

REVIEW

Ecological and evolutionary significance of molt in lowland Neotropical landbirds

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ABSTRACT

The slow-paced life history of many Neotropical birds (e.g., high survival and low fecundity) is hypothesized to increase lifetime fitness through investments in self-maintenance over reproduction relative to their temperate counterparts. Molt is a key investment in self-maintenance and is readily shaped by environmental conditions. As such, variation in molt strategies may be a key mechanism underlying life-history trade-offs and adaptation to new environments. Here, we review molt strategies from a diversity of lowland Neotropical landbirds and examine how variation in molt strategies, characterized by differences in molt insertions, timing, extent, and duration contribute to life-history variation and adaptation to diverse ecological conditions. In addition to our synthesis, we present a case study to examine the relationship between home range size and duration of the definitive prebasic molt of a well-studied subset of Amazonian landbirds. Our results suggest a connection between prolonged molt duration and larger home range size of small-to-medium-sized Amazonian landbirds. Our aims were to identify key gaps in our knowledge of Neotropical bird molt, to stimulate further comparative studies into the evolution of molt strategies, and to highlight how variation in molt strategies may be a key mechanism underlying life-history variation across latitudes.

Keywords: Amazon, forest, lifecycle, life history, molt, moult, Neotropics, tropical birds

LAY SUMMARY

- Songbirds inhabiting Neotropical forests replace feathers, or molt, in a diversity of ways.
- Our review found that closely related species exhibit similar molt strategies.
- Because molt is an investment in self-maintenance and is readily shaped by a bird's environment, variation in molt likely reflects adaptation to different ecological niches.
- To test whether molt reflects adaptation to a bird's ecological niche, we examined differences among molt duration, home range size, and wing length across multiple Amazonian bird species.
- These results suggest that ant-following birds with small wings and large home ranges adaptively slowed molt duration to inhabit a new ecological niche.
- Our findings demonstrate how variation in molt strategies may be a key mechanism underlying life-history variation and ecological differentiation across latitudes.

Significado ecológico e evolutivo da muda em pássaros terrestres Neotropicais de várzea

RESUMO

Uma história de vida lenta em espécies de aves neotropicais (com alta sobrevivência e baixa fecundidade) é relacionada, em hipóteses propostas, com o aumento do fitness ao longo da vida por meio de maiores investimentos em sobrevivência do que em reprodução, se comparados com aves de ambientes temperados. A muda de penas é um investimento indispensável para a manutenção e sobrevivência do indivíduo e facilmente moldado por condições ambientais. Dessa forma, a variação em estratégias de muda pode ser um mecanismo chave na determinação das diferentes histórias de vida e adaptação a novos ambientes. Neste artigo, nós revisamos a estratégia de muda de diversas aves terrestres neotropicais e examinamos como a variação nas estratégias, caracterizada por diferenças em mudas inseridas, tempo de ocorrência, extensão, e duração, contribuem para a variação na estratégia de vida e adaptação a diversas condições ambientais. Junto com esta síntese, apresentamos um estudo de caso para examinar a relação entre tamanho de área de vida e a duração da muda definitiva pré-básica de um subgrupo de aves amazônicas bem estudadas. Nossos resultados

sugerem uma conexão entre mudas de maior duração e áreas de vida maiores para aves amazônicas de pequeno e médio porte. Nossos objetivos são identificar os buracos no conhecimento sobre muda de aves neotropicais, estimular mais estudos comparativos sobre a evolução das estratégias de muda e destacar como a variação em estratégias de muda pode ser um mecanismo importante regendo a variação das histórias de vida em diferentes latitudes.

Palavras-chave: Amazônia, aves tropicais, ciclo de vida, floresta, história de vida, muda, neotrópico

INTRODUCTION

Tropical and temperate systems differ broadly in their climates and seasonality, which, in turn, affects resource availability, predation rates, migration strategies, and competition among breeding and resident birds (Martin 1996, Tieleman et al. 2006, Wiersma et al. 2007). As such, environmental dissimilarities across latitudes have shaped variation in avian life history, which manifest as differences in breeding, migration, and molt strategies across temperate and tropical systems. By comparing these differences, researchers have worked to identify selective forces that gave rise to the latitudinal gradient of slow-paced (tropical) and fast-paced (temperate) life-history strategies (Ricklefs 2000). This pace-of-life gradient is in part the result of tradeoffs between self-maintenance and reproduction. Regardless of breeding latitude, the annual replacement of feathers during the definitive prebasic molt, as well as the number and extent of inserted molts between prebasic molts (see Table 1 for definitions), are essential and energetically costly investments in self-maintenance. Moreover, because molts are energetically costly and shaped by environmental conditions, molt can serve as a key coupling event in the annual cycle linking tradeoffs among self-maintenance, survival, and breeding. Despite the importance of studying Neotropical bird molt to foster a deeper understanding of life-history variation, such research has been lacking (Ryder and Wolfe 2009, Wolfe and Pyle 2012), thereby limiting comparative studies focused on the tradeoffs between breeding and molt across latitudes. Despite the historic paucity of molt research, recent studies aimed at documenting molt strategies of Neotropical birds present an opportunity to comparatively examine how plasticity and lability in avian molt (e.g., insertions, timing, extent, and duration), within and among families, contribute to life-history variation and adaptation to different environments (Guallar et al. 2009, Ryder and Wolfe 2009, Johnson and Wolfe 2017).

In this introduction to Neotropical bird molt, we highlight the importance of understanding molt in the Neotropics to demonstrate how molt represents a critical, yet underappreciated, aspect of avian life histories. We also examine inserted molts (i.e. molts other than the annual prebasic molt; Table 1) and evaluate hypotheses associated with each inserted molt to disentangle relationships

between a species' molt strategy and its ecology. In addition to reviewing inserted molts, we test a novel hypothesis that home range size is associated with the duration of the prebasic molt of Amazonian birds. Our goal is to motivate additional research to investigate how the evolution of avian molt patterns influences life-history variation across latitudes.

Life History Theory and the Definitive Prebasic Molt in Tropical Birds

Life history theory postulates that organisms must allocate and balance time and resources between reproduction and self-maintenance to maximize lifetime fitness (Williams 1966, Martin 1996, Svensson and Nilsson 1997). For temperate birds, events in the annual cycle are often structured around seasonal eruptions of food leading to events that rarely overlap, including intense and discrete periods of breeding, timing of the definitive prebasic molt (see Table 1 for definitions), and migration (Hahn et al. 1992; but see Thomas et al. 2001). These non-overlapping events are consistent with the molt-constraint hypothesis, which posits that birds adaptively avoid simultaneously molting and breeding by scheduling these costly events sequentially in their annual cycle (Nilsson and Svensson 1996, Dawson et al. 2000). When birds are increasingly constrained by seasonality, migration, and/or energetic condition, their behavioral options include either overlapping molt and breeding (although lack of seasonality seems to drive molt-breeding overlap, not the other way around), molting faster to shorten the overall duration, suspending molt (phenological shifts), or a mixture of the aforementioned strategies (Hera et al. 2011, Johnson et al. 2012, Rohwer and Rohwer 2013); however, each of these strategies has varying fitness consequences. Contrary to pronounced seasonal changes in climate and food availability in temperate latitudes, Neotropical systems are often less seasonal, such that the timing of events in the annual cycle of Neotropical residents is less constrained by climate (e.g., onset of winter), food availability, breeding season length, and/or migration. In near-equatorial communities, syntopic species can experience different life cycle phenologies, such that in any given month of the year, at least one species is showing a peak in breeding or molt (Johnson et al. 2012, Stouffer et al. 2013). For example, in the

central Amazon, 3 species of leaf tosser in the family Furnariidae (*Sclerurus mexicanus*, *Sclerurus ruficularis*, and *Sclerurus caudacutus*) all exhibit a peak breeding season from February through June; alternatively, three species of central Amazonian woodcreepers in the same family, Furnariidae (*Certhiasomus stictolaemus*, *Dendrocincla fuliginosa*, and *Hylexetastes perrotii*), exhibit a peak breeding season between June and December (Johnson and Wolfe 2017). Release from highly seasonal temperate environments can directly affect tradeoffs between breeding and survival such that Neotropical birds may shift more energy to self-maintenance (including molt) rather than breeding and seasonal movements as in temperate species. Increased self-maintenance serves as one hypothetical mechanism underlying increased survivorship of tropical birds (Morton 1971, Hau et al. 2008, Johnson and Stouffer 2012, Stouffer and Johnson 2013). Additionally, increased longevity of tropical birds may further shift energetic tradeoffs towards increased investment in self-maintenance and higher survival and away from annual investments in reproduction.

To date, several lines of empirical evidence suggest that birds at tropical latitudes make a disproportionate investment in molt and self-maintenance rather than reproduction each year (Class and Moor 2013, Wagner et al. 2013). For example, Class and Moor (2013) demonstrated that adult Rufous-collared Sparrows (*Zonotrichia capensis*) in the eastern Andes of Ecuador adjusted the timing of events during the end of the breeding season when food was experimentally supplemented. Food-supplemented adults initiated molt earlier than control groups suggesting that, when resources are not limited, individuals readily invest in self-maintenance rather than in an extension of the breeding season. This finding stands in contrast to results from similar experiments conducted in temperate systems, in which food-supplemented birds late in the breeding season are more likely to invest in increased reproductive effort and offspring care (Ruffino et al. 2014) rather than molt. Evidence from Hawaiian birds further underscores how resource availability can influence tradeoffs between reproduction and the timing of molt in tropical systems. Several species in the Hakalau Forest National Wildlife Refuge on the Big Island of Hawaii invested in molt rather than breeding when experiencing weather-related food limitations. Specifically, birds started their prebasic molt during the breeding season, 1–2 mo earlier than normal, when faced with diminished food resources associated with abnormally cold weather (Freed and Cann 2012). Although Hawaiian birds showed plasticity in the timing of molt in response to resources, food limitations constrained the extent of molt (resulting in suspended and asymmetrical flight feather molt), which can affect survival (Freed and Cann 2012).

In addition to how energy is allocated, evidence also suggests that overlap in the timing of molt and breeding may be more common among Neotropical birds than their temperate counterparts (Foster 1975, Moreno 2004); however, the frequency of molt-breeding overlap among most tropical species is poorly documented and requires further study. Given reduced seasonal constraints at tropical latitudes, some species exhibit more variable breeding seasonality and long molt duration which, when coupled with prolonged durations of the definitive prebasic molt, may facilitate molt-breeding overlap (Johnson et al. 2012, Johnson and Wolfe 2014), although it is possible that this overlap occurs more at the population than the individual level in many species (Pyle et al. 2016). Despite the capacity of many tropical birds to simultaneously molt and breed, data primarily from temperate taxa suggest that overlapping these events can affect fitness indirectly via reduced feather quality (Dawson et al. 2000, Hera et al. 2009), carotenoid ornamentation (Badyaev and Vleck 2007), and structural plumage coloration (Griggio et al. 2009). The few well-studied Neotropical examples demonstrate the increased costs of molt-breeding overlap. For example, Echeverry-Galvis and Hau (2013) examined Slaty Brushfinches (*Atlapetes schistaceus*) in Colombia, where some birds overlapped molt and breeding and others did not. They found that individuals with overlap replaced remiges with smaller feathers, leading to lighter and shorter wings. Additionally, birds that overlapped breeding and molt had slower flight speeds during experimental escape attempts, thereby subjecting these birds to potentially elevated levels of predation risk (Echeverry-Galvis and Hau 2013). Other species with exceptionally long molt durations, such as the White-plumed Antbird (*Pithys albifrons*), may have no other option than to overlap molt and breeding (Moreno 2004, Johnson et al. 2012, Johnson and Wolfe 2014; see “Molt as an adaptive trait” below).

Inserted Molts in Neotropical Passerines and Near-Passerines

As field ornithologists continue to describe molt strategies of Neotropical landbirds, a striking consistency has emerged across latitudes: an inserted molt within the first molt cycle, called the preformative molt (Table 1), is present, and appears to be a shared attribute across bird taxa (Dickey and Van Rossem 1938, Pyle 1997, 2008, Guallar et al. 2009). The near-ubiquity of the preformative molt (Pyle 2008, Ryder and Wolfe 2009, Wolfe and Pyle 2012, Johnson and Wolfe 2017) can be explained by three non-exclusive hypotheses: (1) the preformative molt is contemporarily non-adaptive and reflects a vestigial trait shared across disparate taxa, (2) strong historical selective pressures shared across latitudes gave rise to convergent

TABLE 1. Important molt and plumage definitions following Pyle (2008), Howell (2010), and Wolfe et al. (2014).

Terminology	Description
Prebasic molt	Prebasic molts occur approximately annually in most birds, are complete to nearly complete, and delineate molt cycles. The first prebasic or prejuvinal molt results in the juvenal plumage. The prejuvinal molt usually occurs soon after hatching and often replaces natal down. Juvenal plumage is the first pennaceous coat of feathers. The prejuvinal molt is ubiquitous (occurring in all birds) and is complete in extent (replacing all feathers). Howell et al. (2003) considered the prejuvinal molt comparable with later prebasic molts and, therefore, synonymous with the first prebasic molt.
Preformative molt	Results in the formative plumage. Synonymous with the first prebasic molt of Humphrey and Parkes (1959). The presence and extent of the preformative molt are extremely variable across birds. The preformative molt is unique because it occurs only within the first molt cycle and lacks counterparts in subsequent molt cycles. Sometimes 2 preformative molts occur within the first molt cycle, in which case the later-evolved preformative molt is referred to as the “auxiliary preformative molt.”
Prealternate molt	Results in the alternate plumage. The presence and extent of the prealternate molt are extremely variable across birds. When it occurs, it is often the third molt in the first cycle (in addition to the preformative molt) and the second molt found in each subsequent molt cycle (in addition to the prebasic molt).
Definitive plumage	Here, we follow the Wolfe et al. (2014) definition that “definitive” is used only to describe plumages derived from definitive molt cycles (second or later molt cycle for the majority of species). Definitive molt cycles are defined as having molts with counterparts in subsequent cycles. Thus, most cycles that exhibit preformative molts are not considered definitive, because the preformative molt occurs only within the first cycle.

evolution of the preformative molt across disparate taxa, or (3) ancestral preformative molts are maintained through strong contemporary selective pressures shared across latitudes. The regular occurrence of the preformative molt suggests that it is a symplesiomorphic character among species of birds, but the fact that molt is an energetically expensive process suggests that preformative molt serves an adaptive purpose. Selective pressures that maintain preformative molts may include the need to replace poor-quality juvenal feathers (which are grown quickly to facilitate rapid fledging and predator avoidance; Martin 2015) with higher quality formative plumage, or the need to replace cryptic juvenal with formative plumage for sexual and social signaling. Both pressures are likely to be widespread across avian taxa. We propose that a concerted effort to compare the timing, extent, and duration of preformative molts across diverse taxa is needed to assess how variation in plumage maturation and sexual signals may have shaped this ubiquitous molt.

Despite the taxonomic and geographic ubiquity of preformative molt, the extent—or number of feathers replaced—of this molt shows substantial variation across taxa, ranging from limited, to partial, to incomplete, to complete (*sensu* Pyle 1997); limited preformative molts appear to be exceedingly rare in Neotropical passerines (Pyle 1997, Guallar et al. 2009, Ryder and Wolfe 2009, Johnson and Wolfe 2017). Thus, the preformative molt in both temperate and Neotropical landbirds typically includes the replacement of all juvenal body feathers and some to most wing coverts, as well as a variable number of flight feathers, depending on taxon (Pyle 1997, Guallar et al. 2009, Ryder and Wolfe 2009, Johnson and Wolfe 2017). Moreover, because the number of feathers replaced (extent) during the preformative molt varies across species, we suggest birds

replace those feathers most necessary to survive until their next molt. Variation in the extent of preformative molts could also reflect selection to acquire a plumage necessary to attract a mate although, in some taxa, adult plumage acquisition in males can be delayed until subsequent prealternate or definitive prebasic molts depending on social system drivers (i.e. some manakins, McDonald 1993, Ryder et al. 2008; some antbirds and tanagers, Johnson and Wolfe 2014, 2017). For example, White-crowned Manakin (*Dixiphia pipra*) adhere to a complex social structure where young males likely do not have access to reproductive opportunities and, as such, their plumage is not fully mature until their second, third, and possibly fourth prebasic molt (Johnson and Wolfe 2017). If the extent of the preformative molt reflects a balance between replacing those feathers most important to survival and reproduction, and is limited by energy constraints, then we predict that differences in a species' habitat, foraging ecology, and reproductive behavior will result in predictable patterns of variation in preformative molt extent.

In general, Neotropical bird families characterized by numerous ecologically and behaviorally diverse species (e.g., Thamnophilidae, Thraupidae, Cardinalidae, and Tyrannidae) exhibit correspondingly diverse preformative molt extents, whereas subfamilies and families with ecologically and behaviorally similar species (e.g., Dendrocolatinae, Pipridae, and Turdidae) do not. We can imagine several scenarios that provide testable hypotheses for relationships between preformative molt and behavioral ecology in Neotropical birds. For example, virtually all woodcreepers (Dendrocolaptinae) exhibit complete preformative molts, and subsequent formative plumages are strikingly similar to their juvenal plumages (Johnson and Wolfe 2017), suggesting that formative plumages

among woodcreepers are not used for signaling, but rather for structural properties. Given that woodcreepers forage, rub, and roost on tree bark and limbs, it is not surprising that complete preformative molts are likely adaptive to an abrasive lifestyle. Likewise, virtually all manakins (Pipridae) exhibit partial preformative molts, whereby they replace body feathers and a variable number of wing coverts, but no flight feathers. Although manakins occupy a diversity of habitats from coastal scrub to cloud forest, they frequent shaded, understory shrubs to perch and to eat fruit. Presumably, the ecological guild occupied by manakins does not predispose them to the level of abrasion that woodcreepers experience, resulting in less extensive preformative flight-feather molts. In contrast, in the ecologically diverse antbird (Thamnophilidae) and tanager (Thraupidae) families, we find a concordant diversity of preformative molt extents from complete (e.g., *Frederickena viridis* [Thamnophilidae], *Tachyphonus surinamus* [Thraupidae]; Johnson and Wolfe 2017), to incomplete (*Cymbilaimus lineatus* [Thamnophilidae], *Tangara gyrola* [Thraupidae]; Ryder and Wolfe 2009, Johnson and Wolfe 2017), to partial (*Thamnomanes ardesiacus* [Thamnophilidae], *Saltator grossus* [Thraupidae]; Johnson and Wolfe 2017). Viewed cumulatively, these relationships support our assertion that behavior and habitat shape preformative molt extent. Given that only anecdotal and correlative observations exist to date, research and experiments aimed at understanding the abiotic and biotic drivers of variation in preformative molt extent represent promising scientific endeavors.

In addition to habitat and behavior, other elements of a species' ecology, as well as temporal (seasonality) and spatial (habitat quality or predation) factors, such as the timing of breeding/fledging, may influence preformative molt extent. For example, young Wrentits (*Chamaea fasciata*) that fledge late in the breeding season tend to have less extensive preformative molts than those fledged earlier in the season (Elrod et al. 2011). This “early brood – extensive molt hypothesis” may also contribute to intra-specific variation observed in preformative molt extents in more seasonal tropical environments (Rockey 2016). In addition, selective pressures associated with nest or post-fledging predation could drive tradeoffs between the speed of feather growth and quality, where higher predation results in faster growth (Dawson et al. 2000). For example, minimizing the time spent in the nest to avoid predation (i.e. maximizing feather growth rates), may result in tradeoffs via lower feather quality. Neotropical birds have adapted to higher nest predation rates coupled with a slower pace of life by producing fewer young per year (lower clutch sizes and fewer broods) than temperate birds (Cody 1966, Ricklefs 1980, Skutch 1985, Martin 1995, Ryder et al. 2008), thereby increasing the amount of food

per nestling (Martin 2015). Excess food may be used by tropical nestlings to molt flight feathers more quickly, relative to their temperate counterparts, thereby giving tropical fledglings an advantage when escaping depredation (Martin 2015).

Tradeoffs between the speed of molt and juvenile feather quality should be most apparent when comparing those species subject to variable levels of nestling and fledging predation. Species subject to less nest predation can invest more time and energy in the creation of quality feathers, thereby reducing the need to produce a “cheap-and-fast” juvenile plumage. This is analogous to shade-tolerant trees (e.g., beeches [*Fagus* spp.]), which slowly grow much denser, rot-resistant wood relative to their early-successional counterparts (e.g., aspen [*Populus* spp.]), which are under much greater pressure to take advantage of sunny conditions. These hypothetical relationships suggest that species with poor-quality juvenile plumage adapted their preformative molt, which occurs shortly after fledging, to replace poor-quality juvenile feathers grown in the nest. If tradeoffs between the speed and quality of the prejuvenile molt exist and contemporary levels of nest predation are similar to those that evolutionarily shaped the timing of the prejuvenile molt, then we predict that time spent in the nest will be negatively correlated with the extent of preformative molt; i.e. birds subject to less nest predation risk will spend more time and energy investing in quality juvenile plumage and not in the preformative molt. These relationships might be obscured if depredation of recently fledged birds results in additional selective forces that promote the growth of high-quality juvenile feathers in the nest to evade predators upon leaving the nest (Martin 2015). These ideas could be readily tested in birds occupying islands that are historically free of nest predators.

Although the presence of preformative molts is ubiquitous in both temperate and tropical landbird communities, the incidence of additional inserted molts such as an auxiliary preformative molt (Table 1; documented in a single Neotropical resident, *Percnastola rufifrons*; Johnson and Wolfe 2014) or a prealternate molt appear to be rare among resident Neotropical birds, especially in forest-dwelling species (Ryder and Wolfe 2009, Johnson and Wolfe 2017). In Neotropical systems, prealternate molts are most commonly found in Nearctic–Neotropic migrant species, where they tend to initiate and often complete their prealternate molt on their tropical wintering grounds (Pyle 1997, Howell 2010). These prealternate molts often result in brilliantly colored male breeding (alternate) plumages, such as the plumages of wood-warblers (Parulidae). Interestingly, migration distance is correlated with the extent of the prealternate molt (Svensson and Hedenström 1999, Terrill et al. 2020) giving

rise to two competing hypotheses regarding the evolution of prealternate molts in migratory species. The first hypothesis, proposed by Pyle and Kayhart (2010) and subsequently supported by Terrill et al. (2020), posits that the prealternate molt evolved in response to increased wear from heightened solar exposure associated with summering and wintering latitudes and that this molt was subsequently co-opted primarily by males to enhance female choice and sexual selection (Wolfe and Pyle 2011, Terrill et al. 2020). The subsequent adaptive value of the prealternate molt for sexual selection may reflect honest signaling where the carotenoids and melanin deposited in migrant plumage during the prealternate molt reflect the disease, stress, and overall habitat quality experienced on their tropical wintering grounds. By serving as a signal of physiological condition and habitat quality on the wintering grounds, the prealternate molt in migratory species may carry over to indirectly influence reproductive success on temperate breeding grounds. Conversely, Simpson et al. (2015) examined wood warblers (Parulidae) and suggested that a colorful plumage characterized their ancestral plumage; these colorful plumages may have made migratory warblers more susceptible to predators in novel habitats encountered during migration. As such, Simpson et al. (2015) hypothesized that the seasonal loss of colorful plumage after the prebasic molt was an adaptive response to evading predators during fall migration. Thus, the prealternate molt arose to reacquire the ancestral colorful breeding plumage. The proposed hypotheses by Pyle and Kayhart (2010), Wolfe and Pyle (2011), Simpson et al. (2015), and Terrill et al. (2020) are not mutually exclusive but may interact to influence patterns of prealternate molt extent and seasonal dichromatism across Neotropical migratory species.

Considering that prealternate molts may serve as an adaptation associated with the rigors of migratory behaviors (Howell 2010, Pyle and Kayhart 2010, Wolfe and Pyle 2011, Simpson et al. 2015, Terrill et al. 2020), it is not surprising they appear rare among sedentary Neotropical species. Where prealternate molts do occur among forest-dwelling and resident Neotropical landbirds, they appear most common in tanagers (Thraupidae), and to date have been documented in *Cyanerpes*, *Thraupis*, *Habia*, *Hemithraupis*, *Volatinia*, *Sporophila*, *Oryzoborus*, and *Lanio* (Dickey and van Rossem 1938, Ryder and Wolfe 2009, Johnson and Wolfe 2017) genera. Prealternate molts also occur in other families as well (e.g., *Pachyramphus* in Tityridae, E. Johnson and R. Terrill pers. obs., Johnson and Wolfe 2017; *Myiarchus* in Tyrannidae, Pyle 1997, Guallar et al. 2009). Many species in these genera frequent canopies, forest edges, and open grasslands and may sustain a disproportionate amount of feather damage from the sun (Terrill et al. 2020), which is conceptually similar to the

hypothetical framework used to explain inserted molts in Nearctic–Neotropic migrants (Pyle 1998, Pyle and Kayhart 2010, Wolfe and Pyle 2011).

The effects of exposure to solar irradiance as a driver of prealternate molts in resident tropical species are further supported when examining the few documented molt strategies of Afrotropical passerines and near-passerines occurring in closed-canopy Congolese forest, where prealternate molts appear rare, much like their Neotropical counterparts (Dowsett-Lemaire and Dowsett 1991, Dowsett-Lemaire 1997, King et al. 2004). However, outside these forests, some African and Australian birds such as widowbirds (*Euplectes* spp.) and fairywrens (*Malurus* spp.) are renowned for prealternate molts resulting in dramatic changes in seasonal dichromatism (Mulder and Magrath 1994, Craig 2017). Widowbirds and fairywrens both occur in high ultraviolet environments, which may have led to the evolution of an inserted molt to replace worn plumage, providing an evolutionary opportunity for repurposing by sexual selection—similar to warblers (Parulidae; Pyle and Kayhart 2010, Wolfe and Pyle 2011). In the Neotropics, seedeaters (*Sporophila*) occur in brushy and sunny environments and often exhibit inserted prealternate molts like those found in widowbirds (although not as extensive) and fairywrens. Seedeaters typically undergo a partial to incomplete prealternate molt prior to the breeding season resulting in a striking male breeding plumage (Wolfe et al. 2009). Interestingly, plumage maturation appears to be dynamic in at least one species, Black-bellied Seedeater (*Sporophila melanogaster*), where young males take two years to acquire the adult male breeding plumage (Fontana and Repenning 2014, Repenning pers. comm.). Once these males acquire a matured alternate plumage they sometimes revert to a female-like alternate plumage; individuals may remain in this female-like alternate plumage for a breeding season prior to acquiring the matured male-like alternate plumage anew (Fontana and Repenning 2014). This pattern of reverting in-and-out of a breeding plumage may occur in other seedeater species, where individuals in some years may invest in self-maintenance by forgoing aggressive encounters with brightly colored males (Hawkins et al. 2012). Oscillating patterns of investing in self-maintenance over reproduction may be a feature of other Neotropical species, just more difficult to observe without the seasonal and sexual dichromatism found in seedeaters.

Molt as an Adaptive Trait

To date, most molt research associated with a species' has focused on phenological overlap and trade-offs with other life-history events, as well as circannual *zeitgeber* and circadian rhythms (Stiles and Wolf 1974, Foster 1975, Gwinner 1975, Langston and Rohwer 1996, Dawson et al. 2001, Romano et al. 2017). Contrary to our select examples

of molt-centric research detailed above, many ecological studies have implicitly treated molt as a nuisance variable that birds must balance in relation to those events that more directly influence fitness, such as breeding and migration. This bias was supported by a survey of Neotropical ornithological research, which found only 1,030 references for molt, but 105,000 for breeding, and 58,100 for migration (Wolfe and Pyle 2012). Despite the disproportionate amount of research focused on breeding and migration relative to molt, ornithologists are beginning to appreciate the ecological and evolutionary importance of molt strategies, whereby birds can vary the duration, speed, extent, and number of molts necessary to exploit novel ecological and behavioral niches.

We are increasing our knowledge of how molt varies with many of the ecological facets of Neotropical birds. For example, Johnson and Wolfe (2014) studied molt variation in a community of antbirds (Thamnophilidae) from the central Amazon and found that sexually dichromatic species adhere to three general molt strategies: (1) partial preformative molts resulting in female-like plumage within the first year of life, (2) partial preformative molts in which males and females become sexually dichromatic, or (3) complete preformative molts resulting in the adult-like plumage aspect shortly after fledging. In this third category, accelerated plumage maturation in some Amazonian antbirds is accomplished by advancing the timing of adult-like feathers acquired during an otherwise prolonged preformative molt (more adult-like in those species that undergo complete preformative molts), or by acquiring a male-like plumage aspect as a consequence of the preformative molt. Rapid acquisition of adult-like plumage is hypothesized to facilitate the acquisition of territories in those species that rapidly disperse from natal territories compared to species where the male formative plumage is juvenal- or female-like in appearance (Johnson and Wolfe 2014). Thus, variation in molt extent may influence patterns of natal dispersal and territory acquisition.

Another example of how Neotropical birds modify molt strategies is through changing the duration of feather replacement. Greater variation in molt durations exhibited by Neotropical passerines and near passerines (Johnson and Wolfe 2014), when compared to temperate birds (Rohwer et al. 2008), suggests that seasonally stable resource availability has provided opportunities for flexible molt durations; whether subsequent variation in molt strategy facilitated or is simply an outcome of occupying novel ecological niches remains unresolved. One of the most striking examples of prolonged molt duration occurs among obligate ant-following birds. Obligate ant-following birds in the Neotropics feed on arthropods fleeing marauding army ants (Ecitoninae); these birds wander widely in search of active ant swarms resulting in large home

ranges (Willis and Oniki 1978). At ant swarms, obligate ant-following species often form hierarchies where larger and more dominant species forage at the front of the swarm while smaller species are found in the back (Willis and Oniki 1978). One common obligate ant-following species, the White-plumed Antbird (*P. albifrons*), relies on its speed and small size to minimize confrontations with larger species while darting in-and-out of high-quality foraging spots. Given their foraging strategy, White-plumed Antbirds face a substantial tradeoff in their sustained flight efficiency (longer wings) and relatively diminutive size; specifically, small and stubby wings (i.e. short wing aspect ratio) make it difficult to maintain large home ranges, particularly during molt when the replacement of remiges results in gaps among flight feathers making it difficult to fly (Rohwer et al. 2009). The combination of small wings and large home ranges begs the question: how can these birds molt remiges in a way so as not to compromise their lifestyle? We suggest that an incredibly slow molt duration provides a solution to this conundrum where single primaries and secondaries are replaced one at a time, resulting in a molt duration of ~300 days (Johnson et al. 2012), making White-plumed Antbird the world's slowest-molting passerine. Most other passerines replace multiple primaries at once, which results in a faster molt duration (Rohwer and Rohwer 2013). The single replacement of remiges minimizes the size of gaps between feathers and allows White-plumed Antbirds to retain the structural integrity of their wing during the prebasic molt. Other diminutive forest-dwelling species may be faced with similar constraints resulting in associations between large home ranges and slow molt durations. In this context, molt duration may aid species such as White-plumed Antbird in filling unoccupied niche space or simply reflect an evolutionary outcome of being a small tropical bird with a large home range.

Molt as an Adaptive Trait: Case Study

To test our hypothesis that White-plumed Antbird and other small forest-dwelling Neotropical species may slow molt in concordance with a large home range, we examined associations between a species' home range, molt duration, and morphometrics.

METHODS

Our data were compiled from published and unpublished sources for 22 species captured at the Biological Dynamics of Forest Fragmentation Project (BDFFP), located ~80 km north of Manaus, Brazil (Appendix Table 3). Specifically, we formulated a series of linear models where a species' home range (assessed through radio telemetry and spot-mapping; Stouffer

2007, Johnson et al. 2011, L. L. Powell unpublished radio telemetry data) served as the response variable and associated wing chord, mass, molt duration, and an interaction between molt duration and wing chord (assessed through banding data; Johnson et al. 2012, Johnson and Wolfe 2017) were used as explanatory variables. We included mass and wing chord to account and control for allometric relationships between body size and home range size. We selected top models using Akaike Information Criterion corrected for small sample size (AIC_c ; Sugiura 1978, Anderson and Burnham 2002) and examined adjusted R^2 values associated with models to further investigate model fit and correlations. To account for phylogenetic relationships among species, we used phylogenetic generalized least squares models (pgls; Butler and King 2004) in package *caper* (Orme 2013) in R (R Core Team 2014). We employed 1,000 pseudoposterior trees from Jetz et al. (2012) provided on the Hackett et al. (2008) backbone, and examined phylogenetic generalized least squares models, and calculated AIC_c values over the pseudoposterior trees; we used the means of each value from each model to report associated AIC_c and adjusted R^2 values.

RESULTS

The model including molt duration was the best in the model set and carried 92% of the AIC_c weight (Table 2) illustrating a positive correlation between molt duration and the size of a species' home range ($\beta = 0.219$, 95% CI = [0.121, 0.317], adj. $R^2 = 0.48$). Although this relationship appears to support the notion that Neotropical species' molt duration increases as home range size increases, this relationship appeared sensitive to the inclusion of our two-obligate ant-following species, *P. albifrons* and *Gymnophytis rufigula*, which take ~300 and ~270 days to molt, respectively (Figure 1). After removing *P. albifrons* and *G. rufigula* from the analysis, we found that wing chord replaced molt duration as the top model (Table 2) where study species' home range was positively correlated with wing chord ($\beta = 0.132$, 95% CI = [0.008, 0.256], adj. $R^2 = 0.16$; Figure 1); substantial model selection uncertainty clouds the strength of this relationship whereby the wing:molt duration and the intercept-only models also carried weight and were within 2 AIC_c units of the top-ranked model (Burnham and Anderson 2002).

DISCUSSION

Our results suggest that allometric relationships exist between a species' wing chord and their home range size. This makes sense given previously documented relationships between those birds that travel greater

TABLE 2. Results from the phylogenetic generalized least squares (pgls) model selection examining relationships between a species' estimated home range size (response variable), and molt duration, mass, and wing chord (explanatory variables). We present model selection results where (A) all species were considered and (B) with the removal of the two obligate ant-following species. Models were ranked based on corrected Akaike Information Criterion (AIC_c); AIC_c weights (w_i), number of parameters (k), and adjusted R^2 for exploratory purposes. The [wing:molt duration] indicates an interactive effect between two explanatory variables, molt duration, and wing chord. All species used in the analysis were captured at the Biological Dynamics of Forest Fragmentation Project (BDFFP) located ~80 km north of Manaus, Brazil.

Model	AIC_c	w_i	k	adj. R^2
(A) All species included				
Molt duration	158.25	0.92	2	0.48
[Wing:molt duration]	163.37	0.07	4	0.43
Wing	170.02	0.00	2	0.08
Intercept-only	170.47	0.00	1	na
Mass	171.79	0.00	2	0.00
(B) <i>Pithys albifrons</i> and <i>Gymnophytis rufigula</i> removed				
Wing	108.50	0.39	2	0.16
[Wing:molt duration]	108.60	0.37	4	0.29
Intercept-only	110.42	0.15	1	na
Mass	112.41	0.05	2	0.00
Molt duration	112.84	0.04	2	0.00

distances and their relatively longer wings (Mulvihill and Chandler 1991, Marchetti et al. 1995). When examined together, our two analyses demonstrate that certain Neotropical birds, such as small obligate ant-following species, may exhibit slower molt duration to escape constraints imposed by allometric scaling and maintain large home ranges with shorter wings. These modifications may be adaptive for species, such as *P. albifrons*, enabling their role as the smallest obligate ant-following species in the Neotropics. Alternatively, these patterns may simply reflect the evolutionary outcomes of occupying these guilds in lowland Neotropical forests.

The interplay between a species' ecology and variation in molt timing, insertions, durations, and extents should be examined to better understand how selective pressures have shaped specific molt strategies. These molt strategies, in turn, influence those evolutionary forces that affect relative investments Neotropical birds make in their molt (self-maintenance) and reproduction. We have only started to scratch the surface of the ecology and evolution of molt in Neotropical birds. Descriptions of molt strategies from understudied Neotropical bird communities will continue to provide deeper insights into how birds adapt to new environments as well as predict limitations that preclude potential adaptation.

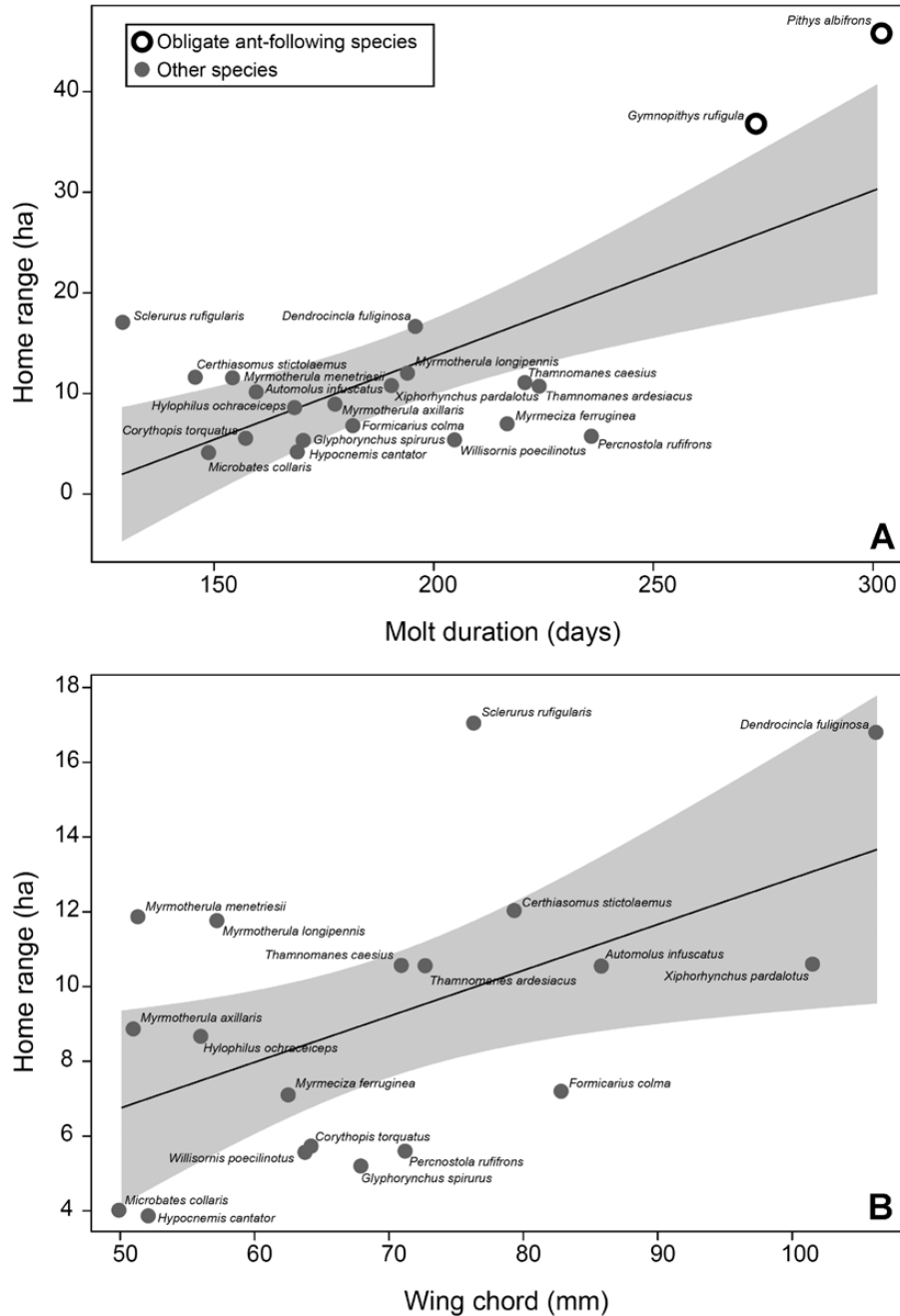


FIGURE 1. (A) A visualization of our top phylogenetic generalized least squares (pgls) model containing a species' estimated home range size (response variable), and molt duration (explanatory variable). (B) A visualization of our top phylogenetic generalized least squares (pgls) after the removal of two obligate ant-following species (*Pithys albifrons* and *Gymnopithys rufigula*). After the removal of these two obligate ant-following species, the top model (A) found that a species estimated home range size (response variable) was best explained by wing chord (explanatory variable). All species used in the analysis were captured at the Biological Dynamics of Forest Fragmentation Project (BDFFP) located ~80 km north of Manaus, Brazil.

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Data availability: Analyses reported in this article can be reproduced using the data provided by Wolfe et al. (2021).

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APPENDIX TABLE 3. Data used in linear regression examining relationships between a species' estimated territory size (response variable), and molt duration, home range, mass, and wing (explanatory variables). All species used in the analysis were captured at the Biological Dynamics of Forest Fragmentation Project (BDFFP) located ~80 km north of Manaus, Brazil.

Species	Molt duration (days) ^a	Home range (ha) ^{b, c, d, e}	Mass (g) ^b	Wing (mm) ^f
<i>Automolus infuscatus</i>	160	10.6	34.8	85.7
<i>Certhiasomus stictolaemus</i>	146	12.0	12.9	79.6
<i>Corythopsis torquatus</i>	157	5.7	15.9	64.2
<i>Dendrocincla fuliginosa</i>	196	16.8	37.4	106.3
<i>Formicarius colma</i>	182	7.3	46.2	82.9
<i>Glyphorhynchus spirurus</i>	171	5.2	13.6	68.0
<i>Gymnopathys rufigula</i>	271	36.7 ^g	29.0	75.0
<i>Hylophilus ochraceiceps</i>	168	8.6	10.0	56.0
<i>Hypocnemis cantator</i>	170	4.0	11.8	52.1
<i>Microbates collaris</i>	149	4.0	10.7	50.1
<i>Myrmeciza ferruginea</i>	217	7.1	24.6	62.6
<i>Myrmotherula axillaris</i>	178	8.9	7.6	50.7
<i>Myrmotherula longipennis</i>	194	11.9	8.4	57.2
<i>Myrmotherula menetriesii</i>	155	11.9	8.1	51.6
<i>Pernostola rufifrons</i>	236	5.6	28.9	71.2
<i>Pithys albifrons</i>	301	36.7 ^g	20.1	69.8
<i>Sclerurus rufigularis</i>	129	17.1	21.2	76.3
<i>Thamnomanes ardesiacus</i>	221	10.6	18.1	72.8
<i>Thamnomanes caesius</i>	224	10.6	17.5	71.2
<i>Turdus albicollis</i>	128	27.3	49.2	102.6
<i>Willisornis poecilinotus</i>	205	5.6	16.8	63.6
<i>Xiphorhynchus pardalotus</i>	190	10.6	37.7	101.6

^a Johnson et al. (2012).^b Johnson et al. (2011).^c Willis and Oniki (1978).^d Bierregaard and Lovejoy (1989).^e Harper (1989).^f Averaged from BDFFP banding data (1979–2014).^g Conservative estimate produced by radio-tracking just 3 birds per species for these two wide-ranging ant followers.