PROGRESS IN OUR UNDERSTANDING OF MOLT PATTERNS IN CENTRAL AMERICAN AND CARIBBEAN LANDBIRDS

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Progress in our understanding of Neotropical bird molt

Abstract. – Information pertaining to molt extent, strategy and timing refine our understanding of the avian life cycle. Despite the importance of describing bird molt, published accounts of molt patterns from Neotropical avifauna remain scarce. In this study we summarized published and unpublished information on molt patterns and timing for resident landbirds found in the Caribbean, Mexico, and Central America. Information on molt could be located for only 34.1% of all resident species, and for only 17.4% of the species was there information on both timing of prebasic molts and extent of preformative molts. Our results suggest the timing of prebasic molts and the extent of preformative molts largely coincide with those of temperate North American landbirds and that significantly fewer resident Neotrpoical landbirds undergo prealternate molts than do Nearctic-Neotropical migrant species.

Keywords: molt, moult, Neotropics, molt extent, molt duration, preformative, prebasic, prealternate

INTRODUCTION

Birds are arguably the most ubiquitously distributed vertebrate taxon throughout the globe (Gill 1995). Feathers provide uniquely avian flight and thermoregulatory capabilities allowing birds to persist in desert, marine, arctic and tropical habitats. The cyclical replacement of feathers, or molt, is the process which facilitates the global success of birds and is, ironically, the least understood phase of the avian life cycle (Pyle 1997, Howell et al. 2003, Ryder and Wolfe 2009, Howell 2010). For example, in November 2011, we used Google Scholar to search articles using the keyword 'tropical' associated with the following phrases: 'bird molt' (and 'moult'), 'bird breeding' and 'bird migration.' We found 1,030 results for molt/moult, 105,000 for breeding, and 58,100 for migration. Disproportionate research effort has led to asynchrony in our collective understanding of the avian life-cycle, particularly in the Neotropics (Ryder and Wolfe 2009, Wolfe et al. 2010).

Understanding the duration, timing, extent, and spatial occurrence of bird molt provides insights into the plasticity and phylogenetic conservation of feather replacement which can influence species distribution. For example, Svensson and Hedenström (1999) found that migratory behavior in Old-World Warblers (Sylviidae) was associated with the presence of an extra inserted molt, the prealternate molt, which presumably aids in mitigating feather wear associated with annual movements between wintering and breeding areas. If the evolution of the prealternate molt preceded annual migrations in Sylviidae, then the prealternate molt probably enabled migratory behavior within the family. Documenting the presence of molt also informs theory regarding plumage coloration and breeding behavior. For example, Pyle and Kayhart (2010) postulated that distinct breeding plumages are more common in migratory landbirds because the presence of the prealternate molt, which may have evolved due to increased solar exposure in migratory species, facilitated subsequent evolution of bright pluamges in males due to sexual selective pressures. Similarly, Wolfe and Pyle (2011) suggested that migratory landbird species rely upon inserted molts as honest signals representative of the parasites, stress, and food resources experienced in tropical latitudes during the establishment of territories on northerly breeding grounds.

In addition to advancing our collective understanding of avian natural history and evolution, molt studies provide the tools necessary to monitor wild bird populations. For example, molt extent often varies by age class, thereby enabling knowledgeable scientists to categorize cohorts and identify trends in productivity (Skalski et al. 2005). Accounts of molt occurrence, duration, and extent have been published for North America (Pyle 1997, Pyle 2008) and Europe (Jenni and Winkler 1994); no comparable resource exists for Central and South American avifauna.

Since the Neotropics represents the next western-hemispheric frontier in contemporary molt studies, and molt strategies in Neotropical species are subject to different environmental constraints than those of Nearctic species, we believe it important to measure our collective progress documenting duration and extent of molt in resident Neotropical avifauna. Here, we provide a literature review of molt data available from Mexico, Central America, and the Caribbean and then compare it to similar literature available from North America. We also compare the number of species exhibiting prealternate and eccentric preformative molts among North American and Central American/Caribbean landbirds. Finally, we examine differences in timing among definitive prebasic molts in North American and Central American/Caribbean landbirds.

METHODS

We restricted our literature and data search to landbird molt information from "Central America," defined here as mainland nations from Mexico south through Panama, and Caribbean Islands from Cuba south through Trindad and Tobago. Central American species are further defined as those that do not breed in the United States. We noted number of species detailed, and whether molt extent and duration were discussed in each source (Table 1). In addition to published sources, we analyzed IBP's (Institute for Bird Populations) MoSI (Monitoreo de Sobrevivencia Invernal; Desante et al. 2005) capture data which was gathered from 170 stations in 14 Caribbean and Central American countries, from 2003 through 2011. MoSI contributors recorded data on body molt, flight-feather molt, and molt limits in six wing-feather tracts to infer the extent of preformative molt and timing of prebasic molts.

Photos of resident tropical birds included in MoSI's ALAS project were also used to infer molt extent; ALAS is a digital-image catalogue of open wings focused on furthering our understanding of molt and ageing in Neotropical landbirds. We also gathered data from IBP's MoMS (Molt Migration and Stopover; Pyle et al. 2009) project which provided data from six banding stations in Mexico from 2007 through 2010. All North American (United States and Canada) bird molt data (occurrence, extent and duration) were gathered from Pyle (1997). Taxonomy follows the American Ornithologists Union (AOU 1998) through the 52nd Supplement (Chesser et al. 2011).

The two databases, Central America/Caribbean (tropical hereafter) and North America (temperate hereafter) were used to summarize the total number of landbird species with available molt data from each region. From these two totals, we derived percentages of tropical and temperate landbirds with partial, incomplete, eccentric, and complete preformative molts. We also determined what percentage of tropical and temperate landbird species exhibit prealternate molts. Timing of the prebasic molt was defined as the proportion of primary molt documented for temperate and tropical species by month. We examined statistical differences between the extent of the preformative molt and presence of the prealternate molt among temperate and tropical landbird species using chi-squared analyses. Finally, we examined timing of the prebasic molt between temperate and tropical landbird species using a t-test of mean distributions.

RESULTS

According to AOU and other resources, there are 394 North American (temperate) and 945 Central American/Caribbean (tropical) landbird species currently recognized. In North America, all 394 landbird species have associated information on molt timing, duration and extent. Of the 945 tropical landbird species, we identified 322 species (34.1%) with some associated molt information. More specifically, out of the 945 tropical landbird species, we identified 164 species (17.4%) with information on both timing and extent of molt.

We found no significant difference between the proportion of species exhibiting different preformative molt extents ($\chi^2 = 2.89$, $P = 0.242$) or proportion of species exhibiting eccentric preformative molts ($\chi^2 = 1.01$, $P = 0.759$) among temperate and tropical landbird species. Conversely, there was a significant difference between the proportion of temperate (28.2%) and tropical (20.4%) landbird species exhibiting prealternate molts ($\chi^2 = 4.7$, $P = 0.031$). Finally, we found no significant difference between the timing of the prebasic molt among temperate and tropical landbird species ($t = 0.179$, $P = 0.86$; Fig. 1).

DISCUSSION

In this study we located and reviewed molt information for 322 of the 945 (34.1%) landbird species that breed in the Central America/Caribbean (tropical) region. When compared to North American (temperate) landbird species, we found no significant difference in the extent of the preformative molt. This result may reflect phylogenetic conservation of molt extent among temperate and tropical taxa; or, conversely, the convergent evolution of preformative molt extent. It may also reflect wide variation in prefromative molt extent, a plastic trait readily shaped by variable environmental constraints. Phylogenetic analyses of preformative molt extent are necessary to elucidate the evolutionary relationships between concordant patterns of feather replacement across taxa and latitudes, and as influenced by varying environmental factors.

Interestingly, we found a significant difference between the presence of the prealternate molt between latitudes, where 20.4% of the tropical and 28.2% of the temperate landbird species exhibited prealternate molt. Out of the 28.2% of the temperate landbird species that exhibit prealternate molts, 52.9% of the species are Nearctic-Neotropic migrants. This finding further supports Pyle and Kayhart's (2010) assertion that the prealternate molt probably evolved to mitigate the effects of increased solar exposure (more hours of sun per year) on feathers relative to resident species (Temperate or Neotropical).

Our analysis found no significant difference between the timing of definitive prebasic molts among tropical and temperate landbirds. Timing of the prebasic molt in temperate species is constrained by the timing of breeding, migration, and low food availability in the winter (e.g. cf. Wolfe et al. 2009a). We believe similar timing among tropical species is probably influenced by three factors: (1) a majority of tropical species appear to undergo the prebasic molt after the breeding season which typically occurs from May through Jul; (2) resource availability is likely highest after rains for most species, which then synchronize prebasic molts; and/or (3) lack of competition from Nearctic-Neotropic Migrants, which are absent or largely so in July through September. We believe these results are not exportable to South America where, for example, resident Central Amazonian landbird species appear to more-commonly molt and breed year-round (Johnson et al. 2012).

Differences in seasonality and resource phenology, along with preliminary evidence from South America (Johnson et al. 2012) make us confident that the timing of the prebasic molt varies greatly in equatorial and southern hemispheric regions relative to Central American avifauna. However, studies focused on resident South American birds show a high degree of similarity among preformative molt extent relative to bird species reviewed in this study (Ryder and Wolfe 2009). Furthermore, prealternate molts in resident tropical birds in equatorial regions appear to be rare (Ryder and Wolfe 2009).

Collectively, we lack the published studies necessary to begin generalizing molt patterns and strategies to all tropical landbirds. Given recent advances in using molt to categorize tropical bird age (Wolfe et al. 2010, Johnson et al. 2011) and increased number of published molt accounts (Guallar et al. 2009; Wolfe et al. 2009a, 2009b), we hope that our collective understanding of Neotropical molt will begin to rival our current understanding of temperate bird molt. Increasing the depth of knowledge pertaining to Neotropical bird molt will inevitably further our ability to monitor tropical bird populations and elucidate the evolutionary history of the tropical avian life-cycle.

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TABLE 1. Sources of information including region of focus and number of study species. Note that many separate references include molt information on the same species.

Source	Number of Species	Region
Dickey and van Rossem (1938)	89	El Salvador
Snow and Snow (1964)	46	Trinidad
Diamond (1974)	10	Jamaica
Foster (1975)	36	Northwestern Costa Rica
Prys-Jones (1982)	10	Dominica
Pyle et al. (2004)	15	Southeast Cuba
Wolfe et al. (2009a)	27	Tortuguero, Costa Rica
Wolfe et al. (2009b)	10	Central Costa Rica
Guallar et al. (2009)	35	West-Central, Mexico
Chase Mendenhall Notes	21	Costa Rica
Peter Pyle specimen and field notes	66	Various locations
Monitoreo de Sobrevivencia Invernal (MoSI)	189	Central America, Caribbean
Molt Migration and Stopover (MoMS)	9	Western Mexico

FIGURE 1. Proportion of species undergoing primary flight feather replacement by month in temperate and tropical regions.