

RATES VERSUS COUNTS: FALL MOLTS OF LUCY'S WARBLERS (*VERMIVORA LUCIAE*)

Author(s): Sievert Rohwer, Adolfo G. Navarro, Gary Voelker

Source: *The Auk*, 124(3):806-814. 2007.

Published By: The American Ornithologists' Union

DOI: 10.1642/0004-8038(2007)124[806:RVCFMO]2.0.CO;2

URL:

<http://www.bioone.org/doi/full/10.1642/0004-8038%282007%29124%5B806%3ARVCFMO%5D2.0.CO%3B2>

BioOne (www.bioone.org) is an electronic aggregator of bioscience research content, and the online home to over 160 journals and books published by not-for-profit societies, associations, museums, institutions, and presses.

Your use of this PDF, the BioOne Web site, and all posted and associated content indicates your acceptance of BioOne's Terms of Use, available at www.bioone.org/page/terms_of_use.

Usage of BioOne content is strictly limited to personal, educational, and non-commercial use. Commercial inquiries or rights and permissions requests should be directed to the individual publisher as copyright holder.



RATES VERSUS COUNTS: FALL MOLTS OF LUCY'S WARBLERS (*VERMIVORA LUCIAE*)

SIEVERT ROHWER,^{1,4} ADOLFO G. NAVARRO,² AND GARY VOELKER³

¹Department of Biology and Burke Museum, Box 353010, University of Washington, Seattle, Washington 98195, USA;

²Museo de Zoología, Departamento de Biología Evolutiva, Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado Postal 70-399, México D.F. 04510, Mexico; and

³Department of Biology, University of Memphis, 3700 Walker Avenue, Memphis, Tennessee 38152, USA

ABSTRACT.—New specimens from Sinaloa, Mexico, as well as two older specimens, show that both adult and recently fledged Lucy's Warblers (*Vermivora luciae*) often move far south of their breeding grounds to molt in the tropical deciduous forests of northwestern Mexico. Remarkably, the first preformative (= first prebasic) molt is complete in Lucy's Warblers, including the replacement of flight feathers, primary coverts, and rectrices; thus, previous aging criteria based on the wear and appearance of these feathers are invalid. We suggest that the recent conclusion that Lucy's Warblers molt on their breeding grounds (Voelker and McFarland 2002) is an artifact of more collecting in the southwestern United States than in western Mexico during late summer. An index of relative collecting in Mexico and the United States, as well as data from constant-effort mist netting, suggest that most Lucy's Warblers move south to molt. Received 11 November 2005, accepted 22 June 2006.

Key words: aging criteria, collecting effort, Lucy's Warbler, Mexican monsoon, molt migration, *Vermivora luciae*.

Tasas versus Conteos: Mudas de Otoño de *Vermivora luciae*

RESUMEN.—Nuevos especímenes de Sinaloa, México, y dos especímenes más antiguos, muestran que tanto los adultos como los juveniles recién emplumados de *Vermivora luciae* se mueven frecuentemente hacia el sur de su área de distribución reproductiva para mudar en los bosques deciduos tropicales del noroeste de México. Llamativamente, la primera muda preformativa (= primera prebásica) de *V. luciae* es completa, incluyendo el recambio de las plumas de vuelo, las cobertoras primarias y las rectrices. Por lo tanto, los criterios empleados en el pasado para estimar la edad, basados en el desgaste y la apariencia de estas plumas son inválidos. Sugerimos que la conclusión reciente de que *V. luciae* muda en sus áreas reproductivas (Voelker and McFarland 2002) es un artefacto de una mayor colecta a fines del verano en los estados del suroeste de Estados Unidos que en el oeste de México. Un índice de colecta relativa en México y Estados Unidos, así como datos de esfuerzo constante de captura con redes de niebla, sugieren que la mayoría de los individuos de *V. lucidae* se mueven hacia el sur para mudar.

AT LEAST HALF the passerines that breed in western North America and winter mostly south of the United States complete all or part of their fall migration before molting

(Rohwer et al. 2005). We call these movements "molt migrations." Some molt migrants winter where they molt, but most pause to molt and then move farther south for the winter. That so many western passerines migrate before molting has been interpreted as an adaptive response to complementary

⁴E-mail: rohwer@u.washington.edu

ecological "pushes" and "pulls." Dry late-summer conditions in the lowland west are believed to "push" western passerines away from their breeding grounds for molting, whereas abundant food resources associated with the late-summer rains of the Mexican monsoon (Comrie and Glenn 1998) "pull" these migrants to the southwest and western Mexico for molting (Rohwer et al. 2005). In some species, both adults and juveniles are molt migrants, with juveniles migrating in juvenile plumage (Bullock's Oriole [*Icterus bullockii*], Rohwer and Manning 1990; Ash-throated Flycatcher [*Myiarchus cinerascens*], Butler et al. 2006). In other species, molt migrations are undertaken only by adults, whereas juveniles remain behind in the breeding range, where they undergo their postjuvenile molt before migrating (Lazuli Bunting [*Passerina amoena*], Young 1991; Painted Bunting [*P. ciris*], Thompson 1991; western Warbling Vireo [*Vireo gilvus swainsonii*], Voelker and Rohwer 1998; Western Tanager [*Piranga ludoviciana*], Butler et al. 2002).

Variable effort invested in collecting means that simple geographic enumerations of specimens may misinform attempts to deduce the scheduling of molt in relation to migration for species in which some individuals molt on the breeding grounds (Butler et al. 2002) or in which movement south before molting is restricted. Rates, based on collecting effort, are needed to overcome these biases. If juveniles molt on the breeding grounds, a decline in the fraction of late-summer adults shows that adults migrate before molting, provided that there are good samples of juveniles showing that collectors were active in late summer (Young 1991, Voelker and Rohwer 1998, Butler et al. 2002). But for species in which both adults and juveniles move south before molting, changing age ratios cannot establish an early departure by adults.

Voelker and McFarland (2002) predicted that Lucy's Warblers (*Vermivora luciae*) should depart from the drier areas of their breeding range to molt in the region of the Mexican monsoon. Because the 18 presumed molting adults that they examined were collected within the breeding range, Voelker and McFarland (2002) concluded that Lucy's Warbler was not a molt migrant. However, molt-related movements in Lucy's Warbler are difficult to assess, because its

breeding range extends only a limited distance north of the northern limits of the monsoon region. These rains begin earlier and are heavier and more predictable in the south than in the north (Comrie and Glenn 1998); thus, species like Lucy's Warblers, whose southern breeding limits include only the northern part on the monsoon region, may benefit from moving south to areas of greater rain to molt.

Here, we show that Lucy's Warbler is a molt migrant. We further show that the postjuvenile molt in Lucy's Warbler is complete, a result that invalidates aging criteria based on retained juvenile flight feathers, rectrices, and primary coverts (Bent 1953, Curson et al. 1994, Johnson et al. 1997, Pyle 1997). Hereafter, we will refer to the postjuvenile molt as the "first preformative molt" (Howell et al. 2003), replacing the term "first prebasic" from Humphrey and Parkes (1959).

METHODS

Our discovery that Lucy's Warbler is a molt migrant is based on eight critical specimens collected in late July 2005 in Sinaloa on a joint expedition of the University of Washington Burke Museum (UWBM) and the Museo de Zoología, Facultad de Ciencias, at the Universidad Nacional Autónoma de México (MZFC). All specimens were aged by skull ossification and by noting the presence or absence of the bursa of Fabricius. For comparative purposes, we also examined 24 late-summer specimens from the Delaware Museum of Natural History (DMNH) and 12 spring specimens from the UWBM.

To assess seasonal changes in collecting effort for Mexico, we used the database developed at MZFC (Peterson et al. 1998, Navarro et al. 2003). This database covers more than 70 important collections (44 held specimens appropriate to this study) in Mexico, the United States, Canada, and Europe. An initial search of this database revealed that just seven Lucy's Warblers had been collected in Mexico in August and September, which emphasizes the importance of attention to collecting effort in assessing whether or not Lucy's Warbler is a molt migrant. To specifically assess potential biases in collecting effort for Lucy's Warbler, we re-evaluated the 430 specimen records from 25 U.S. and Canadian museums used by Voelker and McFarland (2002).

RESULTS

Extent of the first preformative molt.—With one exception, the critical specimens in Table 1 were aged by skull ossification; bursa data confirmed the skull data for the eight 2005 specimens. Surprisingly, six of the nine immatures listed in Table 1 were molting primaries and had started this molt at P1. Two of these specimens are at very early stages of the primary (P) molt, and the quality of the plumage of these two specimens, as well as that of the three immatures that had not commenced the primary molt (Table 1), matches that of three newly fledged juveniles at the DMNH. All lack rufus in their crowns and are pale rufus in their rumps, known age characters for Lucy's Warblers in juvenile plumage (Pyle 1997). These specimens indicate that the first preformative molt of Lucy's Warbler is often complete and that the aging characters described for Lucy's Warblers that have completed the fall molt—color and wear of the primary coverts, and primary and rectrix wear—are invalid (Bent 1953, Curson et al. 1994, Johnson et al. 1997, Pyle 1997). This means that Voelker and McFarland's (2002) sample of "adults" surely includes molting hatch-year birds without age data on their labels. Additionally, their regression estimate of the duration of the primary molt in "adults" likely includes juveniles without age data on their

labels. Voelker and McFarland (2002) excluded the five molting juveniles from the DMNH (Table 1) with age data on their labels from their estimate of molt duration.

Most temperate passerines retain the juvenile primary coverts until the end of the first potential breeding season, including species that replace some outer primaries in the first preformative molt (Rohwer 1986, Pyle 1997). When juvenile primary coverts are replaced, each is typically molted with its corresponding primary; thus, we carefully assessed replacement of the greater primary coverts in young Lucy's Warblers that were replacing primaries (Table 1). The juvenile primary coverts are edged with buff, as shown by three DMNH specimens in full juvenile plumage (9927, 45561, and 46856) and by our three new specimens that had not commenced the first preformative molt (Table 1). Six juveniles in Table 1 are molting primaries. In two specimens, primary molt had progressed only to P2, so replacement of the coverts could not be assessed without damage to the specimen. In two other specimens, molt had progressed to P5 and P7, and these specimens show new gray-edged primary coverts associated with their replaced inner primaries and buff-edged, juvenile coverts associated with their unreplaced juvenile primaries. In the two remaining immatures, P9 is almost fully grown and all the primary coverts are newly replaced

TABLE 1. Critical specimens demonstrating molt migration in Lucy's Warbler.

Museum no.	Age by skull	Date	Locality	South of breeding range?	Outermost growing primary
UWBM 81158	Ad	27 July 2005	El Fuerte, Sinaloa, Mexico	Yes	P2
MZFC 19637	Ad	27 July 2005	El Fuerte, Sinaloa, Mexico	Yes	P5
UWBM 81346	Ad	27 July 2005	El Fuerte, Sinaloa, Mexico	Yes	P4
MZFC 19638	Ad	29 July 2005	El Fuerte, Sinaloa, Mexico	Yes	P4
MZFC 19636	Im	18 July 2005	Rosario, Sinaloa, Mexico	Yes	All juvenile
UWBM 81348	Im	27 July 2005	El Fuerte, Sinaloa, Mexico	Yes	All juvenile
UWBM 81351	Im	27 July 2005	El Fuerte, Sinaloa, Mexico	Yes	P2
UWBM 81243	Im	27 July 2005	El Fuerte, Sinaloa, Mexico	Yes	All juvenile
DMNH 32623	Im ^a	16 Aug 1956	Litchfield Park, Arizona, USA	No	P2
DMNH 32611	Im	21 Aug 1968	Obregón, Sonora, Mexico	Yes	P7
DMNH 32618	Im	25 Aug 1936	Tucson, Arizona, USA	No	P5
DMNH 32558	Im	28 Sept 1954	Obregón, Sonora, Mexico	Yes	P9
DMNH 32626	Im	5 Oct 1948	Valentine, Arizona, USA	No	P9

^a This specimen had no data on skull ossification but carried remnants of juvenile body plumage.

Museum abbreviations: UWBM = University of Washington Burke Museum; MZFC = Museo de Zoología, Facultad de Ciencias collection at Universidad Nacional Autónoma de México; DMNH = Delaware Museum of Natural History.

and edged in gray. Thus, our four specimens that were collected when the first preformative molt was advanced enough to assess replacement of the greater primary coverts show these coverts to be replaced as their corresponding primaries are replaced.

To further assess whether the first preformative molt is usually complete, we examined (1) the rectrices in 12 spring specimens at the UWBM taken in Arizona in late March and April and (2) the four DMNH immatures with advanced primary molt (Table 1) for replacement of rectrices and primary coverts. The Arizona specimens were examined with the assumption that some of these birds should have fledged the preceding summer. Although some had worn central rectrices, there was no indication of any bimodality in rectrix or primary wear, which would be expected if the first preformative molt were sometimes incomplete. Further, all had replaced their juvenile primary coverts, which were little worn and gray-edged. Three of the four DMNH specimens were replacing the central rectrices (the fourth could not be assessed), which suggests that all rectrices are also replaced in the first preformative molt.

Molting specimens south of the breeding range.—Ten of the 13 specimens listed in Table 1 demonstrate that some Lucy's Warblers move far south of their breeding ground to molt. Eight of these specimens were collected by the authors in Sinaloa in late July 2005; seven near El Fuerte, which is >400 km south of the southern edge of the breeding range shown in Johnson et al. (1997); and one near Rosario, which is >700 km from the southern edge of the breeding range. Three of these newly collected specimens (MZFC 19636 and UWBM 81348, 81243) demonstrate that some immatures migrate south in full juvenile plumage before their first preformative molt. Two additional specimens in Table 1 were taken just north of Ciudad Obregón, Sonora, which is ~300 km south of the southern edge of the breeding range. Both specimens had excellent age data indicating that they were immatures. Voelker and McFarland (2002) did not record DMNH 32558 as molting, no doubt because P9 is fully grown in the left wing but slightly short and sheathed at its base in the right wing. Specimen DMNH 32611 was in heavy molt and taken well south of the breeding range, but Voelker and McFarland (2002) eliminated this specimen because it was

known to be an immature by well-annotated skull-ossification data. Thus, by attempting to exclude hatch-year birds from their analyses, Voelker and McFarland (2002) eliminated the only previously existing specimens molting far south of the breeding grounds (DMNH 32611 and 32558 in Table 1).

The eight Lucy's Warblers we collected in 2005 were all taken in coastal tropical deciduous forest of Sinaloa, which leafs out in response to the late-summer monsoon rains. These specimens and four other Lucy's Warblers we observed, together with an abundance of Ash-throated Flycatchers and Bullock's Orioles, and fair numbers of western Warbling Vireos and Black-headed Grosbeaks (*Pheucticus melanocephalus*) (all molt migrants; Rohwer et al. 2005), suggest that the tropical deciduous forest of western Mexico may be an important molt stopover habitat for woodland-dependent molt migrants. Ciudad Obregón, the locality for the two other molting Lucy's Warblers taken south of the breeding range (Table 1), consisted of a riparian corridor along the Yaqui River with Sonoran desert habitat on the hillsides.

Assessing collecting effort.—To illustrate how seasonal and geographic biases in collecting can affect conclusions about the scheduling of molt and migration, we summarize passerine holdings for the monsoon states of Sonora, Sinaloa, and Baja California Sur in Figure 1. These data came from a database developed by Navarro et al. (2003) for 221,757 Mexican specimens in scientific collections: 10,524 specimens from Sonora, 7,794 from Sinaloa, and 8,713 from Baja California Sur. Parsing these totals into percentages by month (Fig. 1) shows minimal collecting in these states during August and September—peak months for monsoon molting. For all passerine species, only 273 specimens have been collected in Sonora in September (2.6% of all Sonora specimens), only 281 have been collected in Sinaloa in August (3.6% of Sinaloa specimens), and only 222 have been collected in Baja California Sur in September (2.5% of Baja Sur specimens; Fig. 1). Yet Sonora, Sinaloa, and Baja Sur appear to be the most important states for migrant passerines that move to the region of the Mexican monsoon to molt (Thompson 1991, Young 1991, Voelker and Rohwer 1998, Butler et al. 2006).

Because both age classes migrate before molting in Lucy's Warbler, the fraction of adults in samples of adults and juveniles, split by region

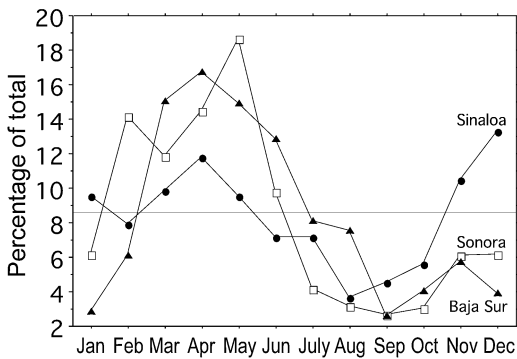


FIG. 1. Collecting effort by month for Sinaloa, Sonora, and Baja California Sur, Mexico, expressed as a percentage of all passerines from these states in 44 scientific collections. If collecting effort had been constant across all months, points would fall around the 8.3% line.

and date, cannot be used to assess collecting effort. This index helps correct biases in collecting effort in species where adults and immatures have different molt-migration schedules (Young 1991, Voelker and Rohwer 1998, Butler et al. 2002). For species in which both adults and juveniles move south before molting (Rohwer and Manning 1990, Butler et al. 2006), other corrections for variation in collecting effort are required.

The late-summer monsoon is more intense in Mexico than in the United States (Comrie and Glenn 1998). Thus, one approach to correcting for seasonal changes in collecting effort is to compare the numbers of spring and molting-season specimens taken in Mexico and the United States (Table 2). We defined April and May specimens as spring-taken and use samples from these cooler months, immediately after spring arrival in March, as an index of the effort collectors might devote to a region during the molting season. For the molting season, we included

specimens from 15 July to 30 September, following the molt dates established for Lucy's Warblers by Voelker and McFarland (2002; their fig. 1). Although Voelker and McFarland's (2002) regression analysis suggests that the molt in adult Lucy's Warbler ends shortly after mid-September, we included birds taken through 30 September, because juveniles usually molt later than adults in other species and appear to do so in Lucy's Warbler as well (Table 1).

The 2×2 contrast for this comparison (Table 2) shows that the percentage of molting-season Lucy's Warblers is much higher for Mexico (43%) than the United States (16%). If spring collecting effort reliably indexes fall collecting effort in these regions, this analysis offers clear evidence of movement south before molting. If anything, we would presume that collecting effort has been relatively low in late summer in Sonora (where collecting was usually conducted on expeditions), compared with late summer in the United States (where collectors often made day trips to acquire specimens). This bias, if it exists, would further exaggerate the contrast in Table 2. On the other hand, if there had been little collecting directed at Lucy's Warblers in April and May in Mexico, the contrast we show in Table 2 would diminish or disappear all together. We doubt that there has been any disproportionate bias against collecting Lucy's Warblers in spring in Mexico, because there were 20 Mexican specimens in Voelker and McFarland's (2002) samples from March. Further, April and May represent the two peak months of collecting for all passerines in Sonora (Fig. 1).

Data from constant-effort mist netting strongly illustrate how poorly specimen counts index the seasonal abundance of Lucy's Warblers. In 10 years, >400 Lucy's Warbler captures (349 birds and 59 recaptures) were made at Tanque Verde Guest Ranch near Tucson, Arizona (Lamm 1991). Netting effort was

TABLE 2. Lucy's Warblers collected in the United States or Mexico during the molting season (15 July to 30 September) and during spring (April and May). Although the numbers are low, the relative rate at which specimens were collected in Mexico (all from Sonora) is 2.7-fold higher from the molting season than from spring (Fisher's exact test, $P = 0.007$). Lucy's Warblers breed in northern Sonora, where most of the molting season specimens from Mexico were collected.

	Spring (April to May)	Molting season (15 July to 30 September)	Percentage from molting season (%)
United States	160	31	16
Mexico	12	9	43

constant across all months of a year, but the number of Lucy's Warblers captured varied about two-fold across years; thus, we summarize these excellent data using percentage of captures by month. There were few captures in March, when Lucy's Warblers are arriving, and more in April and May (Fig. 2). In June there is a huge peak, accounting for ~50% of annual captures. This peak likely reflects the seasonal recruitment of young and southward migration of adults from breeding populations north of Tucson. Most Lucy's Warblers disappear from the Tucson area in July, and few were netted in August, September, and October, when they should have been common if a significant fraction of the population molted in Arizona.

The contrast between these constant-effort netting data and the specimen record is stunning (Fig. 2). Even though Lucy's Warblers are just arriving in Arizona in March, March and April have been the peak months for collecting them. Numbers of specimens decline almost monotonically from April through October, and even though most of these specimens were collected in Arizona, specimen counts offer no hint that June is the month of peak abundance for Lucy's Warbler in Arizona (Fig. 2).

DISCUSSION

The present study makes three principal points. First, we show that the first preformative molt (Howell et al. 2003) of Lucy's Warbler

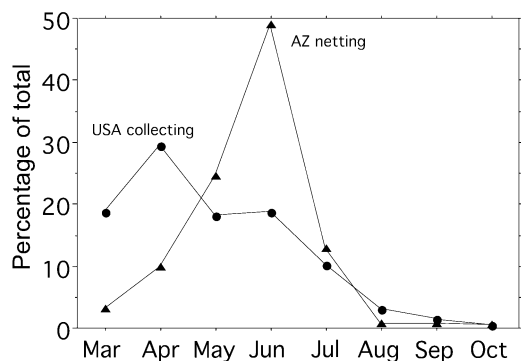


FIG. 2. Percentage of total samples by month (1) for 408 Lucy's Warbler captures at Tanque Verde, near Tucson, Arizona, where netting effort was constant throughout each year, and (2) for 336 Lucy's Warblers (from 26 collections) collected in the United States during the same months.

appears to be complete in hatch-year birds, even though earlier literature suggests otherwise. Second, on the basis of new specimens and a reconsideration of older specimens, we show that Lucy's Warblers should be added to the growing list of birds that move to the region of the Mexican monsoon for molting (Rohwer et al. 2005). Finally, we illustrate how uneven the seasonal distribution of collecting effort has been in the region of the Mexican monsoon (Figs. 1 and 2), and we show how attempts to correct for this uneven effort may modify conclusions based on counts of specimens (Table 2).

Six independently aged juveniles molting their primaries is scarcely a comfortable basis for inferring that the first preformative molt in Lucy's Warbler is always complete (Table 1). Peter Pyle recently sent us photos of a bird netted in November 2005 in Marin County, California (out of normal range), that did not replace the inner two primaries in its first preformative molt. Only Yellow-breasted Chats (*Icteria virens*; Pyle 1997) and Oriente Warblers (*Teretistris fornsi*; Pyle et al. 2004) are known to have partial (eccentric) molts of their primaries in their first fall; thus, Lucy's Warbler appears to be the first parulid and one of only a few passerines known to have complete preformative molts (Jenni and Winkler 1994, Pyle 1997). More molting specimens with internal age data are badly needed to assess the frequency of partial replacement of the primaries in Lucy's Warbler.

Our new specimens add to the world's collections the first molting adult Lucy's Warblers collected well south of the breeding range. This makes Lucy's Warbler the first western breeder with a breeding range lying mostly within the northern reaches of the Mexican monsoon that has been documented to be a molt migrant (Rohwer et al. 2005). Although Voelker and McFarland (2002) showed that some Lucy's Warblers molt in their breeding range, further analysis of their data shows a low relative frequency of molt-season specimens from the United States and a high relative frequency of molt-season specimens from Mexico. For this analysis, the number of spring-taken specimens for these regions provided an index of collecting effort (Table 2).

In the monsoon states of Sonora, Sinaloa, and Baja California Sur, collecting has been minimal for all passerines in August and September, the months when North American molt migrants

move there to molt (Fig. 1). In these molting months, collecting has been one-fourth to one-seventh of that in these same states during months more popular with collectors (Fig. 1). Constant-effort mist netting near Tucson shows remarkable seasonal variability in the number of captures of Lucy's Warblers (Fig. 2), presumably associated with spring arrival, breeding recruitment, and late-summer departure. By contrast, specimen counts decline from early spring (when collectors are eager to be out and birds are in nice plumage) to late summer (Fig. 2), which demonstrates that indirect attempts to correct for collecting effort, even if they are as crude as the analysis in Table 2, are essential for drawing correct conclusions about the scheduling of molt and migration when adults and young move south before molting.

Similar efforts to correct for the combination of seasonal and regional biases in collecting might challenge the published conclusions for Virginia's Warbler (*Vermivora virginiae*; Voelker and McFarland 2002) and for Gray Vireo (*Vireo vicinior*; Voelker 2000). Both species have southerly breeding ranges, making southward movements before molting difficult to demonstrate because of minimal collecting in the monsoon region during August and September (Fig. 1). Ultimately, the best measures of collecting effort will likely be the numbers of other specimens in the world's collections that were collected at comparable times and places; but until the world's collections are accessible online, such analyses remain impractical (Peterson et al. 2005).

Rohwer et al. (2005) showed that an important variable associated with whether or not immatures migrate before or after they molt is the quality of the juvenile plumage. In species where juveniles molt before migrating but adults molt after migrating, the juvenile body plumage is more decomposed than that of adults, having fewer barbs per unit rachis and fewer barbules connecting these barbs (Göhringer 1951, L. Butler et al. unpubl. data). In species where both adults and juveniles migrate before molting, the juvenile plumage is more similar to that of adults, presumably to reduce flutter drag during migration (D. R. Froehlich and S. Rohwer unpubl. data). Lucy's Warblers also fit this pattern: the quality of their juvenile plumage is more like that of adults than is the case for other species of *Vermivora*, such as

the Orange-crowned Warbler (*V. celata*) from the northwest, in which neither adults nor juveniles migrate before molting (L. Butler unpubl. data). Thus, Lucy's Warblers reinforce the trend for the juvenile body plumage to be of high quality (closely resembling that of adults) in molt migrants in which juveniles migrate in juvenile plumage (Rohwer et al. 2005: fig. 8.1).

ACKNOWLEDGMENTS

We thank D. Froehlich, P. Pyle, J. Marks, and an anonymous reviewer for help with the manuscript. The Burke Museum's Endowment for Ornithology and Mexico's SEMARNAT-CONACyT Sectorial Fund (C01-0265) supported our fieldwork. We thank R. Faucett for arranging the expedition, and R. Faucett, V. Rohwer, S. López, E. García, and Ma N. Medina for help in the field. Our new specimens have been deposited at the University of Washington Burke Museum (UWBM) and at the Museo de Zoología, Facultad de Ciencias collection at Universidad Nacional Autónoma de México (MZFC). We especially thank G. Hess, Collections Manager at the Delaware Museum of Natural History (DMNH), for quickly arranging a second loan of their late-summer Lucy's Warblers to S.R. We thank curators of the following collections for access to their Mexican specimen data and for previous loans to G.V.: American Museum of Natural History, Academy of Natural Sciences of Philadelphia, Bell Museum, Museum für Naturkunde Berlin, British Museum (Natural History), Museum Alexander Koenig, Übersee-Museum Bremen, Carnegie Museum of Natural History, California Academy of Sciences, Canadian Museum of Nature, Cornell University, Denver Museum of Natural History, Delaware Museum of Natural History, Fort Hays State College, Field Museum of Natural History, Senckenberg Museum Frankfurt, Instituto de Biología UNAM, Instituto de Historia Natural y Ecología Chiapas, University of Kansas, Los Angeles County Museum of Natural History, Natuurhistorische Museum Leiden, Louisiana State University, Museo de las Aves de México Saitillo, Museum of Comparative Zoology, Moore Laboratory of Zoology, Moscow State University, Museum Mensch und Natur Munich, Museum of Vertebrate Zoology, Royal Ontario Museum, San Diego Natural History Museum, Museum für Naturkunde Stuttgart, Southwestern College,

Universidad Autónoma de Baja California, University of Arizona, University of British Columbia, University of California Los Angeles, Florida Museum of Natural History, University of Michigan Museum of Zoology, University of Washington Burke Museum, United States National Museum, Western Foundation of Vertebrate Zoology, and Peabody Museum Yale University. The Texas Cooperative Wildlife Collection, Barrick Museum, and Utah State University also provided specimens to G.V.

LITERATURE CITED

- BENT, A. C. 1953. Life Histories of North American Wood Warblers. U.S. National Museum Bulletin, no. 203.
- BUTLER, L. K., M. G. DONAHUE, AND S. ROHWER. 2002. Molt-migration in Western Tanagers (*Piranga ludoviciana*): Age effects, aerodynamics, and conservation implications. *Auk* 119:1010–1023.
- BUTLER, L. K., S. ROHWER, AND M. ROGERS. 2006. Prebasic molt and molt-related movements in Ash-throated Flycatchers. *Condor* 108: 647–660.
- COMRIE, A. C., AND E. C. GLENN. 1998. Principal components-based regionalization of precipitation regimes across the southwest United States and northern Mexico, with an application to monsoon precipitation variability. *Climate Research* 10:201–215.
- CURSON, J., D. QUINN, AND D. BEADLE. 1994. Warblers of the Americas: An Identification Guide. Houghton Mifflin, Boston.
- GÖHRINGER, R. 1951. Vergleichende untersuchungen über das juvenile- und adultkleid bei der Amsel (*Turdus merula* L.) und beim Star (*Sturnus vulgaris* L.). *Revue Suisse de Zoologie* 58:279–358.
- HOWELL, S. N. G., C. CORBEN, P. PYLE, AND D. I. ROGERS. 2003. The first basic problem: A review of molt and plumage homologies. *Condor* 105:635–653.
- HUMPHREY, P. S., AND K. C. PARKES. 1959. An approach to the study of molts and plumages. *Auk* 76:1–31.
- JENNI, L., AND R. WINKLER. 1994. Moults and Ageing of European Passerines. Academic Press, San Diego, California.
- JOHNSON, R. R., H. K. YARD, AND B. T. BROWN. 1997. Lucy's Warbler (*Vermivora luciae*). In *The Birds of North America*, no. 318 (A. Poole and F. Gill, Eds.). Academy of Natural Sciences, Philadelphia, and American Ornithologists' Union, Washington, D.C.
- LAMM, D. W. 1991. Lucy's Warbler banding in southeastern Arizona. *North American Bird Bander* 16:9–10.
- NAVARRO, 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. J. Collar, C. T. Fisher, and C. J. Feare, Eds.). *Bulletin of the British Ornithologists' Club*, vol. 123A.
- PETERSON, A. T., C. CICERO, AND J. WIECZOREK. 2005. Free and open access to bird specimen data: Why? *Auk* 122:987–990.
- 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.
- PYLE, P. 1997. Identification Guide to North American Birds, part 1: Columbidae to Ploceidae. Slate Creek Press, Bolinas, California.
- PYLE, P., A. MCANDREWS, P. VELÉZ, R. L. WILKERSON, R. B. SIEGEL, AND D. F. DESANTE. 2004. Molt patterns and age and sex determination of selected southeastern Cuban landbirds. *Journal of Field Ornithology* 75:136–145.
- ROHWER, S. 1986. A previously unknown plumage of first-year Indigo Buntings and theories of delayed plumage maturation. *Auk* 103:281–292.
- ROHWER, S., L. K. BUTLER, AND D. R. FROELICH. 2005. Ecology and demography of east-west differences in molt scheduling of Neotropical migrant passerines. Pages 87–105 in *Birds of Two Worlds: The Ecology and Evolution of Migration* (R. Greenberg and P. P. Marra, Eds.). Johns Hopkins University Press, Baltimore, Maryland.
- ROHWER, S., AND J. MANNING. 1990. Differences in timing and number of molts for Baltimore and Bullock's orioles: Implications to hybrid fitness and theories of delayed plumage maturation. *Condor* 92:125–140.
- THOMPSON, C. W. 1991. The sequence of molts and plumages in Painted Buntings and implications for theories of delayed plumage maturation. *Condor* 93:209–235.
- VOELKER, G. 2000. Molt of the Gray Vireo. *Condor* 102:610–618.

- VOELKER, G., AND S. L. MCFARLAND. 2002. Molt patterns and molting grounds of Lucy's and Virginia's warblers: Similar yet different. *Wilson Bulletin* 114:255–263.
- VOELKER, G., AND S. ROHWER. 1998. Contrasts in scheduling of molt and migration in Eastern and Western warbling-vireos. *Auk* 115: 142–155.
- YOUNG, B. E. 1991. Annual molts and interruption of the fall migration for molting in Lazuli Buntings. *Condor* 93:236–250

Associate Editor: E. H. Burt, Jr.