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BREEDING SEASONS, MOLT PATTERNS, AND GENDER AND AGE CRITERIA FOR SELECTED NORTHEASTERN COSTA RICAN RESIDENT LANDBIRDS

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ABSTRACT.—Detailed accounts of molt and breeding cycles remain elusive for the majority of resident tropical bird species. We used data derived from a museum review and 12 years of banding data to infer breeding seasonality, molt patterns, and age and gender criteria for 27 common landbird species in northeastern Costa Rica. Prealternate molts appear to be rare, only occurring in one species (*Sporophila corvina*), while presupplemental molts were not detected. Most of our study species (70%) symmetrically replace flight feathers during the absence of migrant birds; molting during this period may limit resource competition during an energetically taxing phase of the avian life-cycle. *Received 30 August 2008. Accepted 19 February 2009.*

Temporal patterns of molt and breeding seasonality are largely unknown for many resident tropical species (Dickey and van Rossem 1938, Snow and Snow 1964, Snow 1976) in contrast to Nearctic-Neotropic migrants (hereafter 'migrants'). One might assume differential molt sequences and extent between latitudes given different natural histories of resident tropical birds in relation to their migrant counterparts. However, preliminary studies indicate that most neotropical residents exhibit molt strategies similar to those in temperate latitudes (Dickey and van Rossem 1938, Diamond 1974, Foster 1975, Prys-Jones 1982, Pyle et al. 2004, Ryder and Wolfe 2009, Wolfe et al. 2009). These strategies include partial to incomplete preformative molts and complete prebasic molts that often occur in June–September, following breeding.

Molt and breeding events are energetically demanding and, for the most part, independent phases of the avian life cycle (Snow and Snow 1964, Payne 1972, Avery 1985, Pyle 1997). However, overlap between molt and breeding has been documented in a few temperate landbirds (Bancroft and Woolfenden 1982, Thompson and Slack 1983, Zaias and Breitwisch 1989, Hemborg 1999) and some resident tropical landbirds (Dickey and van Rossem 1938, Snow and Snow 1964, Foster 1975, Avery 1985). Breeding and molt seasonality influence the temporal dynamics of the avian life cycle, but other factors including climate and resource availability may also affect timing of molt (Aidley and Wilkinson 1987, Bensch et al. 1991, Jones 1995). Little has been published concerning temporal patterns of molt among resident tropical species in relation to competition from overwintering migrants despite continued interest in factors influencing timing of molt (Snow and Snow 1964). Given the energetically taxing nature of molt, we believe temporal patterns of molt among resident species may be influenced by resource competition associated with presence or absence of migrant birds. Molt is a critical facet of avian natural history and molt ecology has utilitarian characteristics which aid in understanding population structure and demographic trends.

Capture-recapture, capture-telemetry, and capture-observational data are often used to quantify demographic trends of resident neotropical landbirds (Greenberg and Gradwohl 1997, Sandercock et al. 2000, Cohen and Lindell 2004). Accurately modeling population structure requires methodology pertaining to identification of age and gender classes. Thus, understanding the extent and sequence of molt for a given species is critical for accurate age classification and subsequent demographic analyses.

The Tortuguero Integrated Bird Monitoring Project (TIBMP) was established in 1994 on the northern Caribbean coast of Costa Rica, near the village of Tortuguero, to monitor migrants as well as resident bird populations through constant-effort mist-netting (Ralph et al. 2005). We used 12 years of banding data from TIBMP coupled with a review of museum specimens to provide information on molt and breeding seasonality, and useful criteria for identification of age and gender

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for 27 resident bird species of northeastern Costa Rica.

METHODS

Nine monitoring sites were near the village of Tortuguero on the northeast coast of Costa Rica in Limon Province (83° 31′ 7″ W, 10° 33′ 51″ N; elevation 0–20 m). One 'central' station was operated at least five times every 10 days while the remaining 'satellite' stations were operated at least once every 10 days. Between 10 and 15 12-m mist nets were operated at each site by JDW and others from August to May, 1994–2006 (Ralph et al. 2005). Species studied were selected based on high capture rates during preliminary banding efforts (1994–2000). Protocols pertaining to captured birds follow Ralph et al. (1996).

Banding efforts were not sustained during June and July. Breeding seasonality during these months was inferred based on brood patch and cloacal protuberance data obtained during May and August, juxtaposition of the prebasic molt, and presence of juveniles. Recaptured individuals in many cases were used to verify age; our sample sizes include recaptured individuals as well.

Findings based on banded birds at Tortuguero were augmented by those from specimens examined at the National Museum of Natural History (USNM) by Pyle in early August 2001. All specimens from selected species collected in southern Mexico through northern Panama were examined and, in a few cases, specimens collected in South America were also examined. Ages of birds were inferred when collected and, in many cases, there were no specimens collected while in active molt. Plumage succession and molt timing could often be assumed based on molt limits and extent of feather wear (Pyle 1997). Criteria developed with specimens in 2001 were confirmed or re-examined with analysis of banding data from 1994 to 2006. Banding/specimen data were augmented with information provided by Stiles and Skutch (1989).

The partial to incomplete nature of the preformative molt in most neotropical resident landbird species can be used to facilitate accurate age-class categorization of captured birds (Pyle 1997). Feather characteristics, regarding molt limits and retained juvenile (HY) plumage among tropical residents, appears to be similar to those of temperate species. For example, retained juvenile retrices are often duller in coloration, more worn (in relation to definitive retrices) and tapered. Formative-plumaged individuals are often identifiable by retained primary coverts which typically lack distinctive edging, luster, and are typically more worn in relation to definitive primary coverts and contrast in wear with replaced greater coverts. Definitive flight feathers are typically more truncate in relation to retained juvenile flight feathers. We specifically looked for each of these criteria for banded birds (using standardized data forms) and museum specimens.

Molt and age terminology, including standard abbreviations, follow those of Pyle (1997) as modified by Howell et al. (2003). The first basic plumage is referred to as juvenile plumage (Juv), followed by the preformative molt (PF), first prealternate molt (PA1; if existing in the species), second prebasic molt (PB2), and definitive prealternate (DPA; if existing) and definitive prebasic (DPB) molts. Primaries and primary coverts are numbered from the innermost (primary 1) to the outermost (primary 9 or 10), secondaries and the greater coverts are numbered from the outermost (secondary 1) to the innermost tertial, and rectrices are numbered from the central pair (rectrix 1) to the outermost pair (rectrix 5 or 6). ''Partial'' for molt extent, indicates that no flight feathers (primaries, primary coverts, secondaries, or rectrices) were replaced (except the tertials or central rectrices in some individuals) and ''incomplete'' indicates that some but not all flight feathers were replaced. An ''eccentric molt pattern'' refers to an incomplete molt in which molt of primaries begins at a central feather (other than primary 1) and proceeds distally, and molt of secondaries begins with a central feather (other than secondary 1) and proceeds proximally to the tertials (Pyle 1997, Pyle et al. 2004). The ''typical molt sequence'', which can be incomplete during preformative molts, refers to a molt proceeding distally from primary 1 and proximally from secondary 1, as is typical of definitive prebasic molts.

Age classification follows the calendar-based system described by Pyle (1997). Age codes include HY (hatching year), indicating a bird in the calendar year of its hatching; SY (second year), indicating a bird in its second calendar year (HY/SY indicates a bird in its first plumage cycle, being HY until 31 Dec and SY after 1 Jan); TY (third year), indicating a bird in its third calendar year; AHY (after-hatching year), indicating a bird in at least its second calendar year; ASY (after-second year), indicating a bird in at least its third

calendar year; ATY (after-third year), indicating a bird in at least its fourth calendar year; and U (unknown), indicating a bird that may or may not be in the calendar year of birth. Month ranges in parentheses indicate the timing for which ages can be identified; e.g., ''HY/SY (Oct–Sep)'' indicates a bird with indicative criteria, usually based on an aspect of juvenal or formative plumage and the timing of prebasic molts, can be classified to HY from September to December and SY from January to October (Pyle 1997, Pyle et al. 2004). Age-classification can be complicated due to breeding seasonality overlap with 1 January; a phenomenon more commonly encountered in tropical latitudes. Generally, juveniles are in the bottom 2/3's of wing chord ranges. Wing chord samples represent actual ranges (mm) recorded from field and museum specimens. Color descriptions within species accounts follow recommendations by Smithe (1975). Question marks indicate data uncertainty expressed by the authors.

SPECIES ACCOUNTS

Leptotila cassini (Grey-chested Dove; $n = 32$ specimens, 90 captures). Breeds: January–September. Molt: PF incomplete-complete (year round?), DPB incomplete-complete (year round with strong peaks in Mar–Oct). Molt of primaries during PF proceeds in typical sequence in September–May; both PF and DPB may be suspended during winter. During both PF and DPB, 1–7 secondaries can be retained (25% of museum specimens had uniform secondaries); PF may be incomplete but confirmation is needed. Juvenile primary 10 is often blunt-tipped (tip 5–6 mm wide), the formative primary 10 tends to have a moderately narrow tip (4–5 mm wide), and the definitive primary 10 is thinner (tip <4 mm wide) and distinctly tipped cinnamon. HY/SYs (Aug–Jul) and AHY/ASYs (Aug–Jul) best separated by shape and color of primaries and secondaries, combined with placement of retained feathers, as in *L. verreauxi* (Pyle 1997). Gender similar in all plumages, although AHY/ASYs with bright purplish napes are invariably male and wing chord enables identification of most individuals: F = 128–135 mm, M = 134–140 mm.

Glaucis aeneus (Bronzy Hermit; $n = 22$ specimens, 235 captures). Breeds: October–August. Molt: PF complete (?) (May–Nov), DPB complete (May–Dec). Juveniles (year-round?) often have buff in the supercillium, crown, and nape, and buff or whitish tipping to back feathers, tertials, and most wing coverts, absent in definitive plumage. More pointed rectrices with a deeper white triangle at the tip (>5 mm along shaft) and brownish along outer webs not extending toward the shaft may represent HY/SYs; more study needed. Bill corrugations present in HY/SYs year-round. Gender is similar in all plumages. Wing: F = 48–58 mm, M = 50–61 mm.

Threnetes ruckeri (Band-tailed Barbthroat; $n = 29$ specimens, 136 captures). Breeds: January–August (?). Molt: PF complete (Sep–Nov), DPB (Sep–Nov) complete. Juveniles (Feb–Sep) have cinnamon tipping to head and nape feathers, upper-breast mostly blackish with small amounts of tawny (in relation to uniform tawny in older birds) and more pointed rectrices. AHY females average slightly less and paler tawny on breast (although there is much overlap); this criteria coupled with wing-chord length can aid in identification of gender for some individuals. Bill corrugations present in HY/SYs in January–October. Wing: F = 51–59 mm, M = 54–62 mm.

Phaethornis longirostris (Long-billed Hermit; $n = 22$ specimens, 342 captures). Breeds: November–July (?). Molt: PF complete (?) (Mar–Nov), DPB complete (Mar–Nov). Juveniles (Dec–Aug) have buff-yellow tipping to crown feathers. Bill corrugation present in HY/SYs, January–September and November–January. Gender similar in all plumages. Wing: F = 54–66 mm, M = 56–66 mm.

Phaethornis striigularis (Stripe-throated Hermit; $n = 35$ specimens, 19 captures). Breeds: year-round with a major peak in March–July (?) and a smaller peak in November–December (?). Molt: PF complete (year round), DPB complete (year-round). Juveniles (Mar–Oct) have dusky backs (greenish in older birds) and cinnamon tipping to body feathers, wing coverts, and secondaries. HY/SYs (Sep–Aug) appear to have duskier-based central rectrices and duskier and cinnamon-tipped inner secondaries, whereas AHY/ASYs (Sep–Aug) tend to have darker-based (more distinct) central rectrices and greenish-tipped inner secondaries (cinnamon-tipped secondaries occasionally documented). Bill corrugation criteria useful year-round. AHY/ASY (at least) females average stronger contrast between duller cinnamon breast and brighter cinnamon belly while males show richer cinnamon breast and belly; however, overlap occurs between genders. Wing: F = 35–39 mm, M = 35–41 mm.

Anthracothorax prevostii (Green-breasted Mango; $n = 17$ specimens, 156 captures). Breeds: March–November. Molt: PF complete (Mar–Dec), DPB complete (Mar–Dec). Juveniles (Feb–Dec) have sides of underparts extensively white with rufous extending from malar to flanks, and relatively narrow outer rectrices with indistinct white tips. U/AHY females (Sep–Aug) are similar except for absence of cinnamon-rufous feathering (or restricted amounts) in malar region and broader outer rectrices with more distinct patterning. U/AHY males (Sep–Aug) have dark green flanks and purplish rectrices with little or no white. No apparent differences between juvenile males and females. Bill corrugations present in HY/SYs April–November and appear to become smooth shortly after completion of PF. Wing: F = 57–70 mm, F = 57–71 mm.

Thalurania colombica (Violet-crowned Woodnymph; $n = 17$ specimens, 73 captures). Breeds: February–October. Molt: PF complete (Apr–Dec) DPB complete (Apr–Dec). Juvenile female (Feb–Dec) has green crown, upperparts uniformly dull green, throat and underparts with light gray, outer rectrices with white tips, and tail fork (longest rectrix 1) <4.5 mm. U/AHY female (Aug–Jul) similar except wing coverts and upper lateral scapulars bright green or turquoise green, brighter than rest of the upperparts, tail fork >4.5 mm. Juv/HY male (Feb–Dec) has crown, throat, and underparts dusky with 25 or fewer iridescent purple feathers, outer rectrices blackish, tinged purple without white tips, and tail fork (longest rectrix 1) <12 mm. U/AHY male (Aug–Jul) has crown and upperparts purple, breast glittering-green, rectrices dark blue, and tail deeply forked. Bill corrugations present in HY/SYs March–November. Wing: F = 44–54 mm, M = 50–59 mm.

Hylocharis eliciae (Blue-throated Sapphire; $n = 27$ specimens, 22 captures). Breeds: December–July (?). Molt: PF complete (Mar–Aug), DPB complete (Mar–Aug). Juv/HY female (Jan–Jun) has culmen blackish, throat with moderate greenish-blue spotting, and outer rectrices usually with cinnamon tips. U/AHY female (Jun–May) has culmen dusky with red wash to basal 50%, not contrasting distinctly with bill tip, throat with more extensive dark-blue spotting, and outer rectrices with or without cinnamon tips. Juv/HY male (Jan–Jun) has culmen dusky with dull to bright red coloration on basal 75% contrasting distinctly with black bill tip, throat with extensive dark-blue spotting and gray edges to feathers creating scaly appearance, and outer rectrices without cinnamon tips. U/AHY male (Jun–May) has culmen with bright red coloration on basal 75% contrasting distinctly with black bill, throat with extensive amount of large, dark blue spots and feathers without gray edges, and outer rectrices lacking cinnamon tips. Bill corrugations present in HY/SYs December–August. Wing: F = 43–52 mm, M = 45–54 mm.

Amazilia tzacatl (Rufous-tailed Hummingbird; $n = 40$ specimens, 211 captures). Breeds: February–November. Molt: PF complete (year-round), DPB complete (year-round); molt peaks in April–November. Juv-HY/SY female (year-round) has upper mandible black, upperpart feathers with cinnamon tipping, green throat feathers broadly edged whitish creating scaled appearance, and belly and vent washed buff yellow. AHY/U female (Oct–Sep) is similar except that upperpart feathers lack cinnamon tipping. HY/SY male (Feb–Dec) has upper mandible black gradually turning to red at basal 75%, bright green throat feathers with little or no whitish edging creating uniform appearance, and belly and vent dark gray, often tinged mauve. U/AHY male (Oct–Sep) is similar to HY/SY male except bill bright-red (basal 75%) with black tip. Juvenile rectrices less often show brownish edging extending to feather tips (Stiles and Skutch 1989); variation occurs for at least some rectrices within both age groups as some juveniles have complete brown tips and some AHY/ASYs have rufous extending to the tip. Bill corrugations can potentially occur year-round. Wing: F = 48–64 mm, M = 48–64 mm.

Amazilia amabilis (Blue-chested Hummingbird; $n = 34$ specimens, 57 captures). Breeds: February–July (?). Molt: PF complete (Feb–Aug), DPB complete (year-round?); AHYs may molt earlier than HYs. Juv/HY female (Feb–Jul) has pale gray chin with green spots, throat with 0–2 turquoise blue feathers, crown dull green, and outer rectrices with gray tipping. U/AHY female (Jul–Jun) is similar but throat with 5–15 bluish feathers and crown with bright green coloration. Juv/HY male (Feb–Jul) has dark green chin, throat with 15–30 bluish feathers, glittering green feathering of crown limited (often 3–4 feathers down center of crown) and outer rectrices with little or no gray tipping. U/AHY male (Jul–Jun) has dark-green chin, glittering-green crown, and outer rectrices without gray tips. Bill corrugations recorded in

HY/SYs in May. Wing: F = 47–54 mm, M = 50–57 mm.

Chloroceryle aenea (American Pygmy Kingfisher; *n* = 91 specimens, 156 captures). Breeds: March–June (?). Molt: PF incomplete-complete (May–Feb), DPB complete (Apr–Jan). Up to four juvenile middle secondaries and possibly some primary coverts retained during PF; occasional secondary retained during DPB. Juv/HYs (May–Sep) have paler underparts and an incomplete breast band (female) or streaks to belly (male). Some HY/SYs (Sep–Aug) can be classified to age by having retained, juvenile, dusky secondaries and primary coverts, contrasting distinctly in wear with greener back and replaced formative secondaries and primary coverts. U/AHYs (Aug–Jul) have uniformly green secondaries and primary coverts. Some AHY/ASYs (Sep–Aug) might be identified with retained definitive secondaries and primary coverts, dull greenish, contrasting only slightly in wear with replaced feathers. Gender distinguished in all plumages: females have distinct green chest-band whereas males lack this band. Wing: F = 52–59 mm, M = 52–59 mm.

Dendrocolaptes sanctithomae (Northern Barred Woodcreeper; *n* = 145 specimens, 32 captures). Breeds: February–November (?). Molt: PF complete (?) (Mar–Dec), DPB complete (?) (Mar–Dec). Juveniles (Jun–Aug?) have slightly looser plumage; otherwise, age classes similar and not distinguishable. Stiles and Skutch (1989) described juveniles as having crown more ochraceous and throat and belly with reduced, finer, and less distinct barring but differences subtle if consistent. Gender similar in plumage; many separated by wing-chord length: F = 117–127 mm, M = 124–133 mm.

Lepidocolaptes souleyetii (Streak-headed Woodcreeper; *n* = 170 specimens, 22 captures). Breeds: February–September. Molts: PF incomplete-complete (?) (May–Oct), DPB incomplete-complete (?) (May–Oct). Dickey and van Rossem (1938) report retention of central retrices during the PF, but more-worn rectrices may represent molt suspension (assuming central rectrices are last replaced, as in woodpeckers) or wear; further study needed. Juveniles (Mar–Oct) have slightly looser plumage; otherwise, age classes similar and not distinguishable. Stiles and Skutch (1989) describe Juveniles as having denser yet less-distinct streaking, duller throats with sooty fringes, and darker bills but differences subtle if consistent. Gender similar in plumage but most separated by wing-chord length: F = 84–94 mm, M = 92–99 mm.

Thamnophilus doliatus (Barred Antshrike; *n* = 212 specimens, 85 captures). Breeds: March–October. Molts: PF incomplete-complete (Mar–Jan), DPB complete (Mar–Jan). The PF can be eccentric with 4–8 inner primaries and outer secondaries, and most or all primary coverts retained. Some can retain all remiges (except tertials) and primary coverts while others may have a complete molt; rectrices are usually replaced. Juv/HY/SY female (Sep–Aug) has cinnamon plumage and flight feathers with eccentric molt limits, the retained inner primaries and outer secondaries with barring. U/AHY female (Sep–Aug) similar except remiges uniformly cinnamon and lacking bars. Juvenile/HY/SY male (Jul–Sep) has black and white body plumage with cinnamon or buff wash to lower underparts, and molt limit criteria as in HY/SY female (except replaced remiges barred black and white). U/AHY males (Oct–Sep) have black and white body plumage without cinnamon or buff wash and uniformly black and white remiges. Males still molting flight feathers in September–January can be classified as AHY/ASY if retained outer primaries and middle secondaries are black and white. Wing: F = 63–71 mm, M = 65–71 mm.

Thamnophilus atrinucha (Western Slaty Antshrike; *n* = 213 specimens, 198 captures). Breeds: February–November (?). Molts: PF partial (Mar–Dec), DPB compete (Mar–Dec). The PF occasionally can include 1–2 tertials and central rectrices; possibly all rectrices in some individuals. Juveniles have loose textured plumage and lack white patch; plumage resembles AHYs of each gender but upperparts of female washed chestnut and duller, male with chestnut feathering present on back. HY/SY female (Jul–Jun) has brownish olive body plumage, dusky primary coverts with cinnamon edges, replaced greater coverts contrasting with retained primary coverts and secondaries, several tertials and rectrices occasionally replaced, fresher, and underparts tinged chestnut. AHY/ASY female (Jul–Jun) is similar but primary coverts with pale tips, greater coverts uniform in quality with primary coverts and secondaries, rectrices without molt limits, and underparts brownish olive without chestnut tinge. HY/SY male (Aug–Jul) has black and gray body plumage, dusky primary coverts and remiges with cinnamon edges, contrasting distinctly with re-

placed, black-and-white greater coverts and (at times) several tertials; underparts often tinged brownish. AHY/ASY male (Aug–Jul) has black and gray body plumage, black primary coverts with white tips, and uniformly black remiges with whitish edging, not contrasting in wear with greater coverts; underparts gray without brownish tinge. Wing: F = 63–70 mm, M = 61–71 mm.

Myrmeciza exsul (Chestnut-backed Antbird; *n* = 30 specimens, 98 captures). Breeds: March–October (?). Molts: PF partial (Mar–Dec), DPB complete (Mar–Dec). The PF includes body and most or all greater coverts but usually not the tertials and no other flight feathers; the alula may rarely be replaced. Juveniles are entirely blackish-brown without contrast between breast and throat; gender similar until PF commences. HY/SY female (Oct–Sep) has grayish head and throat, upperparts tawny, primary coverts brownish, alula brownish with thin or no tawny olive edging (occasionally blackish with distinct pale edge), and primaries and rectrices relatively worn; individuals with replaced alula may best be classified U/AHY. AHY/ASY female (Oct–Sep) is similar but primary coverts dusky with tawny olive edging, alula dusky with distinct whitish edge, and primaries and rectrices relatively fresh; by April–July the edging on adult alula often wears off, however, primary covert condition can still be used for age classification. HY/SY male (Oct–Sep) has blackish head, throat, chest, and belly, alula, and flight feathers as in HY/SY female. AHY/ASY male (Oct–Sep) similar but primary coverts black with tawny edging, alula black with distinct white edge, and primaries and rectrices relatively fresh. Wing: F = 62–68 mm, M = 61–72 mm.

Mionectes oleagineus (Ochre-bellied Flycatcher; *n* = 32 specimens, 123 captures). Breeds: March–July. Molts: PF partial (Aug–Feb), DPB complete (Aug–Feb). The PF includes a variable amount of wing coverts but not the alula, primary coverts, tertials, rectrices or remiges. Juveniles (May–Aug) have throat washed gray and belly washed tawny olive. HY/SY males and females (Aug–Jul) have broad-tipped and more worn primaries 8, 9, and 10, primary coverts brownish with thin, dull, green edging; and rectrices narrow, pointed, brownish, and relatively worn. The primary covert and rectrix criteria can be subtle. AHY/ASY females (Aug–Jul) have moderately tapered and fresher primaries 8, 9, and 10 with primary 8 not emarginated (possibly with slight emargination), primary coverts dusky with broad green edging, and rectrices broad, truncate, dusky, and relatively fresh. AHY/ASY male (Sep–Aug) similar except for thinner and more-pointed primaries 10, 9, and 8 emarginated. Wing: F = 57–64 mm, M = 61–69 mm.

Manacus candei (White-collared Manakin; *n* = 26 specimens, 1,525 captures). Breeds: March–November. Molts: PF partial (Aug–Jan), DPB complete (Jul–Jan). The PF includes a variable number of greater coverts but no flight feathers. Age and gender criteria similar to *Pipra mentalis* regarding plumage of HY/SYs of both genders (Aug–Jul), green body plumage, molt limits among wing coverts, and shape and color of outer primaries and rectrices with differences. Some HY/SY males (Sep–Aug) have gray to light-gray throat and AHY/ASY female (Sep–Aug) can lack or have a grayish throat. Leg color may also be brighter orange in AHY/ASY females than in HY/SYs females; more study needed. AHY/ASY male (Sep–Aug) has black cap, lower back, wings, and tail; white throat and upper back, green rump and yellow belly. Males molting in September can be classified to ASY if outer primary is blackish and narrow, measuring <2.5 mm wide at the distal 8–10 mm end of the feather. SY/TY males may have less white in greater coverts than ASY/ATY males; the second-to-outermost greater covert should be checked for smaller and more triangular white patches, at times washed yellowish in SY/TYs. Wing: F = 49–59 mm, M = 49–59 mm.

Pipra mentalis (Red-capped Manakin; *n* = 31 specimens, 293 captures). Breeds: March–September. Molts: PF partial (Mar–Oct), DPB complete (Mar–Oct). The PF includes a variable number of greater coverts but no remiges or rectrices. Juvenile (Apr–Sep) is green with a brown or olive wash over loosely textured body plumage. HY/SY of both genders (Aug–Jul) has body and tertials entirely green, primary coverts brownish-gray with little or no dull green edging. Molt limits occur within greater coverts. Retained wing coverts and remiges are duller and outer primaries dull-brownish, narrow, and relatively worn. Retained rectrices are narrow, pointed, brownish, and relatively worn. Some to many HY/SY males (Aug–2 Sep) can be assigned to gender by dusky or blackish wash to outer web of one or more tertials (usually secondary 9), one or more body feathers blackish, and/or one or more head feathers red. AHY/ASY female (Aug–Jul) has entire body plumage green, one or more tertials with or without dusky or

blackish wash, primary coverts dusky with distinct bright green edging, back, wing coverts, and remiges uniformly bright green, outer primaries dusky green, broad, and relatively fresh. Rectrices broad, truncate, dusky green, and relatively fresh. AHY/ASY male (Oct–Sep) has red head, black body (including wings and tail). SY/TY age criteria unknown. Wing: F = 51–63 mm, M = 51–63 mm.

Hylophilus decurtatus (Lesser Greenlet; $n = 29$ specimens, 343 captures). Breeds: March–September. Molts: PF partial (May–Dec), DPB complete (May–Dec). PF includes most or all wing coverts but no remiges. Juveniles (Apr–Sep) have loosely textured body plumage, pale brown crown, and brownish suffusion to back. HY/SY (Aug–Jul) has brownish-gray primary coverts with little or no dull green edging, crown dull-gray, sometimes washed brown and/or with green-tinged feathers, and contrasting indistinctly with back at nape (yellow-green); rectrices narrow, pointed, brownish, and relatively worn. AHY/ASY (Aug–Jul) has pearly gray primary coverts with distinct green edging; crown pearly gray without brown or green wash and contrasting crisply with back at nape (yellow-green); rectrices broad, truncate, dusky, and relatively fresh. Gender similar in all plumages. Wing: F = 41–57 mm, M = 48–57 mm.

Thryothorus nigricapillus (Bay Wren; $n = 34$ specimens, 201 captures). Breeds: March–October. Molts: PF partial (Mar–Dec), DPB complete (Mar–Dec). The PF appears to include all greater coverts and, at times, the tertials and central rectrices but no other flight feathers. Juveniles (Feb–Jul) average paler cinnamon with thin chest barring, lacking spotting on lower-underparts. HY/SY (Aug–Jul) has brownish-gray primary coverts with irregular, thin, dull-cinnamon patches on edge, contrasting in quality with fresher greater coverts and, at times, tertials. Outer primaries relatively worn and brownish; rectrices relatively worn, at times with fresher central feathers. AHY/ASY (Aug–Jul) has dusky primary coverts with regular and more square cinnamon-patches extending almost to the shaft, not contrasting in quality with greater coverts or tertials, relatively fresh and dusky outer primaries, and uniformly fresh rectrices. Genders are similar in all plumages, although females average slightly duller and wing chord useful for classifying gender of some individuals: F = 60–67 mm, M = 64–70 mm.

Arremonops conirostris (Black-striped Sparrow; $n = 37$ specimens, 143 captures). Breeds: March–September. Molts: PF complete (Sep–Dec), DPB complete (Sep–Dec). The PF may at times be partial (more study needed), and the PF and DPB apparently can be suspended. Juv/HYs (Apr–Sep) have underparts washed yellow with dusky streaks, head pattern indistinct and streaky, and outer primaries and rectrices narrow and tapered. U/AHYs (Oct–Sep) have underparts without yellowish or dusky streaks, head pattern distinct, and outer primary and rectrices broad. Some HY/SYs or AHY/ASYs may be classified to age in November–October by condition of retained feathers during partial or incomplete molts; more study needed. Genders similar in all plumages, although some can be identified by wing chord: F = 68–77 mm, M = 74–81 mm.

Ramphocelus passerinii (Passerini's Tanager; $n = 57$ specimens, 69 captures). Breeds: March–November. Molts: PF partial-complete (Mar–Dec), DPB complete (Mar–Dec). The PF is variable, ranging from partial (as few as 2 greater coverts replaced) to incomplete in eccentric sequence (up to primary 1–4 and secondary 1–3 retained) to complete. All rectrices are often replaced and primary coverts can be retained or replaced with associated primaries. Juveniles (Apr–Jul) have grayer head, paler throat, and tawny washed upperparts and underparts. HY/SYs of both genders (Jul–Jun) have primarily olive brown body plumage lacking dusky or black feathers, molt limits present among wing coverts and/or flight feathers, breast and rump usually with pale orange yellow, lacking red feathers. Duller and browner-winged HY/SYs probably female, but more study is needed. Gender of some HY/SY males (Jul–Jun) can be assigned by having one or more black feathers on body and/or contrastingly red feathers in rump, later-molted flight feathers (especially primary 10, secondaries 4–6, or several rectrices), if replaced, washed sooty or blackish. U/AHY female (Sep–Aug) primarily olive without dusky or black feathers, wing coverts, remiges and rectrices uniformly dark-brown, rectrices broad and truncate, and breast and rump rich reddish-orange, sometimes washed red. Occasional older females may have one or more black feathers. AHY/ASY male (Jul–Jun) has mostly black body plumage and flight feathers, and red rump. Some SY/TYs may be identified by having retained brownish juvenal or formative flight feathers (e.g., secondary 6) or

body plumage, slightly-dusky remiges (males), and/or yellowish to the sides of the rump and undertail region; more study needed. Wing: F = 69–78 mm, M = 72–83 mm.

Thraupis episcopus (Blue-grey Tanager; $n = 32$ specimens, 219 captures). Breeds: February–September. Molts: PF partial (May–Oct), DPB complete (May–Oct). The PF includes most or all lesser coverts, none to all median coverts, and 0–9 greater coverts; some replace all greater coverts as well as several tertials, and several central rectrices. Juveniles of both genders (Apr–Sep) have body plumage washed grayish. HY/SY female (Sep–Aug) has brownish primary coverts with little or no greenish or brownish edging, molt limits present in the wing coverts, replaced feathers contrastingly brighter and greenish-turquoise, and rectrices fresher, narrow, brownish, and washed dull greenish; outer primaries dull brownish, narrow, and relatively worn. HY/SY male (Sep–Aug) is similar to HY/SY female except that replaced formative greater coverts average more blue and brighter. AHY/ASY female (Sep–Aug) has blackish primary coverts with distinct turquoise green edging; wing coverts uniform in color and wear, rectrices broad, truncate, dusky, and washed bright greenish, and outer primaries dusky, truncate, and relatively fresh. AHY/ASY male (Sep–Aug) similar except wing coverts distinctly more blue and brighter. Wing coverts in all age/gender groups show a cline from brighter and more blue lesser coverts, to duller and more green median coverts, to duller and more green secondary coverts. Wing: F = 81–88 mm, M = 80–92 mm.

Sporophila corvina (Variable Seedeater; $n = 40$ specimens, 962 captures). Breeds: April–August and November–February. Molts: PF incomplete-complete (year round?), DPB complete (year round), PA possible. Molts and plumages confusing and perhaps unique; fledglings from April–August breeding season have an incomplete PF (outer primaries, some rectrices, secondaries 3–6 and/or scattered body feathers retained) whereas fledglings from November–February breeding season appear to retain most or all juvenile plumage until May, when a complete (PF or PB2?) molt likely occurs through the summer. Males (at least) may have a PA1 and DPA (Nov–Feb) including some body plumage and at times one to several tertials and central rectrices; confirmation needed. Juv/HYs (Nov–Sep) or SYs (Jan–Sep) of both genders have entirely gray-brown body plumage, brownish primary coverts, brown greater coverts with thin buffy tips, and rectrices narrow and brownish. HY/SY female (Apr–Aug) similar except body plumage mixed olive and brown, molt limits occur among wing coverts or flight feathers. HY/SY male (Feb–Nov) similar to HY/SY female except incoming body plumage and flight feathers black or dusky-black. U/AHY female (Sep–Aug) has entirely brownish olive body plumage, dusky primary coverts with distinct brownish olive edging, uniformly brownish olive wing coverts and dusky flight feathers, and rectrices broad, truncate, and dusky. U/AHY male (Sep–Aug) has entirely black body plumage and flight feathers. Wing: F = 47–57 mm, M = 47–57 mm.

Oryzoborus funereus (Thick-billed Seed Finch; $n = 38$ specimens, 149 captures). Breeds: April–September. Molts: PF partial (Aug–Nov), DPB incomplete-complete (Aug–Nov). The PF includes body and most, or all wing coverts (occasionally up to 5 juvenile greater coverts can be retained) but no flight feathers. The DPB appears to be complete (most commonly), although, it apparently can also be eccentric (more commonly during the PB2?) with up to four inner primaries and primary coverts, and four outer secondaries retained; more study needed. Juveniles (Jun–Sep) have pale grayish brown body plumage and loosely textured feathers; genders are similar, however, some juvenile males may have slightly duskier flight feathers. HY/SYs of both genders (Aug–Sep) have entirely tawny body plumage lacking dusky centers to feathers, molt limits among greater coverts or between these and brown primary coverts, and rectrices relatively thin and worn. Some HY/SY males (Aug–Nov) can be identified by plumage averaging richer tawny and/or with one or more dusky to blackish feathers; crown feathers often with dusky centers, and remiges and rectrices often washed dusky. AHY/ASY female (Sep–Aug) has entirely tawny body plumage, crown without dusky-centered feathers, wing coverts uniform in wear, primary coverts dusky, and rectrices relatively broad and fresh. AHY/ASY male (Oct–Sep) has entirely black body plumage and flight feathers. Some SY/TY males (Sep–Aug) may be identified by having black plumage except tawny wash on belly and vent. AHY/ASYs showing eccentric patterns may be identifiable as TYs (with retained dusky-washed juvenile feathers) or ATYs (with black retained feathers); more study needed. Wing: F = 49–56 mm, M = 49–59 mm.

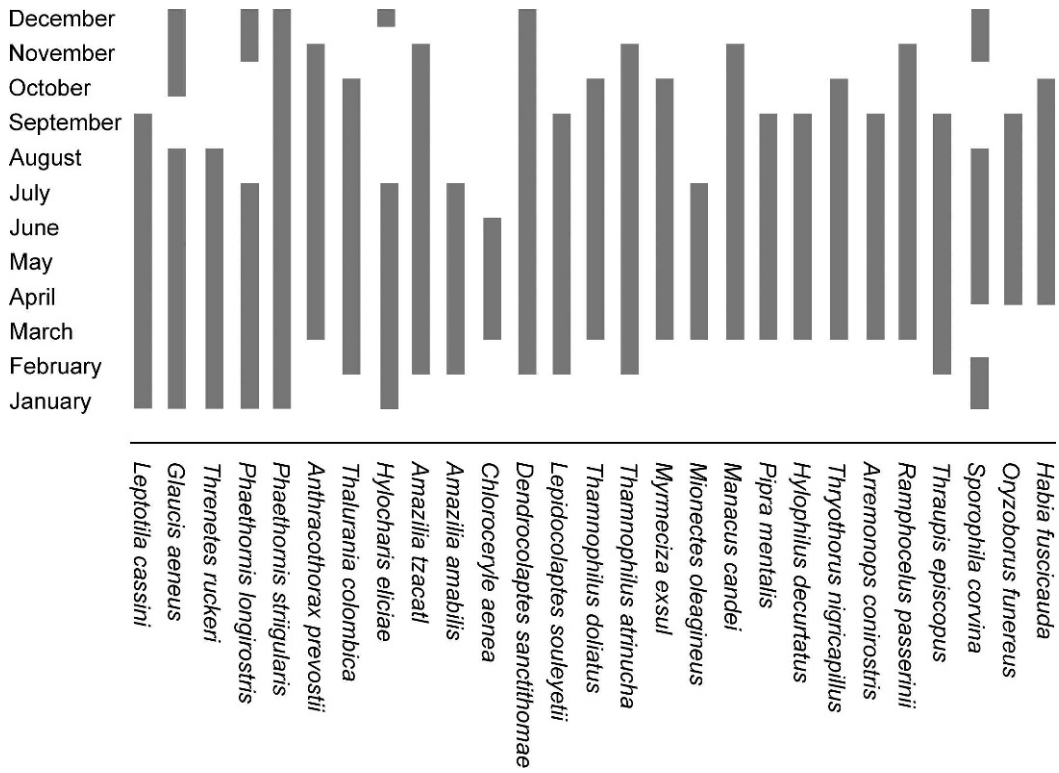

FIG. 1. Breeding seasonality for 27 resident bird species captured in Tortuguero, Costa Rica from 1994 to 2006. Breeding seasonality was inferred based on presence of brood patch, cloacal protuberance, juxtaposition of the prebasic molt, and presence of juveniles coupled with a specimen review.

Habia fuscicauda (Red-throated Ant Tanager; $n = 39$ specimens, 76 captures). Breeds: April–October. Molts: PF partial (Aug–Dec), DPB complete (Aug–Dec). The PF includes most or all lesser and median coverts, and a variable number of greater coverts but few or no flight feathers; look for several tertials and several central rectrices at times to be replaced. Juveniles of both genders (Feb–Oct) have body plumage washed tawny, brownish olive upperparts, and brownish olive on sides and chest. HY/SY females (Aug–Jul) have upperparts olive, throat yellow, molt limits among greater coverts, and rectrices tapered, worn, and greenish (at times reddish), the central feathers occasionally replaced. AHY/ASY female (Aug–Jul) has upperparts brown, throat yellow to orange, uniform greater coverts, and rectrices truncate, fresh, and washed olive, tawny or greenish. HY/SY males (Aug–Jul) have upperparts brown, throat bright-red, and molt limit and rectrix criteria as in HY/SY female. AHY/ASY male has dark red upperparts; throat bright-red and molt limit and rectrix criteria as in AHY/ASY female. Some older females can resemble AHY/ASY males except for pinkish throat and light-red back, while some AHY/ASY males can have interspersed greenish feathers. Wing: F = 83–94 mm and M = 85–104 mm.

DISCUSSION

We provide molt patterns, breeding seasonality, and age and gender criteria using 12 years of banding data and a museum review for 27 resident birds in northeastern Costa Rica. Three potential factors may confound our data: (1) data presented were collected by hundreds of volunteers promoting observer bias and data-quality heterogeneity; (2) the specimen review is largely-based on specimens collected outside the study area; and (3) banding operations were not sustained during June and July. Continuing data collection will further increase the precision of our molt and breeding accounts. Potential complications asso-

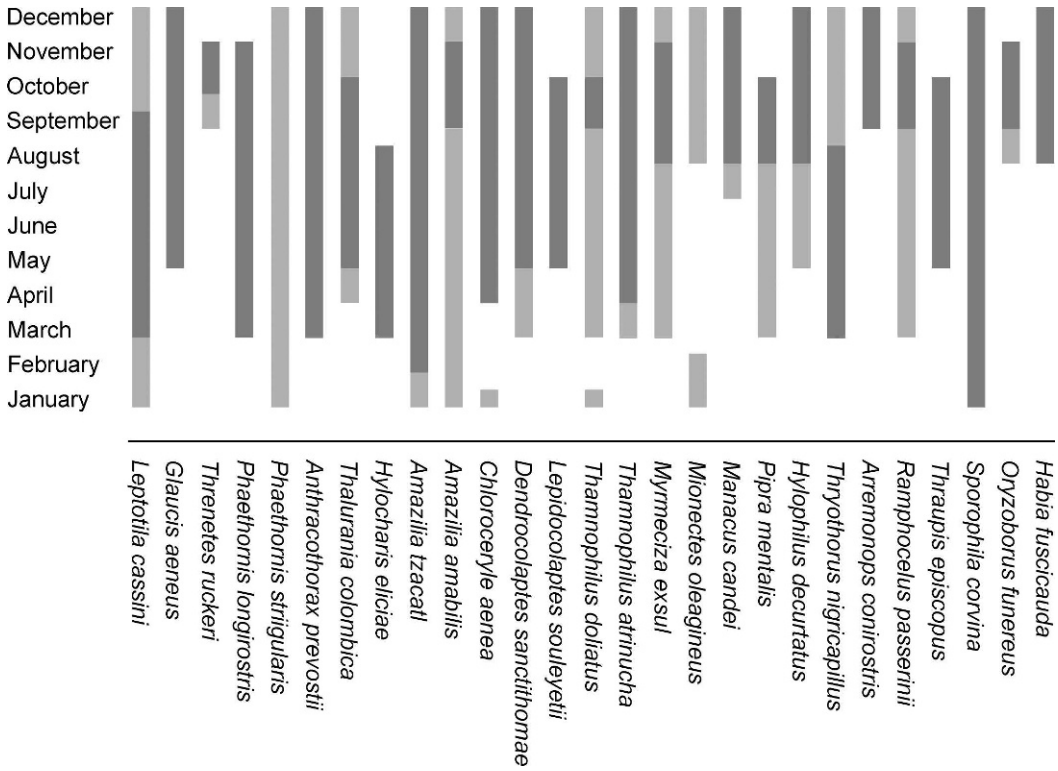

FIG. 2. Timing of the prebasic molt for 27 resident bird species captured in Tortuguero, Costa Rica from 1994 to 2006. Darker portions of the figure indicate symmetrical flight-feather replacement of captured birds at Totuguero. Banding activities were suspended during June and July; molt criteria for June and July were based on the juxtaposition of molt patterns during May and August, and specimen review. Symmetrical flight-feather replacement during June and July was based on juxtaposition of molt patterns of captured birds during May and August.

ciated with data collection exist; however, our study provides novel information associated with basic phases of the avian life cycle and utilitarian data pertaining to age and gender classification.

Plumage and molt-based criteria can be readily used to classify age in 59% of our study species (in-hand). Molt-based aging criteria remain elusive for hummingbirds and (apparently) woodcreepers due to complete preformative molts. Plumage-based gender criteria can be used for 70% of our study species in post-juvenile plumages. Ultimately, molt and plumage-based criteria can be used to place the majority of captured study species into discreet age and gender categories.

Breeding seasons (derived from TIBMP banding data) differ in duration and, in some cases, seasonality from other published accounts of temperate and neotropical birds (Skutch 1950, Snow and Snow 1964, Snow 1976, Sinclair 1978, Stiles and Skutch 1989, Marini and Durães 2001). For example, the breeding activity of avian communities in Minas Gerais, Brazil peaked in November while breeding activity in Costa Rica peaks in April and May (Skutch 1950, Marini and Durães 2001; Fig. 1). The asynchronous nature of breeding among closely related taxa presents a problem for neotropical field ornithologists. Breeding season variability throughout the tropics becomes more dramatic in systems influenced by stochastic precipitation regimes or lowland systems near the equator where birds may breed yearround or immediately following precipitation events (Snow and Snow 1964, Poulin et al. 1992). The apparent variation in breeding seasons across the Neotropics complicates classifying age of tropical landbirds; for example, 19% of our study species are believed to breed across 1 January, the definitive date used to categorize age class. Applying temperate models, such as the calendar-year age-classification system, may not be appropriate in tropical latitudes due to

asynchronous breeding seasons represented by certain taxa. Bimodal breeding seasons are another interesting phenomenon best represented by *Sporophila corvina*. Whether this phenomenon is resource-based or predator induced is unclear and merits further research.

Our data show that annual molt-cycle seasonality is apparently less distinct in some neotropical residents, whereas most demonstrate more structured seasonality (Fig. 2). The majority (70%) of our study species symmetrically replaced flight feathers during the absence of migrant birds (Apr–Aug); this may reflect the presence of protracted molts or a strategy which potentially decreases resource competition during molt, an energetically demanding phase of a bird's life cycle.

The data presented here are important in making resident neotropical bird age and gender criteria readily available for future researchers. We encourage other tropical banding efforts to publish similar studies. The future synthesis of such information will advance our understanding of avian natural history and promote further research in tropical latitudes.

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