora celata	112	111	1.0000			
Dendroica coronata (*coronata* group)	21	35	0.0810	130	87	0.0030 [a]
Melospiza lincolnii	150	104	0.0050	55	56	0.0960
Zonotrichia leucophrys	49	53	0.7660			

[a] Supports hypothesis of latitudinal segregation.

TABLE 4. Samples of males and females of southerly wintering bird species collected in Mexico within December–February, and in southern Central America (Costa Rica or Panama) on any date. *P*–equity represents the probability that the Mexican sample was taken from a population with equal numbers of males and females. Barnard's exact *P* is the probability that the sex ratios in Mexico and in southern Central America are the same; this statistic and Central American sample sizes are provided generally only for species with skewed sex ratios ($P < 0.05$) in Mexico.

	Mexico			Southern Central America		
Species	Males	Females	*P*–equity	Males	Females	Barnard's exact *P*
Archilochus colubris	22	40	0.030	10	11	0.420
Empidonax flaviventris	29	19	0.193			
E. minimus	119	167	0.005	2	3	0.965
Catharus ustulatus	66	28	0.0002	29	17	0.415
Dendroica petechia (*aestiva* group)	115	63	0.0002	91	87	0.010 [a]
D. magnolia	26	23	0.775			
D. virens	41	13	0.0002	58	38	0.056
Mniotilta varia	44	38	0.581	34	15	0.077
Seiurus aurocapilla	39	17	0.005	12	15	0.028 [a]
S. noveboracensis	16	18	0.864			
S. motacilla	24	13	0.099			
Oporornis formosus	26	11	0.020	54	26	0.797
O. tolmiei	58	32	0.008	3	3	0.576
Wilsonia citrina	24	12	0.065			
W. pusilla	120	92	0.063	90	69	1.000
Icteria virens	105	65	0.003	2	4	0.199
Piranga rubra	94	66	0.032	120	86	0.928
Pheucticus ludovicianus	37	28	0.321			
Passerina cyanea	95	53	0.001	30	4	0.006 [a]
P. ciris	113	76	0.009	10	6	0.909
Icterus spurius	53	31	0.021	40	16	0.319
I. galbula	62	26	0.0002	49	17	0.615

[a] Supports hypothesis of latitudinal segregation.

males outnumbered females in Mexico, though females outnumbered males in Ruby-throated Hummingbird and Least Flycatcher. Comparing sex ratios of the same species collected in Costa Rica and Panama, only three species (Yellow Warbler, Ovenbird, and Indigo Bunting) presented significantly different ratios in Central American samples. Samples of Yellow Warbler and Ovenbird from Central America held proportionally more females than Mexican samples, and vice versa for Indigo Bunting (Table 4).

In South America, the Swainson's Thrush was represented in collections by 88 males and 75 females. Although males outnumbered females in all geographic regions examined, the proportion of females was significantly higher in South America than in the Mexican sample of that species ($P = 0.011$). The Summer Tanager, a species skewed toward males in Mexico as well as in Central America, showed similar skew toward males in South American collections (33 males, 23 females).

DISCUSSION

Overall, we found evidence of latitudinal sexual segregation in 9 species (20% of 45 studied) wintering in Mexico. In eight of those cases, males wintered to the north in greater proportions than females (the exception was Indigo Bunting). Our results support earlier reports of latitudinal segregation in Yellow-bellied Sapsucker (Howell 1953), Yellow-rumped Warbler (Hunt and Flaspohler 1998), and Indigo Bunting (Johnston

1970). The other six species have not previously been reported to segregate latitudinally, but studies of segregation on Neotropical wintering grounds have been few (Cristol et al. 1999). Six parulid warblers (one-third of warbler species studied) demonstrated the pattern, which may be more prevalent in Parulidae than in other families, such as Tyrannidae. Latitudinal sexual segregation was not evident in any of the six tyrannid species studied.

Some of the cases of latitudinal sexual segregation reported here are supported by greater numbers of males in one geographic region and greater numbers of females in another. However, in Indigo Bunting and Swainson's Thrush, the evidence is limited to variation in the dimensions of the skew toward males. In those species, males are generally better represented in museum collections than females, evidently throughout the winter range. These particular results should thus be interpreted with caution. To demonstrate latitudinal segregation more conclusively, we would prefer to identify geographic areas where opposite skews would be expected, and carry out tests there. Unfortunately, key series of specimens from Central or South America necessary for such tests were sometimes simply not available, pointing to the continuing need for scientific collecting in many regions (e.g. Central American sample sizes for Hooded Warbler and Yellow-breasted Chat were 2 and 6, respectively). Skewed sex ratios in themselves may suggest latitudinal segregation, but could also reflect sampling bias or real skews in overall wintering populations.

In fact, many species showed significant sex ratio skews in the same direction (more males) across much of their winter ranges. For example, among Hermit Thrush specimens, males outnumbered females in Mexico and across the United States during winter (Table 3); other species showed similar patterns (e.g. Summer Tanager and Baltimore Oriole). This pattern may result from greater detectability of males owing to brighter plumage, from more frequent or longer-distance movements by males compared with females, from male preferences for more open habitats, or from collector preferences, among other possible factors. For sexually dimorphic species, such as Summer Tanager and Painted Bunting, collector bias may be strongly influencing sex ratios in collections: some collectors may prefer to collect flashy, colorful males, whereas others may collect just enough of either sex to ensure equal representation. Either practice would obscure natural patterns of uneven sex ratios. Additional methods, such as standardized mist-netting, may be needed to investigate the possibility of latitudinal sexual segregation in such species. Nonetheless, if existing biases are consistent across a species' range, which we assume to be true, they should not affect our ability to discern significant differences in sex ratios among geographic regions.

True patterns of geographic segregation in some species may be too complex to detect by examination of museum-specimen data alone, without new field studies designed to test hypotheses of latitudinal segregation. For example, differential distributions of age classes, well-documented in some species (Cristol et al. 1999), will require inspection of specimens for further analysis.

Some of our results may reflect more complex sex-specific distributions. For example, in the Black-and-white Warbler, a species with extensive wintering populations south of Mexico, males outnumbered females in the northern half of the Mexican winter samples, and females outnumbered males in the southern half. Unexpectedly, in southern Central America, males outnumbered females 34 to 15 (Table 4), whereas in northern Central America (El Salvador), females outnumbered males 17 to 4 (O. Komar unpubl. data). A similar pattern is evident for Wilson's Warbler (Table 4). The question remains, why would males outnumber females in northern Mexico and southern Central America, but be outnumbered by females in intervening areas? Also unexpected was the prevalence of males in the Mexican sample of Lincoln's Sparrow, given that the U.S. sample showed equity in the sex ratio (Table 3). In all those cases, it is possible that latitudinal age segregation occurs, complicating the pattern. Future research should address the question of age segregation in greater detail. Unfortunately, reliable age information for specimens is not available in most museum databases.

Several species previously reported to segregate sexes latitudinally on wintering grounds did not show such patterns in our analysis: Ruby-crowned Kinglet (Humple et

al. 2001), Summer Tanager (Pearson 1980), and White-crowned Sparrow (King et al. 1965). Our inability to detect segregation in those species may result from several factors: (1) segregation may be evident only at extremes of the winter range, given clinal variation in sex ratios; (2) for sexually dimorphic species, samples may be biased by collectors' preferences, such that sex ratios in collections differ from true ratios in nature; or (3) for species that segregate by habitat in winter, samples may be biased by uneven collecting effort among habitats. More generally, either previous documentations were not representative of larger-scale distributional patterns, or our analyses lack statistical power.

Moreover, geographic segregation does not necessarily have to be latitudinal. In fact, we used latitude only as an initial measure to evaluate whether geographic segregation is a common pattern. Geographic segregation might sort out more frequently in other dimensions, such as Atlantic versus Pacific drainage, elevation, temperature, or habitat features that may or may not be correlated with latitude. Habitat features have been shown to differentially influence abundances of sexes at local scales in many wintering parulid warblers (Rappole and Warner 1980, Lynch et al. 1985, López Ornat and Greenberg 1990, Wunderle 1992, Parrish and Sherry 1994, Wallace et al. 1996, Murphy et al. 2001). Local habitat segregation on wintering grounds has been reported in other species as well (Nisbet and Medway 1972, Rappole 1995). All those factors suggest that local patterns of sexual segregation may not be representative across the winter range. Just as habitat use and overall density of many species in winter vary with latitude, so may sex ratios.

Although our results indicate winter latitudinal sexual segregation in several species, our data were not collected in the context of studies designed for such analysis. Although we are unsure of the real biases in the data, we believe that the data come from sufficiently diverse sources so that biases have not obscured real patterns. We hope that the present study inspires new field studies specifically designed to address questions of geographic segregation. In spite of the growing literature on sexual segregation in some long-distance migratory bird species (Cristol et al. 1999, Nebel et al. 2002, results presented herein), this pattern has not been reported for many long-distance Nearctic–Neotropical migrants, nor has it been reported for any Palearctic or Austral migrants. We suggest that such patterns may prove widespread, once broad-scale data sets covering large portions of winter ranges become accessible. Because many winter ranges are in tropical areas, which tend to be undersampled in museum collections, expansion of museum collections of wintering migratory birds would be useful to elucidate these phenomena.

Acknowledgments

We thank M. T. Murphy, G. E. Wallace, and three anonymous reviewers for comments on the manuscript. Museums supplying access to specimens and associated data are listed in the Methods section and in the Appendix. G. Alvarado, J. Dean, G. K. Hess, N. H. Rice, M. B. Robbins, and V. H. Tejera-N. kindly helped us extract data from museum collections. A. Gordillo georeferenced specimen localities for the Atlas of Mexican Bird Distributions. O.K. acknowledges the support of a National Science Foundation Graduate Research Fellowship. The *Atlas of Mexican Bird Distributions* project was funded by CONABIO, CONACyT, DGAPA-UNAM, British Council (Mexico), and the U.S. National Science Foundation.

Literature Cited

American Ornithologists' Union. 1998. Checklist of North American Birds, 7th ed. American Ornithologists' Union, Washington, D.C.

Binford, L. C. 1989. A distributional survey of the birds of the Mexican state of Oaxaca. Ornithological Monographs, no. 43.

Cristol, D. A., M. B. Baker, and C. Carbone. 1999. Differential migration revisited: Latitudinal segregation by age and sex class. Pages 33–88 *in* Current Ornithology, vol. 15 (V. Nolan, Jr., E. D. Ketterson, and C. F. Thompson, Eds.). Plenum Press, New York.

Howell, T. R. 1953. Racial and sexual differences in migration in *Sphyrapicus varius*. Auk 70:118–126.

Humple, D. L., N. Nur, G. R. Geupel, and M. P. Lynes. 2001. Female-biased sex ratio in a wintering population of Ruby-crowned Kinglets. Wilson Bulletin 113:419–424.

Hunt, P. D., and D. J. Flaspohler. 1998. Yellow-rumped Warbler (*Dendroica coronata*). *In*

The Birds of North America, no. 376 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

Johnston, D. W. 1970. Age and sex distribution in Indigo Buntings. Bird-Banding 41: 113–118.

Ketterson, E. D., and V. Nolan, Jr. 1976. Geographic variation and its climatic correlates in the sex ratio of eastern-wintering Dark-eyed Juncos (*Junco hyemalis hyemalis*). Ecology 57:679–693.

Ketterson, E. D., and V. Nolan, Jr. 1983. The evolution of differential bird migration. Pages 357–402 *in* Current Ornithology, vol. 1 (R. F. Johnston, Ed.). Plenum Press, New York.

King, J. R., D. S. Farner, and L. R. Mewaldt. 1965. Seasonal sex and age ratios in populations of the White-crowned Sparrows of the race *gambelii*. Condor 67:489–504.

Lack, D. 1954. The Natural Regulation of Animal Numbers. Clarendon Press, Oxford.

Laskey, A. R. 1935. Mockingbird life history studies. Auk 52:370–381.

López Ornat, A., and R. Greenberg. 1990. Sexual segregation by habitat in migratory warblers in Quintana Roo, Mexico. Auk 107: 539–543.

Lynch, J. F., E. S. Morton, and M. E. Van der Voort. 1985. Habitat segregation between the sexes of wintering Hooded Warblers (*Wilsonia citrina*). Auk 102:714–721.

Morton, E. S. 1990. Habitat segregation by sex in the Hooded Warbler: Experiments on proximate causation and discussion of its evolution. American Naturalist 135: 319–333.

Murphy, M. T., A. Pierce, J. Shoen, K. L. Murphy, J. A. Campbell, and D. A. Hamilton. 2001. Population structure and habitat use by overwintering Neotropical migrants on a remote oceanic island. Biological Conservation 102:333–345.

Navarro S., A. G., A. T. Peterson, and A. Gordillo-Martínez. 2002. A Mexican case study on a centralised data base from world natural history museums. Data Science Journal 1:45–53.

Navarro S., A. G., A. T. Peterson, and A. Gordillo-Martínez. 2003. Museums working together: The atlas of the birds of Mexico. Pages 207–225 *in* Why Museums Matter: Avian Archives in an Age of Extinction (N. Collar, C. Fisher, and C. Feare, Eds.). Bulletin of the British Ornithologists' Club, Supplement 123A.

Nebel, S., D. B. Lank, P. D. O'Hara, G. Fernández, B. Haase, F. Delgado, F. A. Estela, L. J. Evans Ogden, B. Harrington, B. E. Kus, and others. 2002. Western Sandpipers (*Calidris mauri*) during the nonbreeding season: Spatial segregation on a hemispheric scale. Auk 119:922–928.

Nice, M. M. 1937. Studies in the life history of the Song Sparrow, I. Transactions of the Linnaean Society of New York, no. 4.

Nisbet, I. C. T., and L. Medway. 1972. Dispersion, population ecology and migration of Eastern Great Reed Warblers *Acrocephalus orientalis* wintering in Malaysia. Ibis 114:451–494.

Parrish, J. D., and T. W. Sherry. 1994. Sexual habitat segregation by American Redstarts wintering in Jamaica: Importance of resource seasonality. Auk 111:38–49.

Pearson, D. L. 1980. Bird migration in Amazonian Ecuador, Peru, and Bolivia. Pages 273–283 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation (A. Keast and E. S. Morton, Eds.). Smithsonian Institution Press, Washington, D.C.

Perneger, T. V. 1998. What's wrong with Bonferroni adjustments. British Medical Journal 316:1236–1238.

Peterson, A. T., A. G. Navarro-Sigüenza, and H. Benítez-Díaz. 1998. The need for continued scientific collecting: A geographic analysis of Mexican bird specimens. Ibis 140:288–294.

Rappole, J. H. 1995. The Ecology of Migrant Birds: A Neotropical Perspective. Smithsonian Institution Press, Washington, D.C.

Rappole, J. H., and D. W. Warner. 1980. Ecological aspects of migrant bird behavior in Veracruz, Mexico. Pages 353–393 *in* Migrant Birds in the Neotropics: Ecology, Behavior, Distribution, and Conservation (A. Keast and E. S. Morton, Eds.). Smithsonian Institution Press, Washington, D.C.

Remsen, J. V., Jr. 2001. True winter range of the Veery (*Catharus fuscescens*): Lessons for determining winter ranges of species that winter in the tropics. Auk 118:838–848.

Russell, K. B. 1981. Differential winter distribution by sex in birds. M.S. thesis, Clemson University, Clemson, South Carolina.

SELANDER, R. K. 1966. Sexual dimorphism and differential niche utilization in birds. Condor 68:113–151.

SHERRY, T. W., AND R. T. HOLMES. 1997. American Redstart (*Setophaga ruticilla*). *In* The Birds of North America, no. 277 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.

SOKAL, R. R., AND F. J. ROHLF. 1995. Biometry, 3rd ed. W. H. Freeman and Company, New York.

VIDAL, R. M., C. MACÍAS-CABALLERO, AND C. D. DUNCAN. 1994. The occurrence and ecology of the Golden-cheeked Warbler in the highlands of northern Chiapas, Mexico. Condor 96:684–691.

WALLACE, G. E., H. GONZÁLEZ ALONSO, M. K. MCNICHOLL, D. RODRÍGUEZ BATISTA, R. OVIEDO PRIETO, A. LLANES SOSA, B. SÁNCHEZ ORIA, AND E. A. H. WALLACE. 1996. Winter surveys of forest-dwelling Neotropical migrant and resident birds in three regions of Cuba. Condor 98:745–768.

WUNDERLE, J. M., JR. 1992. Sexual habitat segregation in wintering Black-throated Blue Warblers in Puerto Rico. Pages 299–307 *in* Ecology and Conservation of Neotropical Migrant Landbirds (J. M. Hagan III and D. W. Johnston, Eds.). Smithsonian Institution Press, Washington, D.C.

Associate Editor: M. T. Murphy

APPENDIX

Scientific collections contributing specimen data to the *Atlas of Mexican Bird Distributions* project (Peterson et al. 1998; Navarro S. et al. 2002, 2003), and from which data were used in our analyses, include the following: Academy of Natural Sciences, Philadelphia; American Museum of Natural History, New York; Bell Museum of Natural History, Minneapolis; British Museum (Natural History), Tring; Canadian Museums of Nature, Ottawa; Carnegie Museum of Natural History, Pittsburgh; Delaware Museum of Natural History, Wilmington; Denver Museum of Natural History, Denver; The Field Museum, Chicago; Fort Hays State University, Hays (Kansas); Iowa State University, Ames; Louisiana State University Museum of Natural Science, Baton Rouge; Moore Laboratory of Zoology, Occidental College, Los Angeles; Museo de Zoología, Facultad de Ciencias, Universidad Nacional Autónoma de México, México (D.F.); Museum of Comparative Zoology, Harvard University, Cambridge; Muséum Nationale d'Histoire Naturelle, Paris; Museum of Vertebrate Zoology, Berkeley; Natural History Museum of Los Angeles County, Los Angeles; Natuurhistorische Museum, Amsterdam; Peabody Museum, Yale University, New Haven; Royal Ontario Museum, Toronto; San Diego Natural History Museum, San Diego; Southwestern College, Winfield (Kansas); Texas Cooperative Wildlife Collection, College Station; Universidad Michoacana de San Nicolás de Hidalgo, Morelia; University of Arizona, Tucson; University of British Columbia Zoology Museums, Vancouver; University of California at Los Angeles; University of Kansas Natural History Museum, Lawrence; University of Nebraska, Lincoln; U.S. National Museum of Natural History, Washington, D.C.; and Western Foundation of Vertebrate Zoology, Camarillo (California).