

OVERLAP IN MOLT AND BREEDING PHENOLOGY IN THE HISPANIOLAN WOODPECKER (*MELANERPES STRIATUS*)

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Abstract · Molt patterns, often useful for determining age of individuals and, hence, demographic structure of a population, are generally poorly known for resident Neotropical birds. Neotropical woodpeckers are no exception to this latitudinal bias. We focused on the Hispaniolan Woodpecker (*Melanerpes striatus*) to study molt in regards to age and phenology. The objectives of this study were: (1) to provide the first description of the Hispaniolan Woodpecker's molt pattern, and (2) to describe the relationship of molt within the breeding phenology. For six consecutive breeding seasons (March–July) from 2012 to 2017, we monitored a color-banded population of the Hispaniolan Woodpeckers in a mid-elevation (~ 600 m a.s.l.) landscape of wet forest fragments and cattle pastures in the Dominican Republic. We analyzed standardized photos taken during banding sessions to characterize patterns of retained and replaced feathers, resulting in an accurate method for aging. We found similarities in primary covert replacement and differences in secondary replacement patterns to those of congeners. Breeding birds, regardless of sex, were just as likely to be molting as non-breeding birds showing breeding-molt overlap. We suggest possible reasons for this pattern occurring in primarily tropical avian taxa including ample availability of resources and parasitism defense. This is one of the only studies to document this on an individual rather than population level.

Resumen · Sobreposición de la fenología de muda y la reproducción del carpintero de la española (*Melanerpes striatus*)

Los patrones de muda, comúnmente utilizados para determinar la edad de los individuos y, por lo tanto, la estructura demográfica de una población, son poco conocidos para las aves residentes Neotropicales. Los pájaros carpinteros tropicales no son una excepción a este sesgo latitudinal. Nos centramos en el Carpintero de La Española (*Melanerpes striatus*) para estudiar la muda tanto en lo que respecta a la edad y la fenología. Los objetivos de este estudio fueron: (1) presentar la primera descripción del patrón de muda del Carpintero de la Española y (2) describir su relación con la fenología reproductiva. Durante seis temporadas reproductivas consecutivas, de marzo a julio, desde el 2012 a 2017, monitoreamos una población de Carpinteros de la Española marcados con anillos de color, en un paisaje de elevación media (~ 600 m s.n.m) compuesto por fragmentos de bosque húmedo y pasturas en la República Dominicana. Analizamos las fotos tomadas de manera estandarizada durante el anillamiento para identificar patrones retención y reemplazo de plumas viejas y nuevas. En base a estos resultados desarrollamos un método exacto para determinar la edad. Encontramos similitudes en los patrones del reemplazo de las cubiertas primarias y diferencias en patrones de reemplazo de secundarias con patrones descritos para otras especies del género. No hubo diferencia en la probabilidad de encontrar muda en de pájaros carpinteros reproductores y los no reproductores, demostrando la superposición de muda y reproducción. Sugerimos causas por las cuales éste patrón ocurre principalmente aves tropicales, incluyendo un incremento en la disponibilidad de recursos y mecanismos de defensa de parásitos. Este es uno de los pocos estudios que documentan este patrón en un nivel individual en vez de población.

KEY WORDS: Aging · Breeding phenology · Dominican Republic · Life history · Molt pattern · *Melanerpes striatus* · Picidae · Prebasic molt · Preformative molt

INTRODUCTION

Knowledge of feather molt patterns can serve as a valuable tool for both aging birds and to better understand their life histories (Ryder & Wolfe 2009). Application of this information is perhaps best exemplified by the

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extensive documentation of molt patterns in North American passerines and near-passerines by Pyle (1997), which has been widely used to facilitate the study of wild bird populations. Molt limits, the presence of two or more generations of feathers on an individual, allow field ornithologists to determine a bird's age since the different generations of feathers correspond to distinct molt cycles (Pyle 1997). Like temperate breeding species, many resident tropical species have a partial molt following hatching (preformative molt) that can be used to determine age (Ryder & Wolfe 2009, Johnson & Wolfe 2018). However, because tropical taxa tend to have longer and more flexible breeding periods than those in temperate latitudes (Stutchbury & Morton 2001), tropical molt phenology might not correspond to the “standard” temperate molt phenology (Pyle 1997, Johnson et al. 2011). Wolfe et al. (2010) revised age-classification terminology for tropical taxa, whereby birds' age is classified in relation to the corresponding molt episode rather than a calendar-based categorization. Furthermore, molt descriptions are incomplete or wholly lacking for most tropical species, and this latitudinal bias is especially true for woodpeckers (Picidae), that are less likely to be captured using standard mist-netting techniques (Ryder & Wolfe 2009, Johnson & Wolfe 2018).

North American woodpeckers follow a more complex molt strategy compared to most passerines, allowing them to be more precisely aged to third year (or second cycle basic) and after third year (or after second cycle basic). In late summer and early autumn, both juvenile and adult woodpeckers undergo an annual molt (Pyle & Howell 1995, Pyle 1997, Johnson & Wolfe 2018). For most species, the primaries and rectrices are completely replaced during the preformative molt while most secondaries and all primary coverts are retained. During the following molt, the primaries, secondaries, and greater coverts are completely replaced, but only the 0–5 consecutive outer primary coverts are usually replaced, resulting in the presence of retained juvenile feathers and molt limits. Regular retention of basic secondaries and primary coverts also occurs in third and older basic-plumaged individuals (Pyle & Howell 1995, Pyle 1997) but patterns are usually different and more often asymmetrical than those of second basic plumage. Other Antillean woodpecker species exhibit similar molt patterns (Pyle et al. 2004). For instance, while the West Indian Woodpecker (*Melanerpes superciliaris*) and the Cuban Green Woodpecker (*Xiphidiopicus percussus*) mostly follow the molt strategy of North American woodpeckers, both species usually do not retain secondaries during second or later prebasic molts or primary coverts during third or later prebasic molts (Pyle & Howell 1995, Pyle et al. 2004) Other tropical woodpeckers follow these patterns as well, with molt limits for third year or second cycle basic birds found in the primary coverts as well (Johnson & Wolfe 2018).

In temperate regions, molt and breeding usually occur asynchronously, possibly because of physiological costs (Foster 1974, Dietz et al. 1992, Moreno 2004, Johnson et al. 2012). Molt is considered metabolically “expensive” since birds need to account for the energetic costs of growing feathers and heat loss from reduced insulation (Dietz et al. 1992). In contrast, some tropical breeding residents execute their molt cycles during their reproductive periods, a phenomenon possibly attributable to reduced physiological demands resulting from smaller average clutch sizes or release from the seasonal constraints on food resources that would otherwise be faced in temperate environments (Snow & Snow 1964, Foster 1974, Martin et al. 2000, Johnson et al. 2012). Only a subset of tropical residents are known to display this “molt-breeding overlap” in their life histories and it is possible that molt-breeding overlap occurs more at the population level than the individual level (Pyle et al. 2016); nevertheless, molt-breeding overlap may be found to be more widespread among taxa as the natural history of tropical resident birds is more thoroughly investigated (Snow & Snow 1964; Foster 1974, 1975; Zaias & Breitwisch 1990, Mallet-Rodrigues 2005, Johnson et al. 2012).

The Hispaniolan Woodpecker (*Melanerpes striatus*) is a Neotropical woodpecker species endemic to the island of Hispaniola, where it breeds in most habitats and elevations (Latta et al. 2006). Breeding possibly occurs year-round at lower, coastal elevations, such as Punta Cana, but exhibits a defined season of five to six months (March–August) in at least one mid-elevation (ca. 600 m a.s.l.) population (Latta et al. 2006, LaPergola pers. obs.). The species' natural history remains poorly known. All published research on the Hispaniolan Woodpecker thus far has focused on its foraging behavior in relation to morphology or general natural history while neglecting molt cycle (Selander 1966, Short 1974, Wallace 1974). In this study, we provide the first description of the Hispaniolan Woodpecker's molt pattern and describe how molt covaries with breeding phenology. We expected to find patterns mirroring temperate *Melanerpes* spp.: molt limits in second year (or first cycle formative) observed within the secondary coverts and inner secondaries, molt limits in third year (or second cycle basic) involving retained juvenile primary coverts, and molt limits in older (after second cycle basic) being absent or involving asymmetrical retention of primary coverts (Pyle & Howell 1995, Pyle et al. 2004). Moreover, we expected that there would be an absence or limited extent of breeding-molt overlap as the species exhibits an abbreviated (i.e., mostly restricted to a five-to-six month period) breeding season relative to other tropical taxa.

METHODS

Study site and population. As part of a focal study on Hispaniolan Woodpecker breeding biology, we monitored an individually marked population in the small

Table 1. Total number of Hispaniolan Woodpeckers (*Melanerpes striatus*) captured and uniquely banded during course of study in Jarabacoa, Dominican Republic, from 2012–2017.

Year	Adult females	Adult males	Nestlings
2012	4	3	26
2013	13	18	33
2014	34	38	85
2015	18	18	109
2016	10	9	7
2017	10	11	103
Total	89	97	363

community of Piedra Blanca, 3 km east of Jarabacoa (19°07'09.5"N, 70°34'54.8"W; 550–700 m a.s.l.), La Vega, Dominican Republic, during five field seasons Mar–July of 2012–2017. The site consists of private property in a landscape of mixed pine (*Pinus occidentalis* and *P. caribaea*, Pinaceae) and broadleaf wet forest fragments immersed in a matrix of cattle pastures with isolated or clustered royal palms (*Roystonea hispaniolana*, Arecaceae) and small fragments of secondary vegetation and “living tree” (predominantly *Gliricidia sepium*, Fabaceae) fences.

Capture and data collection. To capture adult woodpeckers, we used two approaches: (1) “ambushing” adults in nest cavities (Stanback & Koenig 1994) and (2) an elevated, dual-tower mist-net system (LaPergola & Keynon in prep.). Ambushing involved monitoring active cavities to determine the stage of nesting. We used light-weight, hollow plastic balls (Wiffle balls) covered in duct tape and tied to monofilament nylon line to cover cavity entrances after birds entered to feed chicks or pre-dawn when birds roosted. To reduce the chance of nest abandonment, we used the ambush capture method one or more weeks before egg-laying or ≥ 22 days post-hatch. The mist net tower system involved erecting two 15.2 m tower poles supported with a series of guy lines and, using pulleys and ropes, raising two stacked 12 m mist nets in front of nesting trees. This method allowed us to reduce disturbance at nests and increase sampling to include woodpeckers nesting in substrates too unstable to climb.

Once captured, each bird received a unique four-band combination consisting of two color bands on one leg and a color band and numbered aluminum band on the other. In total, we banded 186 adult birds (89 females, 97 males; Table 1) and 260 nestlings. Of the 260 nestlings, six were recaptured as adults. We assigned sex based on adult crown color, which is black in females and red in males.

From 2014 to 2017, we photographed birds in the hand using a Nikon d7100 camera with an external flash. To the best of our ability, we attempted to standardize lighting conditions by using a white backdrop

and not photographing in direct sunlight. We included a ruler in each photograph for scale, and photographed the band combination, right eye, head profile, crown, dorsal and lateral views of the beak, back, dorsal view of the tail, and dorsal view of the right wing. If birds exhibited asymmetric molt patterns or limits, we photographed both wings. In the hand, we aged birds as accurately as possible using the criteria established by Pyle & Howell (1995), noting the presence/absence of retained juvenile or basic feathers.

Data analysis. Using generic photo-viewing software that came with the computer’s operating system, we examined photographs of wings, labeling wing feathers from which molt they were grown (e.g., primary coverts were grown in the juvenile molt, greater coverts were grown in the formative molt, etc.). Because this is a Neotropical species with a defined breeding season that partially fits with that of North American breeding birds, we used Pyle & Howell’s (1995) terminology to describe the molt cycle relative to age, later adding in newer Wolfe-Ryder-Pyle (Wolfe et al. 2010) terminology more commonly used for tropical birds. We scored birds as “breeding” in analyses if they were known to have an active nest at time of capture, initiated a nest less than one week after capture, or exhibited breeding characteristics (brood patch, cloacal protuberance) when captured. “Non-breeding” birds included both birds known to lack nests within the sampling period and birds that initiated nesting attempts more than one week after capture.

To test whether molt was more likely to be documented in non-breeding than breeding birds we used a Chi-squared test of independence. Body-feather molt and wing-feather molt were examined independently since the presence of symmetric wing-feather molt indicates the beginning of a molt cycle (Pyle & Howell 1995). Body-feather molt included body feathers or wing coverts growing in with blood-supplied pins.

RESULTS

Molt description. While body molt was observed from March to July (Figure 1A), wing molt only occurred from the end of May through at least July (Figure 1B). The preformative molt was incomplete, with body feathers, most to all greater coverts, up to 5 inner secondaries (including the tertials), and all primaries and rectrices replaced but primary coverts and secondaries retained (Figure 2A–C). The second prebasic molt was also incomplete with secondaries replaced, but all birds ($n = 19$) retained some inner primary coverts (Figures 2D–F). Most birds in definitive plumage showed a complete prebasic molt for subsequent molts, occasionally retaining single primary coverts asymmetrically (Figures 2G–I). No prealternate molt was observed. Juveniles had black crowns, similar to females, and

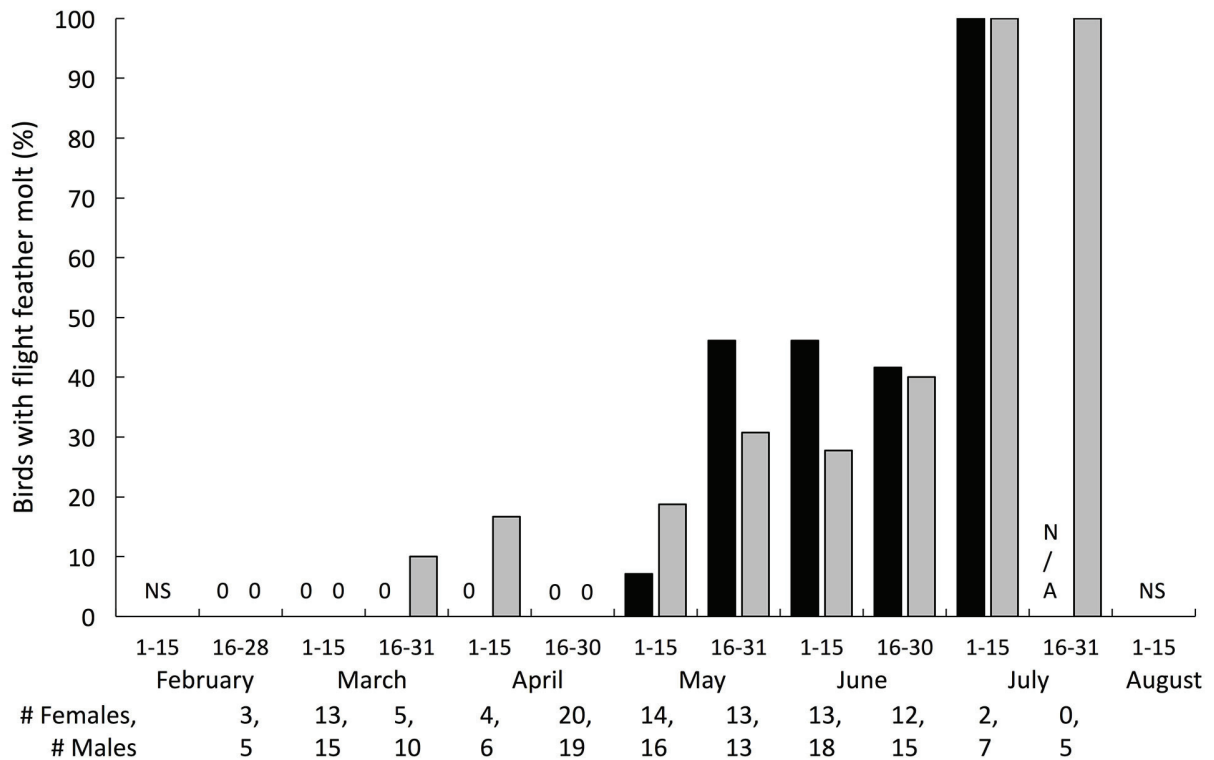
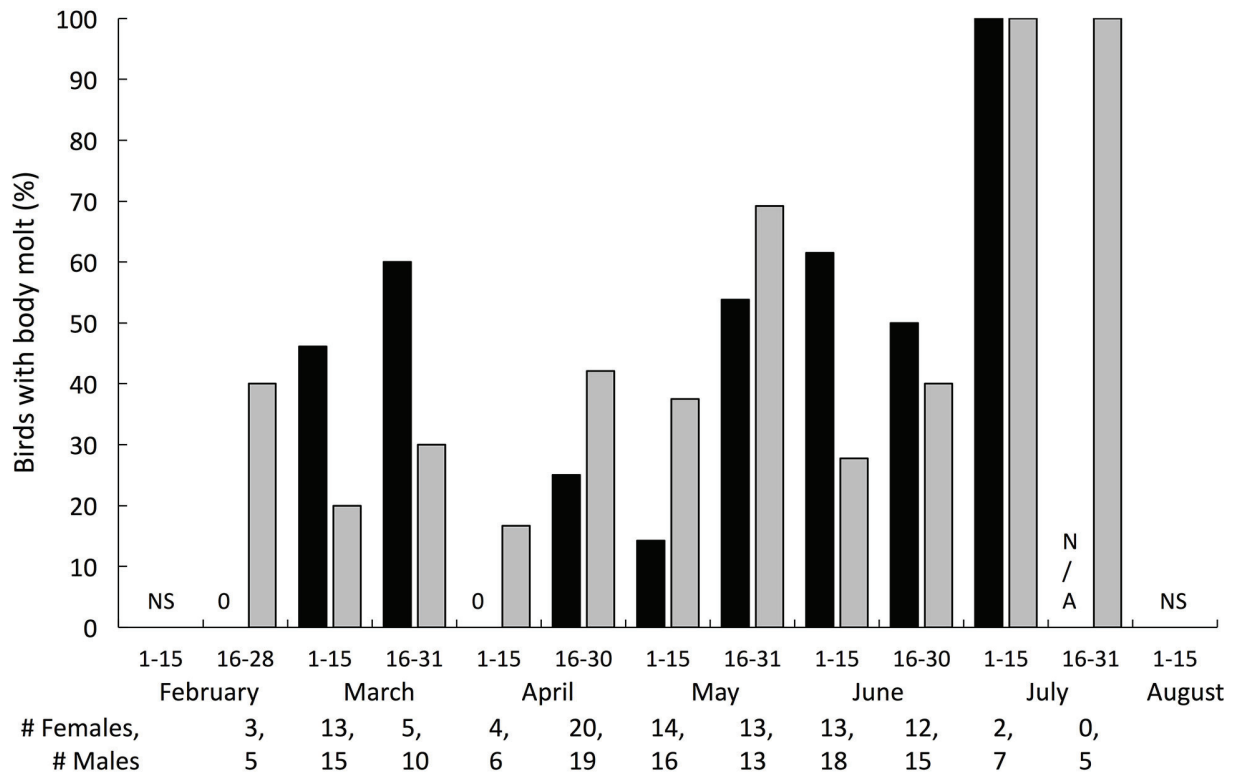


Figure 1. Body feather molt (A) and flight feather molt (B) of Hispaniolan Woodpeckers (*Melanerpes striatus*) documented during the sampling period in Jarabaoca, Dominican Republic, from 2012–2017. Body molt occurred throughout the sampling period for both females (black bars) and males (gray bars), but flight feather molt occurred mostly from early May until late July. Upper and lower numbers below months represent sample sizes for females and males, respectively. “NS” denotes the absence of sampling, and “N/A” appearing above the bar signifies zero captures despite sampling attempts.

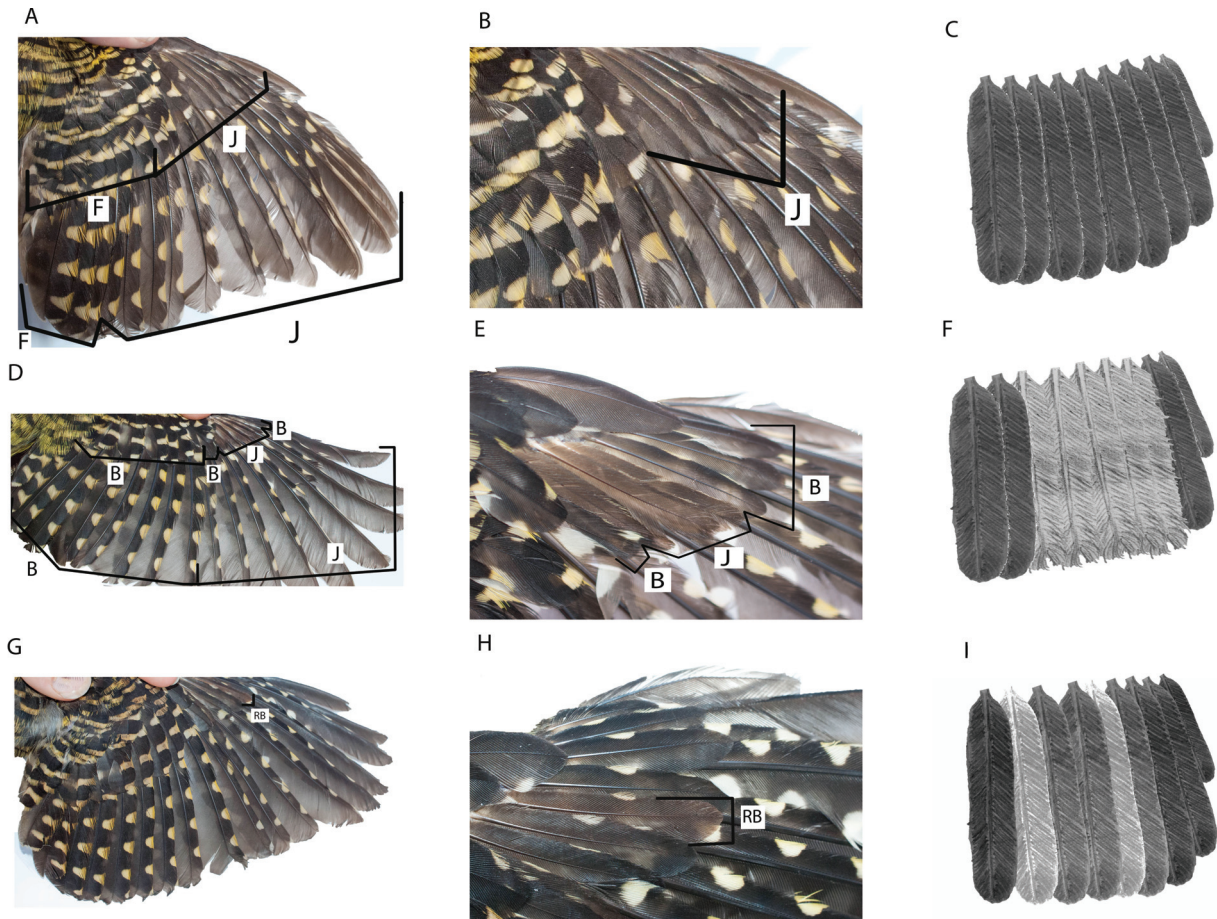


Figure 2. Molt limits for two known-age (banded as nestlings and recaptured as adults) Hispaniolan Woodpecker (*Melanerpes straitus*) (A–F) and one woodpecker first banded as an adult (G–I) in Jarabacoa, Dominican Republic. (A–C) The wing of a known second year (or first cycle formative) bird. The full-wing photo (A) shows that five inner secondaries (including the tertials) were replaced and that the outer two juvenile greater coverts have been retained, resulting in a molt limit with the remaining formative secondary coverts. The close-up photo (B) and diagram (C) illustrate that primary coverts uniformly juvenile. (D–F) The wing of a known third year (or second cycle basic) bird exhibits uniformly basic feathers except for the 5th–8th primary coverts from the outside. The close-up photo (E) and diagram (F) illustrate two generations of primary coverts. (G–I) The wing of a known after third year (or after second cycle basic) bird exhibiting adult basic plumage of one generation except for the retention of two additional generations of basic primary coverts. Although two tertials appear browner they are probably of the same generation as the other secondaries, just more worn due to earlier molt and the increased solar exposure that these feathers endure. The outer three and inner two primary coverts appear new, while the 4th, 6th, and 7th from the outside have been retained one year and the 5th and 8th from the outside has been retained two years as illustrated in the primary coverts close-up photo (H) and diagram (I); this pattern was not symmetrical between the wings. This bird was first banded as an adult in 2013, but the photos (G, H) shows the bird’s plumage when it was recaptured a year later. Feathers are labeled based on the molt in which they were grown: J = juvenile, F = formative, B = basic, RB = retained basic. Photographs: Holly Garrod; drawings: Joshua B. LaPergola.

soon after fledging the males began to molt in a completely red crown (Table 2). Nestlings had gray eyes that started to turn into a creamy yellow after fledging. Adults of both sexes had bright yellow eyes. Birds in juvenile plumage were aged as hatch year (or first cycle juvenile) from Apr–Jul, second year (or first cycle formative) from Feb–Jul, third year (or second cycle basic) from Feb–Jul, and after third year (or after second cycle basic) from Feb–Jul. We recaptured six birds originally banded as nestlings, which matched the predicted molt patterns for their corresponding age class (Table 2).

Molt and breeding phenology. Body molt (Figure 1A) and flight feather molt (Figure 1B) exhibited different phenologies. Body molt occurred throughout the sampling period (from late February to late July) for both sexes (Figure 1A). Flight feather molt occurred mostly later in the sampling period, from early May through late July.

All categories of birds (breeding females, non-breeding females, breeding males, and non-breeding males) did not differ significantly in the proportion exhibiting flight feather molt (Pearson Chi-square test of homogeneity: $\chi^2 = 0.26$, $df = 3$, $p = 0.97$) nor in the proportion exhibiting body molt (Pearson Chi-square

Table 2. Age class and molt pattern of recaptured Hispaniolan Woodpeckers (*Melanerpes striatus*) captured in in Jarabaoca, Dominican Republic, from 2012–2017 after being banded as nestlings. *Age classification: HY = hatch year, SY = second year, TY = third year, ATY = after third year.

Individual	Sex	Hatch date	Recapture date	Age (months)	Age class and diagnostic plumage at recapture*
465	M	22 Mar 2017	8 Jun 2017	2.5	HY – uniform juvenile plumage, molting adult crown
073	F	18 May 2013	7 Mar 2014	10	SY – uniform retained primary coverts, molt limit in greater coverts
018	M	12 Jun 2012	31 May 2014	24	TY – three generations of primary coverts
288	M	8 Apr 2015	29 Mar 2017	24	TY – three generations of primary coverts
317	M	19 Mar 2015	2 May 2017	25.5	TY – three generations of primary coverts
207	M	23 May 2014	3 Jun 2017	36.5	ATY (fourth year) - uniform basic primary coverts

Table 3. Comparison of Hispaniolan Woodpeckers (*Melanerpes striatus*) captured in in Jarabaoca, Dominican Republic, from 2012–2017 undergoing body molt and flight feather molt with sex and breeding status noted.

Sex	Breeding status	Percentage of birds exhibiting flight feather molt	Percentage of birds exhibiting body molt
Male	Breeder	41% (N = 22)	41% (N = 22)
	Non-breeder	38% (N = 16)	69% (N = 16)
	Total	40% (N = 40)	49% (N = 43)
Female	Breeder	42% (N = 26)	42% (N = 26)
	Non-breeder	35% (N = 17)	59% (N = 17)
	Total	39% (N = 38)	53% (N = 38)

test of homogeneity: $\chi^2 = 4.11$, $df = 3$, $p = 0.25$, Table 3). There was no difference between male and female birds exhibiting flight feather molt ($\chi^2 = 0.00$, $df = 1$, $p = 1.00$) and body molt ($\chi^2 = 0.12$, $df = 1$, $p = 0.73$). Among females, there was no difference between breeders and non-breeders that exhibited flight feather molt ($\chi^2 = 0.05$, $df = 1$, $p = 0.83$) and no difference between breeder and non-breeders that exhibited body molt ($\chi^2 = 2.88$, $df = 1$, $p = 0.09$). Among males, there was no difference between breeders and non-breeders that exhibited flight molt ($\chi^2 = 0.21$, $df = 1$, $p = 0.65$), no differences between breeders and non-breeders that exhibited body molt ($\chi^2 = 1.12$, $df = 1$, $p = 0.29$). Non-breeding females and males also did not differ significantly in the prevalence of flight molt (females: 38%, $n = 16$; males: 35%, $n = 17$ individuals; $\chi^2 = 0.02$, $df = 1$, $p = 0.99$) nor body molt (females: 69%, $n = 16$; males: 59%, $n = 17$ individuals; $\chi^2 = 0.35$, $df = 1$, $P = 0.94$).

DISCUSSION

Molt description. We expected molt patterns in the Hispaniolan Woodpecker to mirror those of congeners from temperate areas and closely related species in the Caribbean region (Pyle et al. 2004). While many temperate *Melanerpes* spp. retain secondaries during the second and later prebasic molts, most Hispaniolan Woodpeckers did not, with < 3% of birds retaining any secondary feathers. Hispaniolan Wood-

peckers retained primary coverts in third year (or second cycle basic) birds in a pattern like that of temperate woodpeckers. Likewise, the asymmetric retention of individual secondaries (usually the eighth of 10 secondaries in the Hispaniolan Woodpecker, $n = 6$) and primary coverts in definitive plumaged birds matched what is observed in temperate woodpecker taxa (Pyle & Howell 1995).

Juvenile and female coloration. In many woodpecker species, adult males and females differ in one or a few plumage patches that tend to be brighter or more colorful (often red) in males. Across Picidae, juvenile plumages differ in how much they resemble adult plumages (Winkler et al. 1995). Adult Hispaniolan Woodpeckers match this trend, with females and males differing in the posterior coloration of the crown (black in female and red in males). Juvenile Hispaniolan Woodpecker plumage resembles that of adult females, with males replacing black feathers with red during their preformative molt. This pattern contrasts with that in Acorn Woodpeckers (*Melanerpes formicivorus*), which exhibit a similar type of sexual dichromatism in adults: females and males differ in coloration in only the anterior half of the crown (black in females and red in males). Unlike Hispaniolan Woodpeckers, juvenile Acorn Woodpecker plumage resembles the adult male, with females molting in black crown feathers during the preformative molt (Spray & MacRoberts 1975, Pyle 1997). Pattern

differences between juvenile plumage relative to adult plumage in woodpeckers remains an interesting question and warrants further study (Koenig & Walters 2014).

Molt-breeding overlap. Even though our study population has a defined breeding season (Mar–Aug), individuals exhibited molt-breeding overlap, and breeding birds were just as likely to be molting as non-breeding birds with no differences between males and females. The lack of difference between males and females is perhaps unsurprising given the sharing of parental investment in Hispaniolan Woodpeckers. Because molting and breeding are both energetically expensive, differences in parental investment could select for sexually dimorphic molting strategies. However, both parents in Hispaniolan Woodpeckers provide high levels of parental care, with both sexes incubating and provisioning chicks (LaPergola unpubl. data).

Although molt-breeding overlap may occur regularly in tropical species, which tend to have longer breeding seasons than temperate species, much variation in the prevalence of molt-breeding overlap exists across taxa (Foster 1974, Johnson et al. 2012), including among woodpeckers, and it is possible that overlap occurs more at the population than at the individual level (Pyle et al. 2016). What specifically drives interspecific variation in molt-breeding overlap among woodpeckers is unknown and will likely remain so until more researchers work on tropical woodpeckers. For example, a year-round resident population of Acorn Woodpeckers in central coastal California has a long breeding season (~ 5 months, or ~ 7 months in years with secondary breeding seasons) and exhibits fairly extensive molt-breeding overlap (Koenig & Mumme 1987, Koenig et al. 1995). In contrast, the Red-headed Woodpecker (*Melanerpes erythrocephalus*), which has a shorter breeding season (~ 4 months) and migrates in parts of its range, exhibits very minimal if any overlap (Frei et al. 2017). The Red-bellied Woodpecker (*Melanerpes carolinus*), which has a longer breeding season (~ 5 months) than *M. erythrocephalus* and is not considered migratory, exhibits moderate molt-breeding overlap, at least at the population level (Shackelford et al. 2000). The Golden-fronted Woodpecker (*Melanerpes aurifrons*) is less well studied than its aforementioned congeners, but with a more southerly distribution, no migration, and apparently short breeding season (~ 4 months) in Texas, exhibits minimal molt-breeding overlap (Husak & Maxwell 1998). Together, these data suggest the duration of the breeding season might influence the evolution of molt-breeding, but data from more species are needed to adequately test this hypothesis.

While the selective advantages of molt-breeding overlap remain unknown, one hypothesis proposes that in contrast to more resource-limited and time-constrained temperate breeders, tropical birds have more access to abundant resources, allowing them to

begin molting before breeding ends (Johnson et al. 2012). This hypothesis requires further attention for Hispaniolan Woodpeckers. Although our study population appears to be resident year-round, Neotropical migrants present at the start of breeding and outside the breeding season could alter resource availability. An alternative hypothesis is that resident tropical birds might have a more active immune system due to increased parasite levels, resulting in slower molting process and thus prolonged molt period, which in turn could result in more overlap with the breeding season (Moreno 2004). Nevertheless, the full occurrence and benefits of molt-breeding overlap at the individual level largely remain unexplored. While some studies have documented molt-breeding overlap at the individual level (Hemborg & Lundberg 1998, Echeverry-Galvis & Hau 2013), the majority of studies have focused on this phenomenon at the population level (Moreno 2004, Meet-Rodrigues 2005, Johnson et al. 2012). More complete documentation of molt patterns in tropical species is needed for comparison of life history strategies with temperate regions to increase our understanding of potential evolutionary mechanisms at play in different contexts.

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