THE ROLE OF PREALTERNATE MOULT IN NONBREEDING PERIOD CARRY-OVER EFFECTS IN NEOTROPICAL MIGRATORY SONGBIRDS

by

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ABSTRACT

Feathers serve myriad functions, including flight, thermoregulation, and communication. Because feathers are keratin structures, they cannot be repaired once damaged so birds must shed and regrow new feathers each year through a process called moult. Despite the importance of moult for feather function, it is one of the least understood events in the annual cycle of migratory birds. For Nearctic-Neotropical migratory songbirds that moult twice annually, little is known about the ecology of their prealternate moult, which typically occurs on the stationary nonbreeding grounds prior to pre-breeding (northward) migration. Improving our understanding of prealternate moult is fundamental for identifying how it interacts with other life history stages, breeding and migration, across the annual cycle, knowledge that is critical for determining periods of the year that limit declining bird populations. Here, I provide a detailed quantification of the timing, patterns, and intensity of prealternate moult for six warbler species (Family: Parulidae) on their stationary nonbreeding grounds in Jamaica. I demonstrate that prealternate moult is common for Northern Waterthrush (*Parkesia noveboracensis*), Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), Northern Parula (*Setophaga americana*), and Prairie Warbler (*Setophaga discolor*), and for most species increases in frequency and intensity across the nonbreeding period. I confirm the occurrence of prealternate moult in some Ovenbirds (*Seiurus aurocapilla*). I then assess the role of prealternate moult in carry-over effects from the nonbreeding period to the timing of migration departure for the Black-and-white Warbler, Northern Waterthrush, and American Redstart. First, I assessed the influence of body condition on the timing and intensity of prealternate moult in distinct habitats that differ in moisture regime: dry second-growth scrub forest and wet mangrove. I analyzed stable-carbon isotope ratios (δ^{13}C) from birds' red blood cells to support my understanding of relative habitat quality for the study species. Using the Motus Wildlife Tracking System, I tracked precise dates of migration departure so I could evaluate the influence of habitat quality, body condition, and prealternate moult on departure timing. Moult intensity was generally higher in young birds but its relationship with body condition varied among species, indicating that body condition may not be the most important driver of prealternate moult phenology. For the American Redstart, the effect of age on moult varied with habitat type, suggesting that birds with the poorest quality feathers, associated with poorer quality, open habitat, require a more intense moult than older birds and those in higher quality habitat. I found the first potential evidence of a carry-over effect from prealternate moult to departure timing in a parulid warbler, the American Redstart. Male American Redstarts with later, high-intensity moult departed on migration later, suggesting that prealternate moult can represent an important seasonal interaction in some birds. Ultimately, this study is an important step in beginning to understand the role of prealternate moult in nonbreeding period carry-over effects. To that end, it will be crucial for researchers in the global north to establish equitable partnerships with local neotropical researchers to aid in furthering prealternate moult research on the nonbreeding grounds of many migratory birds.

Keywords: migratory birds, nonbreeding ecology, prealternate moult, carry-over effects

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I want to start by first acknowledging the perspective through which I conducted this research, as a descendant of white settlers, a resident of the Global North, and a scientist trained in Western scientific methods, all of which come with inherent privileges and biases. The field work component of this research took place on the stolen lands of the Yamaye Taíno people, the first indigenous peoples of Yameyeka, also known as Jamaica. As a student at Thompson Rivers University, I am based as an uninvited guest in Secwepemcúlucw, on the stolen lands of the Tk'emlúps te Secwépemc people. Settler-colonialism and the Western scientific agenda have long-dominated the field of environmental science in both Canada and Jamaica, often reinforcing systems of oppression and exclusion. These systems continue to exclude Indigenous peoples and peoples historically displaced because of settler-colonialism and slavery, from the study and management of their lands. I would like to thank those of you who welcomed conversation or provided guidance, as I sought to better understand the role of my research in these dynamics and the inequities driven by Western science: Dr. Matt Reudink, Dr. Lisa Cooke, Dr. Kara Lefevre, Sukh Heer Matonovich, Dr. Amie McLean, Dr. Maggie MacPherson, and Ivy Ciaburri. I have much work to do but learned from all of you.

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CHAPTER 1: INTRODUCTION

Animal migration is one of the most engaging phenomena in the natural world. When colourful migratory songbirds arrive in temperate North America each spring, they spark joy among people of many demographics and inspire them to connect with nature and participate in environmental stewardship. Migratory birds play important roles in our ecosystems, from plant pollination to agricultural pest control (Galloway et al. 2004, Anderson et al. 2016, Díaz-Siefer et al. 2022) and can also act as indicators of environmental health (Morrison 1986, Simons et al. 1999, Zöckler 2005). However, migratory birds face threats such as habitat degradation and loss, changes in global climate, and collisions with buildings (Machtans et al. 2013, Loss et al. 2014, Bairlein 2016, Zurrell et al. 2018, Rosenberg et al. 2019). As a result, migratory birds have declined globally (Bairlein 2016, Zurrell et al. 2018, Rosenberg et al. 2019). In temperate North America alone, we have lost an astounding 2.9 billion birds, or an estimated 29%, of all birds between 1970 and 2017 (Rosenberg et al. 2019). Long-distance migrants, such as Nearctic-Neotropical that migrate to the Caribbean and tropical regions of the Americas during the season we call winter, have experienced more staggering declines than non-migratory, native resident species (Rosenberg et al. 2019).

While Nearctic-Neotropical migrants might spend up to four months on their breeding grounds in Canada and the United States, they spend a greater portion of the year in-transit and on their tropical, stationary nonbreeding grounds (Albert et al. 2020)[1]. Because migratory birds utilize diverse habitats throughout the year that are often separated by thousands of kilometres, understanding the drivers of their population decline (Marra et al. 2015) and identifying actions for conservation (Runge et al. 2015) are uniquely challenging. Gaining this understanding requires identifying the temporal and spatial periods of the annual life cycle in which bird populations are limited (Marra et al. 2015). One such period for long-distance migrants can be the nonbreeding period. For example, dry environmental conditions on the nonbreeding grounds can reduce the

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[1] This period is also known as "overwintering," but that term is north-centric and inaccurate when describing tropical seasons, so I use the terms "stationary nonbreeding," or "nonbreeding" to refer to this period, following Albert and Siegel (2023). Throughout the thesis I use "pre-breeding" and "post-breeding" migration in place of the north-centric spring and fall migration (Albert and Siegel 2023)

annual survival of the American Redstart (*Setophaga ruticilla*) during northward, pre-breeding migration (Dossman et al. 2023). Moreover, such effects can disproportionately impact certain breeding populations. In this example, Dossman et al. (2023) found that American Redstarts that breed further north, and therefore have a longer distance to migrate, were most impacted by dry nonbreeding conditions. Undertaking research to uncover such patterns, then applying this information to implement meaningful conservation actions, requires massive cooperation across international and jurisdictional boundaries (Runge et al. 2015, Albert et al. 2020).

Understanding moult is important for conserving migratory birds

Bird feathers serve myriad functions, including flight, thermoregulation, protection from parasites, visual (and sometimes aural) communication, and others (reviewed in Terrill and Shultz 2023). Because feathers are keratin structures, they cannot repair themselves once damaged (Lennox and Rowlands 1969) and birds must shed and regrow new feathers each year through a process called moult (Figure 1.1). Moult requires protein to support feather synthesis and imposes a high energetic cost (Dietz et al. 1992, Lindström et al. 1993, Cyr et al. 2008, Vézina et al. 2009, Lourenço 2014). The energetic demands of moult can conflict with the energetic demands of the other important annual life stages: migration and breeding (Barta et al. 2008). For this reason, moult, migration, and breeding typically occur at different times during a bird’s annual schedule without overlapping (Figure 1.2; Barta et al. 2008, Wingfield 2008, de la Hera et al. 2012, Kiat et al. 2019), though there are exceptions. For example, moult-migrants pause their migration at a “stopover” location to spend time moulting before proceeding to their final destination (Tonra and Reudink 2018).

Figure 1.1. An example of moult on the wing of a Black-headed Grosbeak (*Pheucticus melanocephalus*), a small Nearctic-Neotropical migratory songbird. This bird grew the black feathers more recently than the brown feathers; hence they are newer, fresher, and in overall better quality. This example illustrates how moult can serve multiple functions: to maintain the structural function of feathers, and to change the colour of a bird's plumage during the year to signal age or intrasexual dominance during the breeding season. Photo taken by Shae Turner.

The environmental conditions that a bird experiences during one life stage can interact with the bird's physiological state and "carry over" to shape their performance (e.g., fitness) during the subsequent life stage, even creating a domino effect across multiple stages, or seasons (Norris and Marra 2007, Harrison et al. 2011). For example, songbirds that spend the stationary nonbreeding period in poor quality habitat tend to have poorer body condition, which can delay pre-breeding migration (e.g., Marra et al. 1998, Studds and Marra 2005, Reudink et al. 2009), in turn delaying arrival to the breeding grounds and culminating in reduced reproductive success when compared with conspecifics from higher quality nonbreeding habitat (e.g., Norris et al. 2004, Reudink et al. 2009). Identifying when and where these carry-over effects occur during the avian annual cycle is critical for fully understanding when, where, and how declining populations are limited (Marra et al. 2015). Some evidence suggests that the conditions a bird experiences preceding moult can influence the timing of that moult (e.g., initiation; Danner et al. 2015) or the production of plumage ornaments important for sexual selection (Saino et al. 2004, Sparrow et al. 2017). The timing of moult, or the moult strategy, can in turn carry over to influence the timing of birds' migration (e.g., Stutchbury et al. 2011). Despite the year-round importance of moult, the potential role of moult in carry-over effects has received far less study than breeding and migration, leaving many gaps in the scientific community's understanding of moult's basic ecology (Bridge 2011, Pyle et al. 2018, Kiat 2023).

Each year, adults of all songbird species moult most or all feathers after the breeding season as part of the "prebasic" moult (Humphrey & Parkes 1959, Pyle 2022, Jenni and Winkler 2020). Some species, including many Nearctic-Neotropical migratory warblers (Family: Parulidae), moult some feathers a second time in the annual cycle, prior to the breeding season (Figure 1.2; Pyle 2022). This second, partial moult is called the "prealternate moult" (Howell et al. 2003). Parulid warblers that undergo prealternate moult typically do so on the nonbreeding grounds, prior to pre-breeding migration (Pyle 2022). Because prealternate moult occurs during an understudied portion of the annual cycle, the nonbreeding period, aspects of parulid prealternate moult such as its patterns, intensity (i.e., percentage of feathers in moult at one time), and timing, are not well understood when compared with the prebasic moult (see Chapter 2). Quantifying prealternate moult phenology is an important first step toward being able to identify if prealternate moult influences subsequent life history stages through carry-over effects. If the prealternate moult period does limit bird populations, such information can be applied to support the prioritization of high-quality nonbreeding habitats for conservation.

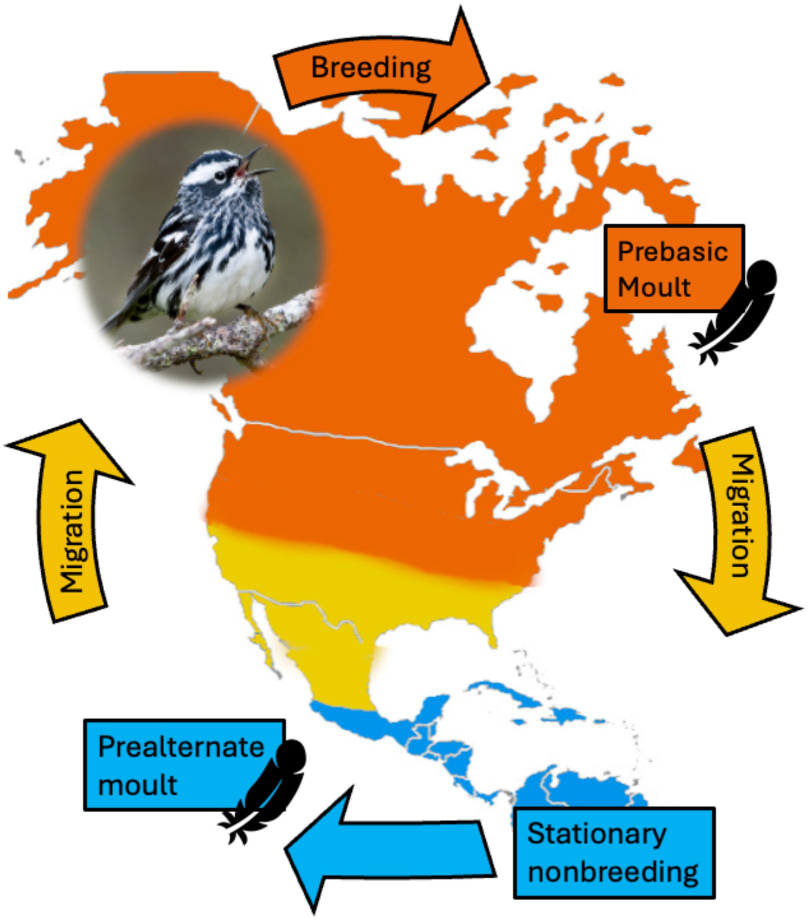

Figure 1.2. Generalized diagram illustrating the annual life cycle of Nearctic-Neotropical migratory birds that undergo prealternate moult on the stationary nonbreeding grounds. Birds arrive to their temperate breeding grounds in Canada and the United States in April – June, undergo prebasic moult after the breeding season, depart on post-breeding migration Aug – Oct, spend the stationary nonbreeding period in the tropics Nov – Apr, and undergo prealternate moult in the two to three months prior to departing on pre-breeding migration. Photo of the Black-and-white Warbler (*Mniotilta varia*) taken by Megan Buers.

Study system

I completed field research from January to April 2023, at Font Hill Nature Preserve (18.0391°N, 77.9411°W, <100 m above sea level), St. Elizabeth Parish, on the southwest coast of Jamaica. I conducted this research as part of a long-term study (1987-present) of a nonbreeding population of Nearctic-Neotropical migratory songbirds. Research at Font Hill has primarily focused on the American Redstart as a model species, but other work has investigated the nonbreeding ecology of the Ovenbird (*Seiurus* *aurocapilla*), Black-and-white Warbler (*Mniotilta varia*), and Swainson's Warbler (*Limnothlypis swainsonii*). The decades-long body of work from this site has been fundamental to the scientific community's understanding of nonbreeding ecology and its influence on the population dynamics of migratory birds through seasonal carry-over effects. Numerous peer-reviewed articles and graduate theses have resulted from work at Font Hill.

Font Hill Nature Preserve is owned by the Petroleum Company of Jamaica and is adjacent to Font Hill Beach Park, a previously popular recreation site for locals and tourists that is no longer in operation. Although hurricane damage during the 2010's altered the shoreline—and forest habitat structure within areas of the nature preserve—this site remains under constant threat from development proposals.

I targeted bird capture in two habitat types: wet mangrove forest and a drier, second-growth scrub forest. The study area included five, 5 to 7 ha plots (Figure 1.3). A cluster of one scrub forest plot and two mangrove plots was separated by 200 m from one mangrove plot adjoining a scrub forest plot.

I captured six warbler species (Family: Parulidae), Ovenbird, Northern Waterthrush (*Parkesia noveboracensis*), Black-and-white Warbler, American Redstart, Northern Parula (*Setophaga americana*), and Prairie Warbler (*Setophaga discolor*), and used the data I collected on their prealternate moult in Chapter 2. In Chapter 3, I focused only on the Northern Waterthrush, Black-and-white Warbler, and American Redstart, the species for which capture rates were highest. For each species, their breeding and nonbreeding ranges are shown in Figure 1.4. Pre-breeding migration timing from Jamaica, and my pre-study knowledge of the extent and timing of the prealternate moult for each species are summarized in Table 1.1.

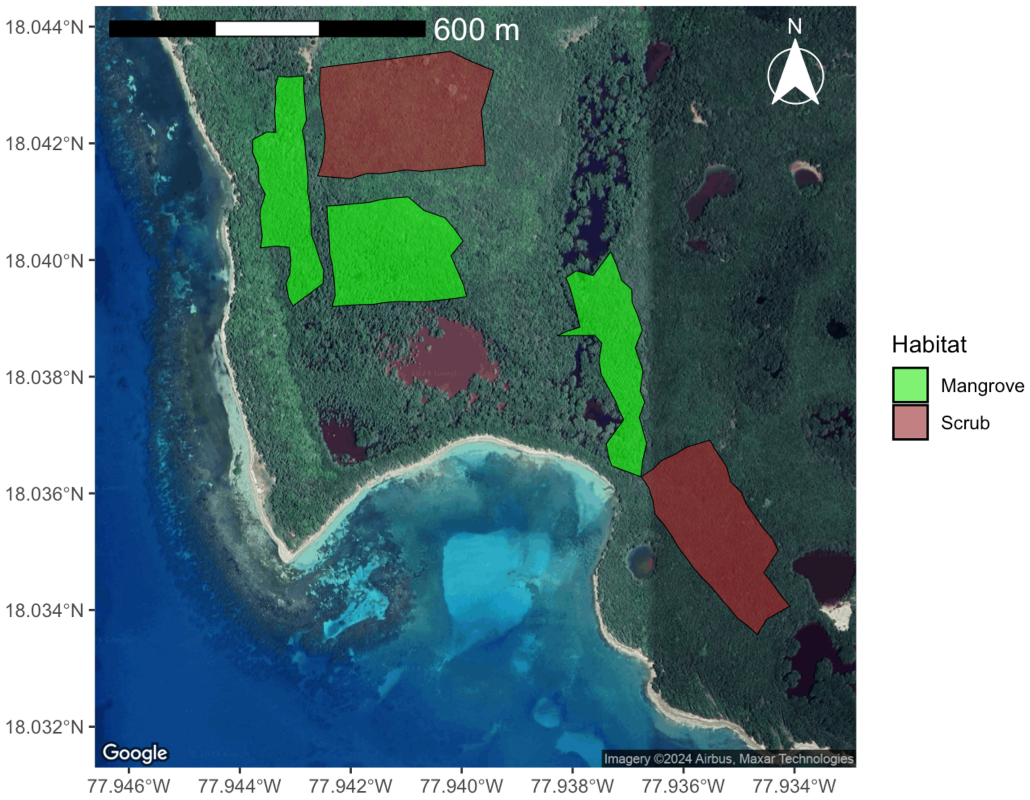

Figure 1.3. Map showing the arrangement of study plots within Font Hill Nature Preserve, (18.0391°N, 77.9411°W, <100 m above sea level), St. Elizabeth Parish, on the southwest coast of Jamaica. Three mangrove plots are shown in green while two scrub plots are shown in brown.

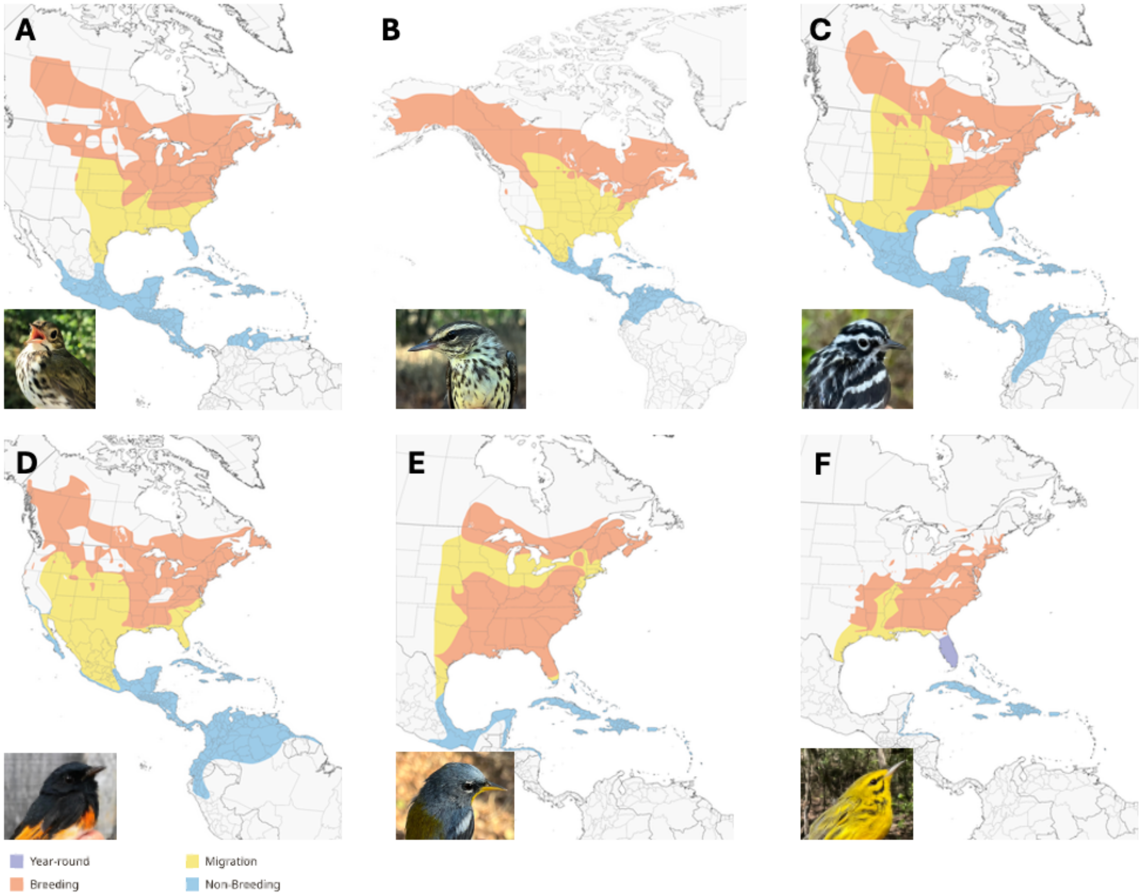

Figure 1.4. Range maps of A) Ovenbird, B) Northern Waterthrush, C) Black-and-white Warbler, D) American Redstart, E) Northern Parula, and F) Prairie Warbler (Birds of the World accounts; Porneluzi et al. 2020, Whitaker and Eaton 2020, Kricher 2020, Sherry et al. 2020, Moldenhauer and Regelski 2020, Nolan Jr. et al. 2020). Photos taken by Shae Turner.

Table 1.1. List of study species, pre-breeding migration timing for a bird departing Jamaica and arriving in northern United States/southern Canada, and my pre-study knowledge of the extent and timing of their prealternate moult. Information on migration timing from eBird data (Fink et al. 2023) and Birds of the World accounts (Kricher 2020; Moldenhauer and Regelski 2020; Nolan Jr. et al. 2020; Porneluzi et al. 2020; Sherry et al. 2020; Whitaker and Eaton 2020). Information on moult from Pyle (2022) and Birds of the World accounts. Definitions of moult extent follow Pyle (2022): Absent = no moult; limited = some, but not all, body feathers and no flight feathers; partial = most or all body feathers and sometimes the tertial and/or central rectrices but no other flight feathers.

Species	Pre-breeding migration timing	Pre-study knowledge of prealternate moult	
		Extent	*Timing*
American Redstart	Departs mid-Apr – early May Arrives mid-May	Absent – limited scattered head and body feathers, occasionally 1-3 greater coverts in Mar – Aug	Mar – Apr
Black-and-white Warbler	Departs mid-late Apr – early May Arrives late April – mid-May	Limited – partial Body feathers	Mar – Apr
Northern Parula	Departs late March – late Apr Earliest departures from the Caribbean in early Feb Arrives mid-May	Absent – limited Body feathers in some individuals	Feb – Apr
Northern Waterthrush	Departs late Apr – early May Arrives early – mid-May	Limited – partial Body feathers	Feb – Apr
Ovenbird	Departs mid-late Apr Arrives late Apr – mid-May	Absent	NA
Prairie Warbler	Departs late Mar – mid-Apr Arrives late Apr – mid-May	Limited Usually head and neck feathers	Feb – Apr

Research goal

The purpose of my thesis is to evaluate the potential role of prealternate moult in nonbreeding period carry-over effects in Nearctic-Neotropical migratory songbirds. Chapter 2 is focused on quantifying the patterns, intensity, and timing of prealternate moult in six parulid warbler species on their nonbreeding grounds in Jamaica to understand variation among species, age, and sex classes across the moult period. For three of those species, Chapter 3 is focused on testing the prediction that nonbreeding habitat quality and body condition influence the timing and intensity of prealternate moult, and in turn, carry over to influence the date birds depart Jamaica for pre-breeding migration (Figure 1.5). Specifically, I predict that birds from high-quality habitat will have better body condition, complete a high-intensity moult earlier, and depart from Jamaica earlier when compared with birds from poor-quality habitats. This thesis concludes with Chapter 4, in which I summarize the significance of my results to the broader field and their implications for environmental management.

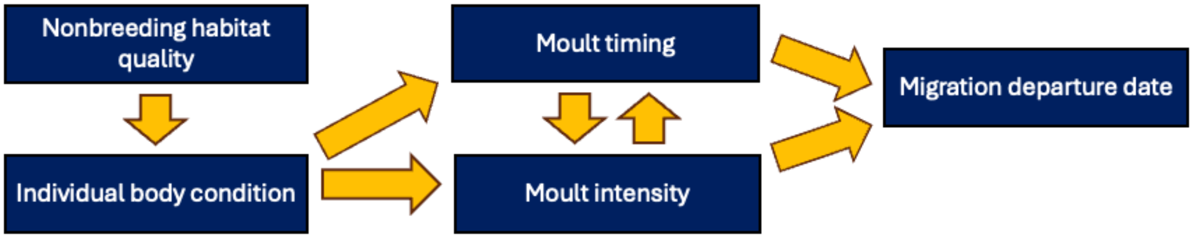

Figure 1.5. Summary of the predicted relationships and their directions between nonbreeding habitat quality, individual body condition, prealternate moult timing and intensity, and pre-breeding migration departure date.

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CHAPTER 2: QUANTIFYING PREALTERNATE MOULT TIMING, PATTERNS, AND INTENSITY IN SIX NEARCTIC-NEOTROPICAL MIGRATORY WARBLERS

ABSTRACT

Moult is vital for maintaining year-round feather function yet is one of the least understood events in the annual cycle of migratory birds. In Nearctic-Neotropical migratory songbirds, prealternate moult has received far less study than prebasic moult because it typically occurs during the least studied period of the annual cycle: the stationary nonbreeding period. Improving our basic understanding of prealternate moult is fundamental for identifying how it interacts with other life history stages across the annual cycle. Here, I provide a detailed quantification of the timing, patterns, and intensity of prealternate moult for six species of parulid warblers on their stationary nonbreeding grounds in Jamaica. I demonstrate that head and body feather moult is common for Northern Waterthrush (*Parkesia noveboracensis*), Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), Northern Parula (*Setophaga americana*), and Prairie Warbler (*Setophaga discolor*), and for most species increases in frequency and intensity later in the nonbreeding period. Black-and-white Warbler and American Redstart demonstrated age-specific patterns in moult intensity, with greater moult intensity exhibited by first-cycle than definitive-cycle birds. I confirm the occurrence of prealternate moult in at least some Ovenbirds (*Seiurus aurocapilla*) and provide the first detailed description of their contour feather moult. These findings represent the first quantification of contour feather moult intensity in these species and will serve as a foundation for investigating the mechanisms that regulate prealternate moult and potential carry-over effects from the nonbreeding grounds.

INTRODUCTION

An understanding of how life history stages interact across the full annual cycle is needed to effectively conserve declining migratory bird populations (Marra 2015a, Rosenberg et al. 2019). This task is particularly challenging for migratory species whose life history stages are separated temporally and spatially across the annual cycle while birds track seasonal resources across thousands of kilometers. Moult, the periodic replacement of feathers, is one stage for which substantial knowledge gaps remain (Bridge 2011, Pyle et al. 2018, Pyle 2022a, Kiat 2023). Moult is vital to maintaining a myriad of feather functions from flight and movement overall (Hedenström 2002, Jenni and Winkler 2020a), thermoregulation (Wolf and Walsberg 2000), visual communication (Hill and McGraw 2006, Santos et al. 2011, Jenni and Winkler 2020a, Terrill et al. 2020), protection from parasites (e.g., Gunderson et al. 2008) and solar radiation, among others (for a full review of feather function, see Terrill and Shultz 2023). Since moult has a high energetic cost (Dietz et al. 1992, Lindström et al. 1993, Cyr et al. 2008, Vézina et al. 2009, Lourenço 2014), moult in migratory birds is typically scheduled not to overlap with breeding and migration (Barta et al. 2008, Wingfield 2008, de la Hera et al. 2012, Kiat et al. 2019), two other energetically costly events, though moult and migration strategies vary (Rohwer 2005). Some evidence suggests that moult strategy and/or timing can carry over to influence birds' migratory timing (e.g., Carlisle et al. 2005, Stutchbury et al. 2011, Kiat and Izhaki 2016), and that conditions experienced prior to moult can influence its timing (e.g., initiation date; Danner et al. 2015), and the production of phenotypic plumage traits likely to have consequences on individual fitness (e.g., Saino et al. 2004, Sparrow et al. 2017). Understanding the frequency, intensity, and timing of moult is imperative given its year-round importance to feather function and its potential to influence subsequent life history stages through seasonal interactions.

Each year, adults of all species of passerines moult most or all contour and flight feathers as part the prebasic moult (Humphrey & Parkes 1959), typically occurring after the breeding season in north-temperate resident and Nearctic-Neotropical migratory birds (Pyle 2022b). Some species replace contour feathers a second time in the annual cycle during a prealternate moult, typically occurring prior to the breeding season (Humphrey & Parkes 1959, Pyle 2022b). The prealternate moult is thought to have evolved to maintain feather function in long-distance migratory birds and as the mechanism through which migrant passerines achieve seasonal dichromatism (Kiat et al. 2018, Terrill et al. 2020, Cuervo et al. 2022). Most Nearctic-Neotropical migrant songbirds that undergo prealternate moult complete it on the stationary nonbreeding grounds (hereafter "nonbreeding grounds") prior to pre-breeding (northward) migration (Pyle 2022b), though the number of species that employ a prealternate moult-migration strategy may be underestimated (Leu and Thompson 2002, Tonra and Reudink 2018, Wright et al. 2018).

Given that the study of migratory birds has long been biased toward the breeding period and breeding grounds (Marra et al. 2015a, Kiat 2023), it's unsurprising that the study of moult has focused heavily on the prebasic moult, leaving a significant knowledge gap in our understanding of the prealternate moult. While detailed information is available for the timing and extent of prebasic moult for almost all Nearctic-Neotropical migrant songbirds, such information ranges from limited to absent for those species' prealternate moult (Pyle 2022b). Not only are many descriptions of the timing and extent of prealternate moult lacking detail when compared with the prebasic moult, but for some species the extent (e.g., Black-and-white Warbler (*Mniotilta varia*)) or occurrence of prealternate moult (e.g., Ovenbird (*Seiurus aurocapilla*)) remain uncertain or unknown. Further, much study of the prealternate moult has focused on wing feather moult and thereby the species that moult wing feathers as part of the prealternate moult. This bias is likely because prealternate moult limits on passerines can be easily detected on the wings of museum specimens (e.g., Pyle and Carnes 2022) and on birds captured on the breeding grounds (e.g., Crary and Rodewald 2012, Jones et al. 2014, Cimprich 2018, Carnes et al. 2021), prior to the prebasic moult. Once prealternate moult is completed, moult limits between the tiny contour feathers of small birds are challenging to detect in the field, becoming near impossible to detect when replaced alternate feathers are the same colour as retained basic feathers. This challenge has likely contributed to a biased focus on prealternate contour feather moult in particular regions of the body that contribute to seasonal dichromatism (e.g., Boone 2006, Boone et al. 2010), leading to a reduced understanding of prealternate moult patterns on other regions of the body. Studying birds in active prealternate moult, whether wild birds captured on the moulting grounds (e.g., Mettke-Hofmann et al. 2010, Renfrew et al. 2011, Danner et al. 2015, Wright et al. 2018) or museum specimens (e.g., Rohwer et al. 1983, Jackson et al. 1992, Voelker and Rohwer 1998, Voelker and McFarland 2002, Sieburth and Pyle 2018), allows for greater capacity to accurately quantify the extent or intensity of prealternate contour feather moult but these studies are relatively few in number.

Of the 46 warbler species (Family: Parulidae) that are Nearctic-Neotropical migrants, 33 (72%) are thought to have a prealternate moult strategy, at least in some individuals, and the occurrence of prealternate moult remains uncertain in additional 5 species (Pyle 2022b). For 8 of the 33 (24%) species thought to have a prealternate moult strategy, there is some level of uncertainty in the apparent extent of that moult (Pyle 2022b). Aside from recent updates to species moult accounts in *Identification Guide to North American Birds, Part I* (2nd Edition; Pyle 2022b), prealternate moult has largely been overlooked in the study of wild Nearctic-Neotropical migratory warblers over the past 24 years. A systematic search of scientific papers in The Web of Science yielded only four papers since the year 2000 related to field study of the prealternate moult in any Nearctic-Neotropical migratory parulid species (conducted June 2024, using the search terms "prealternate moult" or "prealternate molt" alongside each species' common name). Only one of these studies aimed to quantify prealternate moult in all feather groups during active moult; in the Lucy's Warbler (*Leiothlypis luciae*) and Virginia's Warbler (*Leiothlypis virginiae*) (Voelker and McFarland 2002). Studies of the Magnolia Warbler (*Setophaga magnolia*) (Boone et al. 2010) and Yellow Warbler (*Setophaga petechia*; Quinlan and Green 2011, Crary and Rodewald 2012) aimed to understand links between feathers moulted during the prealternate moult and another life history stage, using data collected away from the moulting grounds. I know of one additional published study on the Yellow Warbler (Jones et al. 2014) that was not captured by my search. While this systematic search is likely to have accurately captured work published by scientists based in the Global North, it excludes dissertations (e.g., Ames 2021) and may fail to account for studies of prealternate moult by Neotropical researchers that are not published in global-scope journals, particularly if those studies are descriptive (Ruelas Inzunza et al. 2023, Soares et al. 2023).

Collecting detailed information on the timing and patterns of prealternate moult in all areas of the bird's body is the necessary first step to facilitate future study of the mechanisms that regulate prealternate moult, such as body condition, and how prealternate moult interacts with other life history stages. As such, it will be critical to gather fundamental information of how prealternate moult varies across species, age and sex classes, and eventually across the nonbreeding period range for individual species.

Here, I provide a detailed quantification of the timing, intensity, and patterns of prealternate moult for six species of Nearctic-Neotropical migratory warbler on their nonbreeding grounds in Jamaica. This study represents the most detailed information available for the moult of contour feathers across all areas of the head and body and is the first quantification of moult intensity over time in the species studied.

METHODS

Study species

My study focused on six primarily insectivorous, long-distance, Nearctic-Neotropical migratory species that are commonly captured in Jamaica during their nonbreeding period: Ovenbird, Northern Waterthrush (*Parkesia noveboracensis*), Black-and-white Warbler, American Redstart (*Setophaga ruticilla*), Northern Parula (*Setophaga americana*), and Prairie Warbler (*Setophaga discolor*). While several of these species have been the subject of extensive research on the nonbreeding grounds (e.g., Dugger et al. 2004, Smith et al. 2011, Marra et al. 2015b, Kent and Sherry 2020, Cooper et al. 2021, Kent et al. 2022), relatively little is known about the extent and timing of their prealternate moult, which has been suggested to occur during this portion of the annual cycle (Pyle 2022b, Kricher 2020, Moldenhauer and Regelski 2020, Nolan Jr. et al. 2020, Porneluzi et al. 2020, Sherry et al. 2020, Whitaker and Eaton 2020). The occurrence of prealternate moult in the Ovenbird requires confirmation (Porneluzi et al. 2020, Pyle 2022b); at least some individuals of the other five species complete a limited to partial prealternate moult, as in some but not all contour feathers and typically no wing feathers (Pyle 2022b).

Study site

I conducted this study on the southwest coast of Jamaica within the Font Hill Nature Preserve (18.0391°N, 77.9411°W, <100 m above sea level), St. Elizabeth Parish, from January 13 through April 18, 2023. Precipitation at this site is strongly seasonal, with a wet season typically from August to November (average monthly precipitation >100 mm) and dry season from December through May (average monthly precipitation <25 mm; Powell et al. 2021).

I captured Nearctic-Neotropical migratory warblers in two second-growth dry scrub forest plots and three mangrove plots, ranging in size from 5 to 7 ha each. A cluster of one scrub forest plot and two mangrove plots was separated by 200 m from one mangrove plot adjoining a scrub forest plot. See Cooper et al. (2021) for a description of vegetation structure and composition in these two habitat types. Scrub plots remained dry without standing water throughout the study period, typical conditions for this habitat type during the dry season (Marra et al. 2015b, Cooper et al. 2021). Mangrove plots typically hold 0.3 to 2 m of standing brackish water throughout the dry season (Cooper et al. 2021). Due to relatively low levels of precipitation preceding and during the study period, water levels in the mangrove plots remained low and at times, areas within plots were completely dry. Similar conditions have occurred at the study site in previous dry years (e.g., Cooper et al. 2015, Brunner et al. 2022, Dossman et al. 2023).

Field methods

I captured warblers by mist-netting on 47 days between January 13 and April 18, 2023, using a combination of passive netting and target netting with an audio lure. Each week I captured birds in at least one scrub plot and one mangrove plot. Each capture day usually involved opening at least ten 12 m long mist nets for five to six hours of passive netting after sunrise. I used target netting with an audio lure to capture highly territorial American Redstarts throughout the season, and from March through April to recapture individual Black-and-white Warblers and Northern Waterthrushes. I typically used one or two 12 m mist nets from the array for target netting or erected an additional 6 m mist net. I aimed to recapture as many individuals as possible to observe the progression of moult over time.

I banded each individual with a uniquely numbered United States Geological Survey aluminum band. I determined sex for species with sex-based differences in plumage characteristics (Pyle 2022b): American Redstart, Black-and-white Warbler, Northern Parula, and Prairie Warbler. I was unable to determine sex using morphometric measurements for Ovenbird or Northern Waterthrush (Pyle 2022b). I determined age classes based on moult and plumage characteristics (Pyle 2022b), following the WRP age classification system (Wolfe et al. 2010) most recently modified by Pyle et al. (2022).

Thereby, I assigned moulting individuals to one of two age classes, First Prealternate Moult (FPA, hereafter “first-cycle”) or Definitive Prealternate Moult (DPA, hereafter “definitive-cycle”).

I systematically searched for active contour feather moult (pinfeathers) by blowing on the feathers (Mettke-Hoffman et al. 2010, Wright et al. 2018) in each of 17 patches across the head and body (Figure 2.1; Wright et al. 2018). For each patch, I scored the percentage of feathers in active moult on a scale of 0 to 4, a method I adapted from Greenwood et al. 1983 and Wright et al. 2018. The scale divides the percentage of feathers in active moult into quarters, where 0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100% of active moult per patch. To minimize observer error, moult scores for each bird were collected by one of two skilled observers (SAT and IAC). At the beginning of the field season, we repeated the moult scores on the same birds to standardize our measurements and reduce variability associated with the observer. We periodically repeated this process for feather patches with active moult throughout the season.

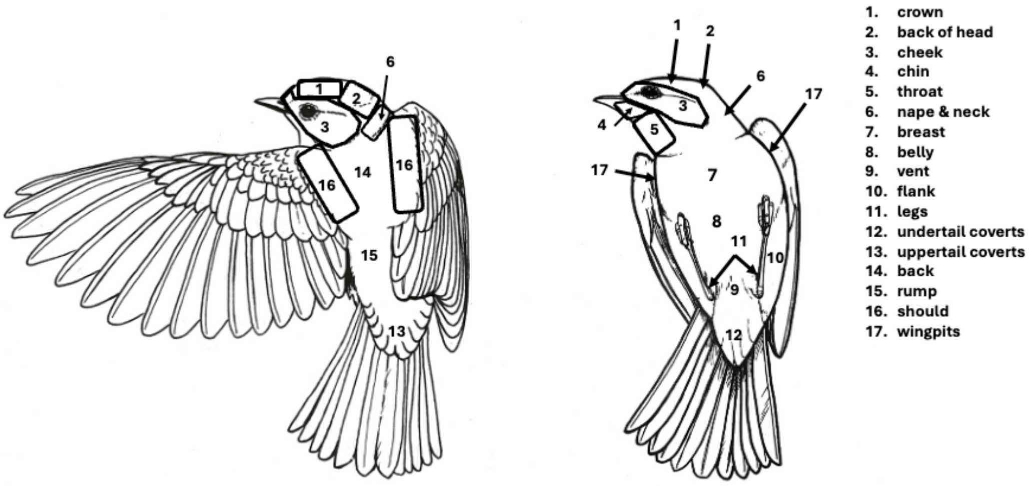

Figure 2.1. Diagram of 17 contour feathers patches in which I scored prealternate moult intensity. Illustration by Stephen Joly.

I considered all instances of contour feather moult to be part of a prealternate moult strategy, rather than part of a protracted or suspended (Jenni and Winkler 2020b, Pyle 2022b) preformative/prebasic moult (Howell et al. 2003), or adventitious feather replacement. Five of the six study species were not moulting during the first 1.5 weeks of capture (at least 4 weeks without moult for most species), so I am confident that I observed seasonal prealternate moult. I captured a Northern Waterthrush in moult on the first day that I captured the species (January 25), so prealternate moult for some individuals of the species may have commenced earlier in January than I could document. I refer to the first observed occurrence of moult for each species as the "observed onset" of moult for that species.

I could not easily distinguish retained contour feathers from those replaced on the nonbreeding grounds prior to capture, except in first-cycle male American Redstarts when recently replaced feathers were black. Prior to the observed onset of moult in the species, plumage appearance varied considerably in males of the other focal species with differing basic and alternate plumage, making it impossible to determine the extent of contour feather moult completed before capture. For example, both first- and definitive-cycle male Black-and-white Warblers displayed wide variation in the number and position of black feathers on the cheeks and throat. For this reason, I used moult intensity, rather than extent, as my moult metric.

I also examined the wings and rectrices for active moult, symmetrical or not, and recorded the number and position of coverts, flight feathers, or rectrices in pin. The study species are not known to moult wing or tail feathers as part of their prealternate moult strategies (though some American Redstarts may moult one to three greater coverts; Pyle 2022b), so the few individuals I observed moulting these feathers likely did so adventitiously, as previously documented in American Redstarts at the study site (Tonra et al. 2014). I exclude this information from the statistical analyses.

Quantifying moult intensity and prevalence

To describe the intensity of active moult per individual, I calculated a combined contour moult index (CCMI) modified from Wright et al.'s (2018) variation of the Greenwood et al. (1983) method. Each bird received a CCMI score on a scale of 0 to 4, the sum of all patch scores divided by the total number of patches (17). The CCMI score divides the percentage of active moult across the entire head and body into quarters; for example, a bird with a CCMI score of 1 was actively moulting between 1 and 25% of all contour feathers.

Since I anticipated differences in moult intensity between the head and body in most species (Chapter 1, Table 1.1), to facilitate comparison I also grouped the feather patches by head (6 patches) and body (11 patches) and calculated a CCMI score for each patch group. To compare moult intensity among moulting individuals across species, I calculated the mean CCMI score for each species including only birds that were actively moulting at capture and had a CCMI score recorded. I then calculated the mean CCMI score for each patch, per species, only including individuals actively moulting that patch at capture (Wright et al. 2018).

For each species' population, I calculated the prevalence of moult by feather patch as the proportion of all captures (including non-moulting individuals) actively moulting each patch (Wright et al. 2018). In all calculations at the population level, I included data from recaptures, regardless of the number of days passed since first (or previous) capture. This decision was informed by multiple observations of moult starting in a new feather patch only one day after the bird was captured and scored for active moult. In each of these cases, I carefully compared patch scores in the field with those from the previous capture to ensure that differing patch scores were not a result of observer error.

For each species, I also aimed to determine the population-level peak in moult prevalence, as in the period where the greatest proportion of weekly captures was moulting. When presenting the results I use the term population-level peak to describe the clear peak only observed in the Northern Waterthrush and Ovenbird.

Statistical analyses

To compare the prevalence of prealternate moult across the six species, I used a Pearson's chi-squared test of the proportion of individuals from each species that were moulting versus not moulting, excluding captures from before the observed onset of moult in each species. I used ANOVA to compare mean moult intensity (CCMI) across species. For all statistical analyses, I evaluated the significance of parameter estimates at a $\alpha = 0.05$. The results did not change qualitatively for Pearson's chi-squared test or ANOVA when I excluded recaptures, so I report test statistics from tests that included recapture data. I performed all statistical analyses in R 4.4.0 (R Core Team 2024).

I used paired t-tests to determine if moult intensity, as measured by CCMI, differed between the head and body patch groups within individuals of each species. To compare the prevalence of head feather moult against body feather moult, I used chi-squared tests of given probabilities of the proportion of moulting individuals of each species moulting head or body feathers. I did not detect differences for any species in the prevalence of active head versus body moult ($p \geq 0.14$), so I do not present the individual test statistics. The results of paired t-tests and chi-squared tests did not change qualitatively when I excluded recaptures, so I report test statistics from paired t-tests that included recapture data.

I examined the influence of Julian date, age, sex, and their interactions on moult intensity (CCMI) for each species using a linear mixed-effect (function *lmer,* R package *lme4*; Bates et al. 2015) or linear model (function *lm*) and a stepwise backward variable removal procedure where I started with the initial full model and iteratively removed non-significant terms ($p > 0.05$) to arrive at a single best fit model. I ran a separate model for each species because exploratory analysis revealed a strong species effect on moult intensity. I tested whether the explanatory variables predicted moult intensity during the moult period by excluding capture data prior to the observed onset of moult. I ran a linear mixed-effect model with the individual as a random effect to account for recaptures for Ovenbird, Northern Waterthrush, and Black-and-white Warbler. I ran a linear model with no random effect for the remaining species because I either had no recaptures (Northern Parula), or the recaptures after the observed onset of moult did not contain all age-sex combinations (American Redstart and Prairie Warbler), making model fitting unreliable. For American Redstart and Prairie Warbler, I ran the model three ways to handle individuals with repeated measurements. First, I included only the first capture record. Second, I included only the second capture record. Finally, I included all capture records without accounting for the effect of individual, for the sake of comparison. The estimates for explanatory variables varied among approaches between 0 and 42.3%, but the results did not differ qualitatively ($p > 0.05$), so here I report the models including only the first capture records (see Appendix A, Table A.1 for the results of all approaches). For American Redstart and Prairie Warbler only, I found a quadratic relationship between moult intensity and Julian date, so I included Julian date^2 as an explanatory variable in the initial model to account for both linear and quadratic components of the relationship. I present results below only for the species in which moult intensity was predicted by at least one significant explanatory variable which included Northern Waterthrush, Black-and-white Warbler, American Redstart, and Prairie Warbler but excluded Ovenbird and Northern Parula.

RESULTS

In total I recorded the presence or absence of contour feather moult 418 times for six focal species combined. Those records came from 349 unique individuals, 54 (15%) of which I recaptured at least once, with 15 individuals recaptured two, three, or four times. The average time between successive captures was 24.8 ± 19.7 days (mean ± SD). In total I determined that 64% of birds were actively moulting at capture ($n = 268$ of 418).

I assigned CCMI scores for 408 captures (first and recaptures combined); I was unable to assign CCMI scores for 10 captures due to high capture volumes and time constraints. For 51 individuals, I successfully scored moult two to five times throughout the season. In Table 2.1, I summarize for each species the percentage of birds I scored for moult more than once (i.e., recaptures), the total number of moult scores, and the percentage of birds moulting at capture.

Each species showed active prealternate moult, involving some scattered head and body feathers or the simultaneous moult of many feathers from multiple tracts. The observed onset of moult in the study species ranged from late January to early March, though for most species, moult commenced in early to mid-February (Figure 2.2). The prevalence of moult generally increased in all species from the observed onset through the end of the study period. After the observed onset of moult, the proportion of moulting individuals varied markedly across species (Pearson's chi-squared test: $X^2_{(5)} = 22.3$, $p < 0.001$, $n_{total} = 342$; see Appendix A, Table A.2 for each species' sample sizes).

Table 2.1. Summary for each study species of the unique individuals captured by age and sex, the percentage of unique individuals scored for moult more than once, the total number of moult scores, the percentage of birds scored for moult that were in active moult, the mean ± SD Combined Contour Moult Index (CCMI) and the range of CCMI values for moulting birds. *n* is the same for percentage in active moult (%) and mean ± SD CCMI unless specified. *n* is the same for mean ± SD CCMI and CCMI range.

Species	Number of unique individuals	Sex ratio (M:F)	Percentage (%) of unique individuals with > 1 moult score (i.e., recaptures)	Total number of moult scores (initial and recaptures combined)	Percentage (%) of scored birds in active moult	Mean ± SD CCMI	CCMI range
Ovenbird	33; 9 first-cycle	NA	12 (*n* = 4)	37[a]	26 (*n* = 10)	0.29 ± 0.23 (*n* = 9[a])	0.06 – 0.59
Northern Waterthrush	95[b]; 39 first-cycle	NA	16 (*n* = 15)	110	67 (*n* = 75)	0.25 ± 0.26	0.06 – 1.41
Black-and-white Warbler	73; 23 first-cycle	29:44	22 (*n* = 16)	99[c]	62 (*n* = 62)	0.74 ± 0.72 (*n* = 61[c])	0.06 – 3.35
American Redstart	100; 26 first-cycle	58:42	15 (*n* = 15)	112[d]	79 (*n* = 89)	0.50 ± 0.47 (*n* = 81[d])	0.06 – 1.88
Northern Parula	21; 8 first-cycle	13:8	0	21	67 (*n* = 14)	0.34 ± 0.23	0.06 – 0.77
Prairie Warbler	27; 19 first-cycle	15:12	4 (*n* = 1)	28	64 (*n* = 18)	0.26 ± 0.21	0.06 – 0.59

[a] One additional Ovenbird was moulting at first capture, but I did not collect the patch scores needed to calculate CCMI.

[b] Four individuals were scored for moult but not aged.

[c] One additional Black-and-white Warbler was moulting at second capture, but I did not collect the patch scores needed to calculate CCMI.

[d] I recorded the presence of active contour moult for an additional 8 American Redstart captures (6 first capture, 1 second capture, 1 third capture) but did not collect the patch scores needed to calculate CCMI.

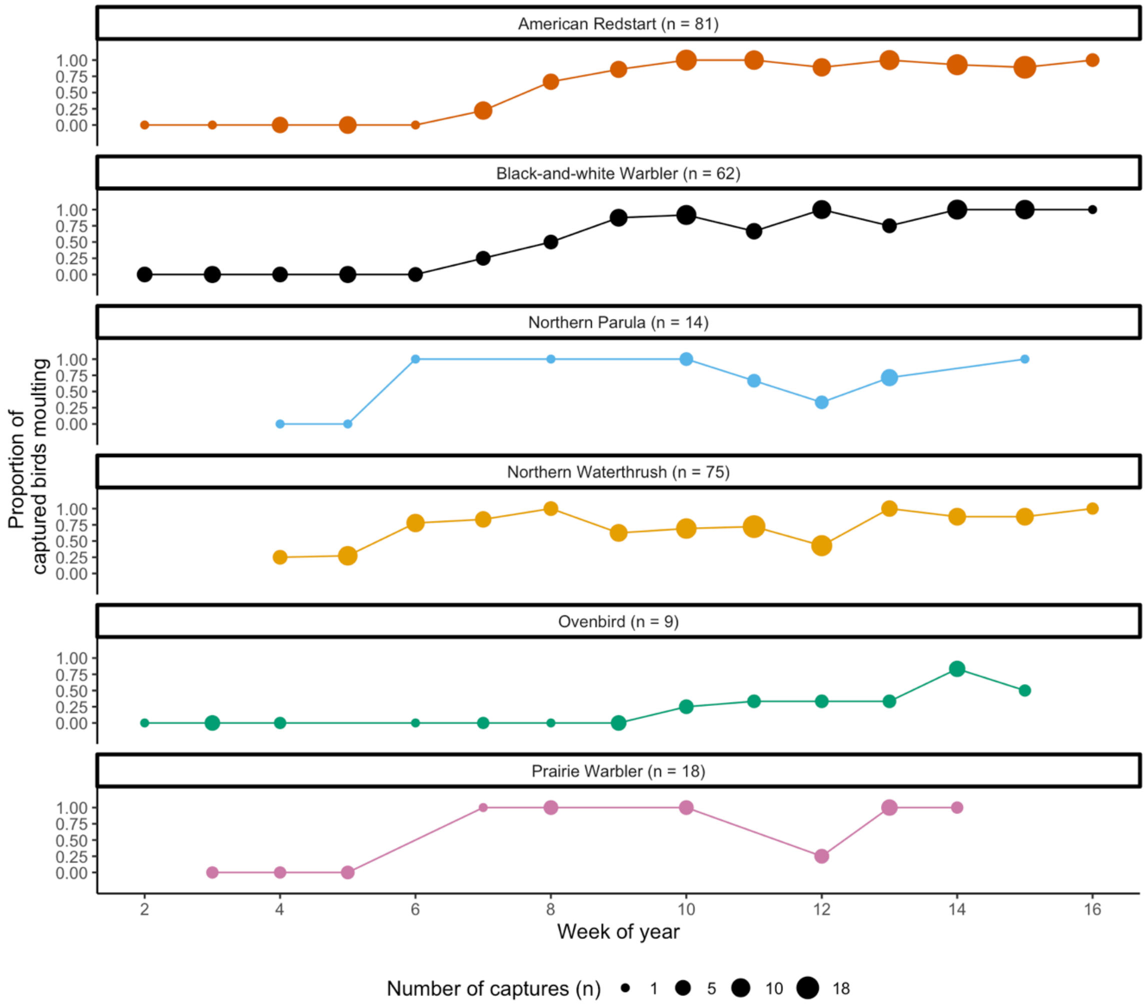

Figure 2.2. The proportion of captured birds of six species moulting by week of year from January 13 through April 18, 2023, at Font Hill Nature Preserve, Jamaica.

I observed both intra- and inter-specific variation in individual moult intensity. However, while mean moult intensity varied across species (ANOVA: $F_{(5)} = 7.39$, $p < 0.001$), all species had a mean CCMI score < 1 (Table 2.1), meaning that on average, birds from all species were not actively moulting more than 25% of their contour feathers at once. Only a few Black-and-white Warblers ($n = 4$) had CCMI scores ≥ 2, as in simultaneously moulting more than 25% of contour feathers.

Species accounts

Ovenbird

I captured moulting Ovenbirds three to six weeks later than other species in this study, between March 9 and April 9 (Figure 2.2). The prevalence of moult within the population peaked from April 3 to April 6 (83% of captures that week were in moult). I observed active moult in all feather patches except for the legs and wingpits, and most frequently on the chin and cheeks (Figure 2.3). I did not detect a difference in moult intensity between the head and the body when comparing CCMI scores for the two patch groups (paired t-test: $t_{(8)} = 1.91$, $p = 0.09$; Figure 2.4). While in other species I found clear statistically significant trends in increasing moult intensity over time, Ovenbirds showed a similar general pattern albeit not statistically significant (Julian date: $df = 15$, $t = 1.68$, $p = 0.11$).

Northern Waterthrush

I captured the first moulting Northern Waterthrush earlier than all other species in this study, on January 25 (Figure 2.2). The prevalence of moult peaked twice during the study period, from February 19 to 25 and March 26 to April 1, with all captures moulting during those weeks. After April 1, moult prevalence remained high (≥ 88% of weekly captures in moult) through April 18. Waterthrush showed active moult in all feather patches except for the belly (Figure 2.3). Active moult was most frequent on the chin, throat, and cheek. Per feather patch, mean moult intensity was greatest on the rump, the only feather patch with more than 50% of feathers in active moult (mean CCMI score > 2; Figure 2.5). Moult intensity also differed by patch group; mean CCMI was greater on the head than the body (paired t-test: $t_{(74)} = 5.58$, $p < 0.0001$; Figure 2.4). When I examined changes in moult intensity over time from the observed onset of moult in the study population (January 25), I found that CCMI increased linearly through the end of the study period (Julian date: $df = 104$, $t = 3.73$, $p = 0.003$).

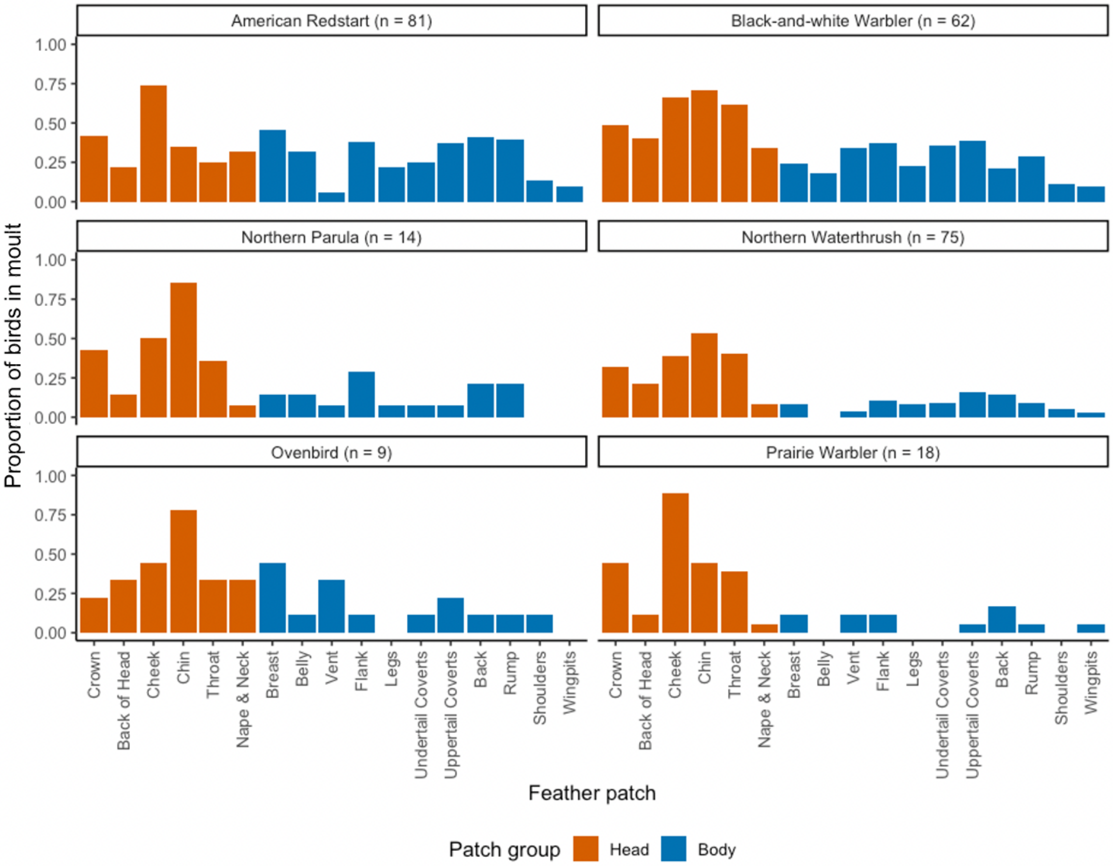

Figure 2.3. The proportions of birds from six species moulting each of 17 contour feather patches captured from January 13 through April 18, 2023, at Font Hill Nature Preserve, Jamaica.

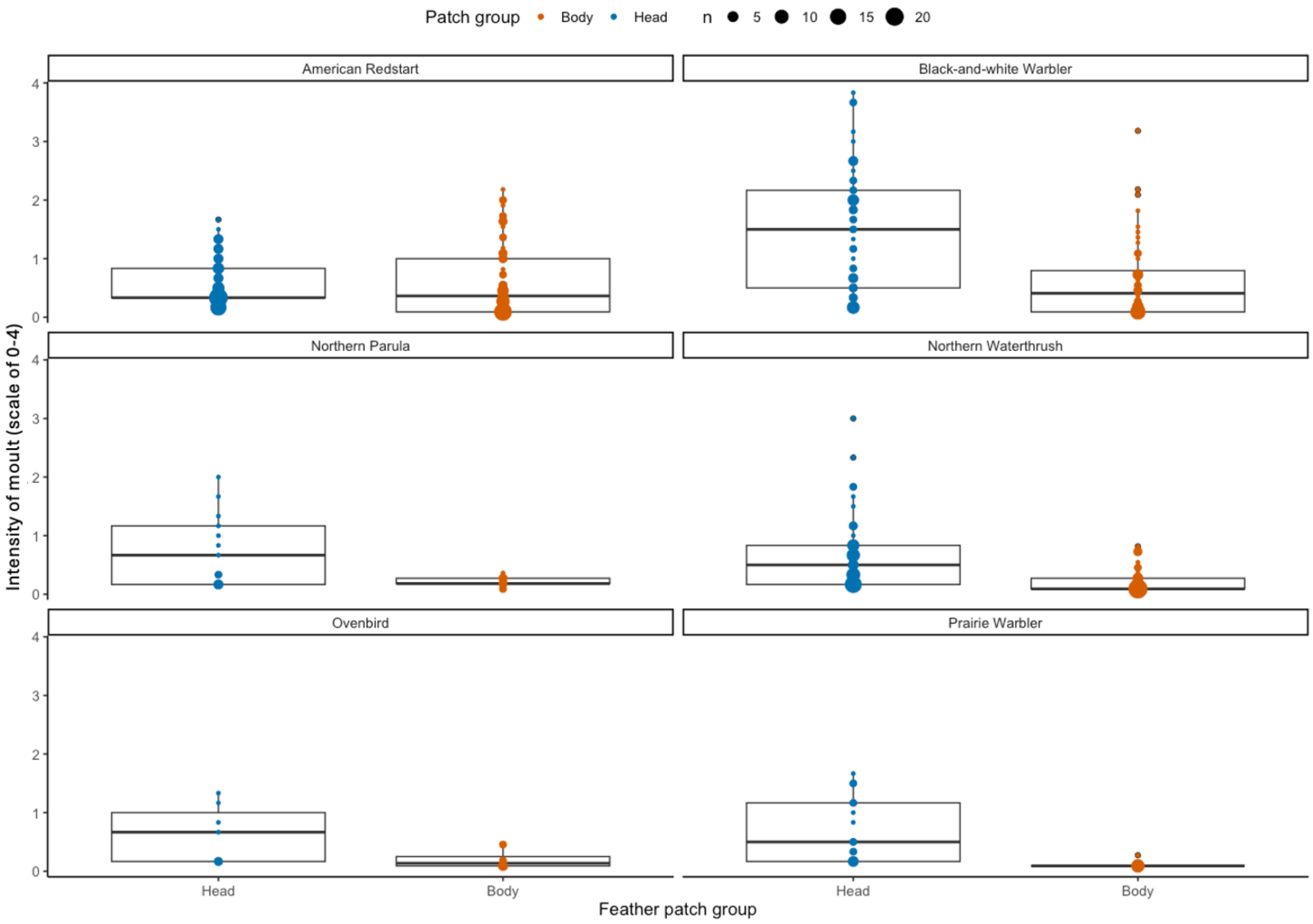

Figure 2.4. The intensity of moult (scale of 0-4) for head feathers and body feathers in six species captured from January 13 through April 18, 2023, at Font Hill Nature Preserve, Jamaica. The size of the circles represents the number (*n*) of birds sampled that had the corresponding moult intensity score for each patch group.

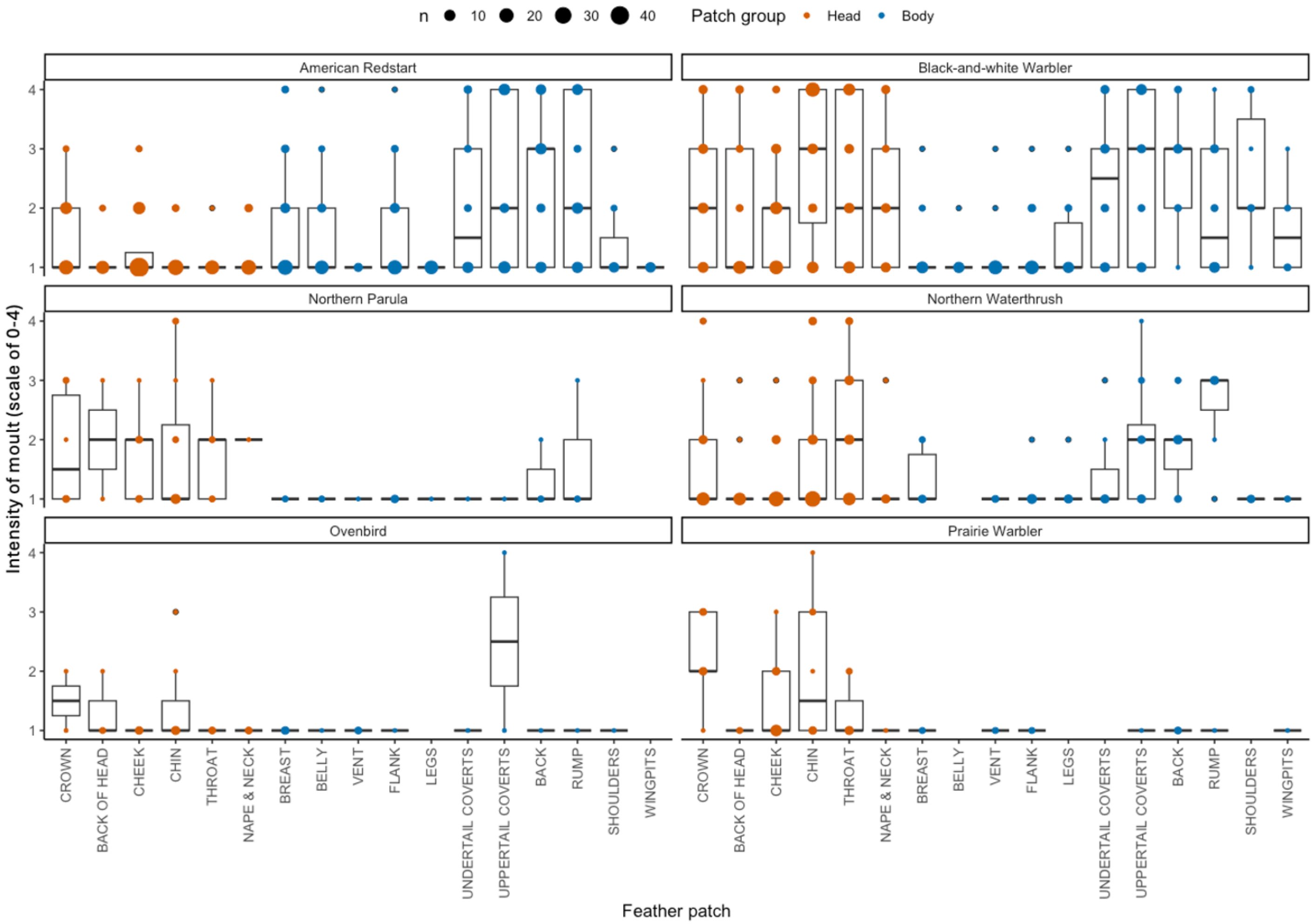

Figure 2.5. The intensity of moult (scale of 0-4) per 17 feather patches in six species captured from January 13 through April 18, 2023, at Font Hill Nature Preserve, Jamaica. The size of the circles represents the number (*n*) of birds sampled that had the corresponding moult intensity score for each patch.

Black-and-white Warbler

Black-and-white Warblers showed active moult between February 15 and April 18 (Figure 2.2). Moult was most prevalent within the population from March 19 onward when most (≥ 75%) or all captures each week were moulting. I observed active moult in all 17 feather patches, and most frequently on the chin, cheek, and throat (Figure 2.3). Mean moult intensity per patch was greatest on the back and chin (mean CCMI scores > 2.8; Figure 2.5), and when compared between the head and body patch groups was greater on the head (paired t-test: $t_{(60)} = 6.70$, $p < 0.0001$; Figure 2.4).

When I examined changes in moult intensity over time from the observed onset of moult (February 15), I found an Age*Julian Date interaction ($df = 62.87$, $t = 3.27$, $p = 0.002$) indicating that CCMI increased more strongly over time in first-cycle than definitive-cycle birds (Figure 2.6). When I examined the age classes separately, both first-cycle (Julian date: $df = 23.29$, $t = 5.12$, $p < 0.001$) and definitive-cycle (Julian date: $df = 69.79$, $t = 7.74$, $p < 0.001$) birds saw an increase in CCMI over time.

American Redstart

I captured moulting American Redstarts between February 12 and April 18 (Figure 2.2). Moult was most prevalent within the population from February 26 onward when most (≥ 86%) or all captures each week were moulting. American Redstarts showed active moult in all 17 feather patches, and most frequently on the cheek, breast, and crown (Figure 2.3). The back, rump, uppertail coverts, and undertail coverts had the greatest mean moult intensities of all patches (mean CCMI scores >2; Figure 2.5). However, moult intensity as measured by CCMI did not differ between the head and body patch groups (paired t-test: $t_{(80)} = -0.70$, $p = 0.49$; Figure 2.4). When I examined the relationship between moult intensity and age from the observed onset of moult in the study population (February 12), CCMI was greater for first-cycle than definitive-cycle individuals (Age: $df = 82$, $t = 3.55$, $p = 0.0007$; Figure 2.7). Moult intensity followed a parabola, with peak CCMI in the middle of the observed moult period based on the quadratic term for time (Julian date: $df = 82$, $t = 2.67$, $p = 0.009$; Julian date^2: $df = 82$, $t = -2.71$, $p = 0.008$; Figure 2.7).

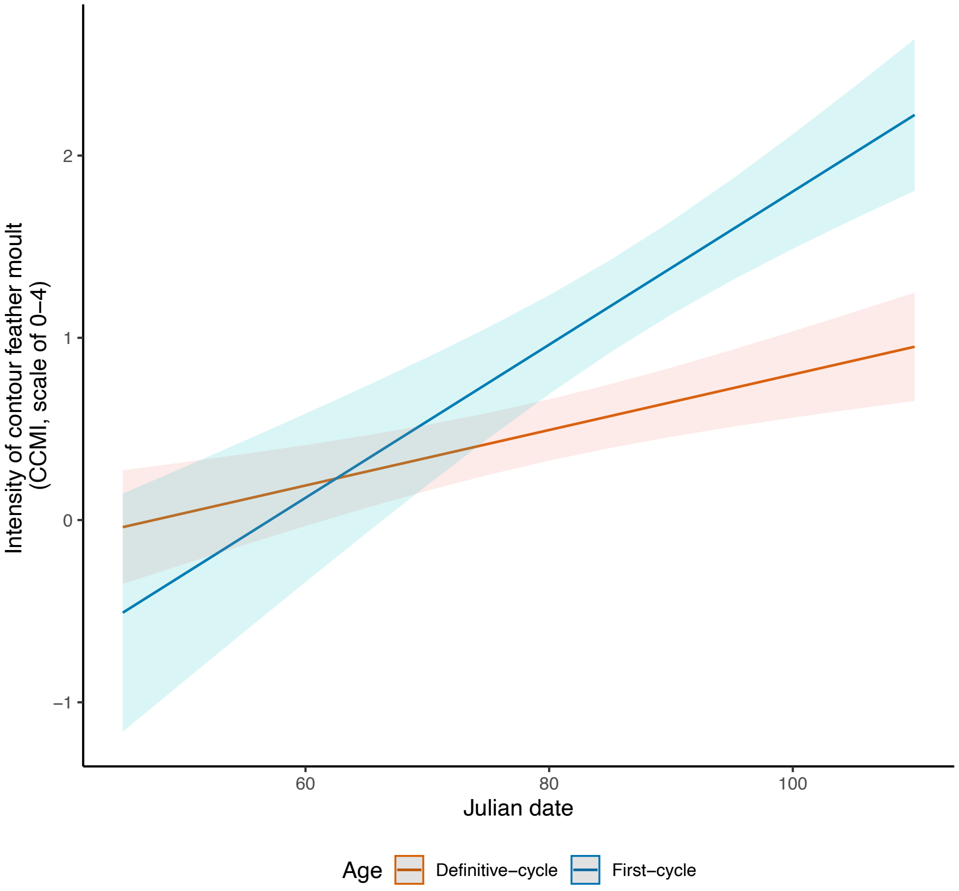

Figure 2.6. Predicted linear relationships between contour feather moult intensity in Black-and-white Warblers, measured as a Combined Contour Moult Index (CCMI) on a scale of zero to four, and Julian date from the observed onset of moult, February 15, 2023, through April 18, 2023, interacting with age class. The solid lines represent the predicted relationship between moult intensity and Julian date for each age class. The shaded areas represent 95% confidence intervals.

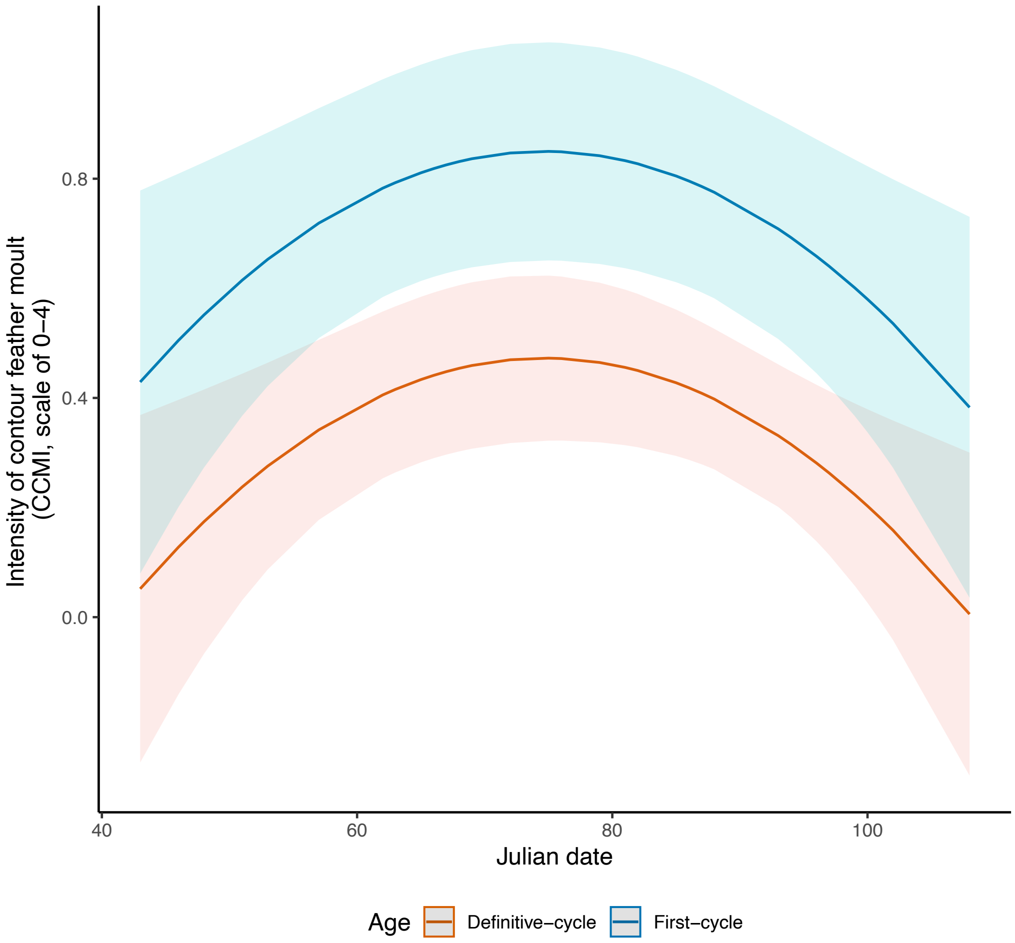

Figure 2.7. Predicted parabolic relationships between contour feather moult intensity in American Redstarts, measured as a Combined Contour Moult Index (CCMI) on a scale of zero to four, and Julian date from the observed onset of moult, February 15, 2023, through April 18, 2023, grouped by age class. The solid lines represent the predicted relationship between moult intensity and Julian date for each age class. The shaded areas represent 95% confidence intervals.

Northern Parula

I captured Northern Parulas in moult between February 6 and April 11 (Figure 2.2). Weekly capture sample sizes were small (n = 1, 3, or 7), making it difficult to determine the population-level peak of moult prevalence. Northern Parulas showed active moult in all feather patches except for the shoulders and wingpits (Figure 2.3). Active moult most frequent on the chin, crown, and cheeks. Per feather patch, mean moult intensity was greatest on the crown, chin, and throat (mean CCMI scores > 1.8; Figure

2.5). Northern Parulas moulted head feathers more intensely than body feathers, based on a comparison of mean CCMI scores for the head and body patch groups (paired t-test: $t_{(13)} = 3.24$, $p = 0.006$; Figure 2.4).

Prairie Warbler

Prairie Warblers showed prealternate moult between February 12 and April 3 (Figure 2.2). All birds captured between February 12 and April 3 were moulting, aside from 3 individuals (first-cycle male, first-cycle female, and definitive-cycle female) captured on March 23, though sample sizes for weekly captures were small ($n \leq 6$). I observed active moult in all feather patches except for the belly, legs, and shoulders (Figure 2.3). Active moult was most frequent on the cheeks, crown, and chin. Prairie Warblers moulted the uppertail coverts most intensely of all 17 patches (Figure 2.5), but moult intensity was greater on the head than the body when comparing the two patch groups (paired t-test: $t_{(17)} = 4.31$, $p < 0.001$; Figure 2.4). Moult intensity followed a parabola, with peak CCMI in the middle of the observed moult period based on the quadratic term for time (Julian date: $df = 17$, $t = 2.96$, $p = 0.009$; Julian date^2: $df = 17$, $t = -3.23$, $p = 0.005$).

DISCUSSION

Here, I provide detailed information on the timing, patterns, and intensity of prealternate moult in six parulid warbler species–information that remains extremely limited for most parulid warblers, despite the critical importance of feather quality for these birds. I demonstrate that head and body feather moult is common in the Northern Waterthrush, Black-and-white Warbler, American Redstart, Northern Parula, and Prairie Warbler, and for most species increases in frequency and intensity later in the nonbreeding period, though timing varied markedly across species. To the best of my knowledge, I provide the first detailed account that some, though likely not all, Ovenbirds complete a prealternate moult on the nonbreeding grounds. I also demonstrate age-specific patterns in the intensity of moult in the American Redstart and Black-and-white Warbler.

The evolutionary drivers behind prealternate moult in birds remain unclear, but the feather wear hypothesis proposed by Pyle and Kayhart (2010), and supported by Wolfe and Pyle (2011), Terrill et al. (2020), and Cuervo et al. (2022), may explain the age-specific differences in moult intensity that I observed in the American Redstart and Black-and-white Warbler. The feather wear hypothesis proposes that prealternate moult evolved primarily to renew feathers for maintaining feather function, rather than for breeding plumage, but was then co-opted during the evolution of seasonal dichromatism. In both the American Redstart (Sherry et al. 2020) and Black-and-white-Warbler (Kricher 2020), first-cycle birds of both sexes replace most or all juvenile contour feathers during the preformative moult. Consistent with the feather wear hypothesis, first-cycle birds may benefit more than definitive-cycle birds from an intense prealternate moult if they are replacing relatively poor-quality contour feathers (i.e., either retained juvenile or formative feathers). In the American Redstart, prealternate moult can contribute to the slow acquisition of black (definitive) feathers in first-cycle males (Rohwer et al. 1983). First-cycle males in this study did not exclusively replace grey contour feathers with black feathers; some new feathers were black, some were grey, and some birds moulted new feathers in both colours simultaneously. This is contrary to the results of Tonra et al. (2014), where the experimentally regrown breast feathers of first-cycle males appeared to be exclusively black. The production of grey alternate feathers in first-cycle males is another example of a prealternate moult that does not contribute to plumage maturation or seasonal dichromatism, suggesting that the replacement of these feathers may be primarily driven by feather maintenance. Further supporting the feather wear hypothesis, the patches most frequently moulted across all species tended to be areas of the body that are exposed to the sun when birds are perching (Terrill et al. 2020): the head, in particular the cheek, chin, and crown, followed by the breast.

In most other parulid warblers that complete a prealternate moult on the nonbreeding grounds, their moult patterns are not known to differ by age or sex class (Pyle 2022b), but more detailed studies of parulid warbler moult on the nonbreeding grounds could elucidate age- or sex-based differences. I observed a pattern of higher moult intensity in first-cycle Black-and-white Warblers and American Redstarts, a pattern that was recently documented in the Prothonotary Warbler (*Protonotaria* critea; Ames

2021). For the American Redstart, Pyle (2022b) reports that prealternate moult is most evident in first-cycle males. While I observed greater moult intensity in first-cycle American Redstarts, I did not detect a significant difference in moult intensity between the sexes. Contrary to Nolan 1978 (as cited in Nolan Jr et al. 2020), I did not find a sex-based difference in moult for Prairie Warblers, but my results may be limited in that I was able to determine moult intensity at capture but not the full moult extent for the moult period. Boone (2006) found age- and sex-based differences in the prealternate moult of the Magnolia Warbler but captured migrating birds post-moult and quantified moult extent based only on the wing coverts and amount of dark streaking on the breast, a part of the plumage that changes in colour from the basic to alternate plumage. For species, age, or sex classes that replace basic contour feathers in the same colour as alternate feathers, as I have documented in all age and sex classes of American Redstarts, it is possible that previous studies of moult and plumage may have missed the replacement of same-colour alternate feathers or mischaracterized late-winter contour feather moult as adventitious rather than obligate. I suggest that by collecting detailed moult data at the feather patch level across the entire head and body during the moult period on the nonbreeding grounds, along with more rigorous mark-recapture efforts through the moult period, further studies can clarify our knowledge of prealternate moult and its potential variation across species, age and sex classes, nonbreeding populations, and years.

Moult intensity often follows a parabolic curve from start to finish, peaking during the middle of moult (e.g., Wright et al. 2018, Hutton et al. 2021, Guallar 2024). I observed this pattern in the American Redstart and Prairie Warbler but only captured a linear increase in moult intensity over time in the other species, indicating that the moult period for the Ovenbird, Northern Waterthrush, Black-and-white Warbler, and Northern Parula may have extended beyond April 18. Individuals from all six study species showed active moult into early or mid-April, coinciding with timing windows for pre-breeding migration departures from Jamaica (Fink et al. 2023; Chapter 1, Table 1.1). This result suggests that for many birds, moult likely overlaps with migratory fattening, and that some birds may continue moulting until departure. Mid-April aligns with early departures for Ovenbird, Northern Waterthrush, Black-and-white Warbler, and American Redstart (Studds and Marra 2007, 2011, Tonra et al. 2013, Cooper et al. 2015), but late departures for Northern Parula and Prairie Warbler (Fink et al. 2023). As far as I know, most Nearctic-Neotropical migrant parulids have prealternate moult schedules that occur before pre-breeding migration (Billerman et al. 2022, Pyle 2022b), likely to avoid energetic conflicts (Froehlich et al. 2005). Because migration constrains their prealternate moult spatially and temporally, and the resources needed to facilitate energetically demanding events vary seasonally in Jamaica (Parrish and Sherry 1994, Strong and Sherry 2000, Johnson and Sherry 2001, Studds and Marra 2007, Studds and Marra 2011), the study species may be faced with trade-offs between migratory fattening and maximizing alternate feather quality by moulting closer to departure (Froehlich et al. 2005). Future studies should explore this potential trade-off and evaluate its consequences by determining if the timing of individual moult is associated with the timing of migratory fattening and pre-breeding migration departure. Collecting such data for the same individuals over multiple years could begin to elucidate whether individuals adjust their moult and migration strategies according to interannual variation in seasonal resource availability during the nonbreeding period.

With an improved understanding of prealternate moult in six species of Nearctic-Neotropical migratory warblers, I can now use data on the timing and intensity of moult to begin to evaluate how prealternate moult interacts across the annual cycle with other crucial life events, including pre-breeding migration. Understanding the individual timing of migration in relation to moult, together with the underlying influence of habitat quality and individual body condition on moult and migration, are the next steps in disentangling the role of prealternate moult in potential nonbreeding period carry-over effects in the study species. This knowledge is critical for determining which life stages limit bird populations in the annual cycle (Marra et al. 2015a). To that end, it will be crucial for researchers in the global north to establish equitable collaborations with local neotropical researchers (Soares et al. 2023) to aid in furthering prealternate moult research on the nonbreeding grounds of many migratory birds.

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CHAPTER 3: PREALTERNATE MOULT LINKS NONBREEDING HABITAT CONDITIONS AND MIGRATION DEPARTURE TIMING IN NEARCTIC-NEOTROPICAL MIGRATORY SONGBIRDS

ABSTRACT

The quality of nonbreeding habitat can carry over to influence the performance of migratory birds during subsequent life history stages. Yet, for birds that undergo prealternate moult during the nonbreeding period, its potential role in seasonal interactions has largely been overlooked. Here, I build on a detailed quantification of the timing and intensity of prealternate moult in three species of Nearctic-Neotropical migratory songbirds to assess the role of moult in carry-over effects from the nonbreeding period to the timing of migration departure: Black-and-white Warbler (*Mniotilta varia*), Northern Waterthrush (*Parkesia noveboracensis*), and American Redstart (*Setophaga ruticilla*). I assessed the influence of body condition on the timing and intensity of prealternate moult in distinct habitats in Jamaica that differ in moisture regime: xeric second-growth scrub forest and mesic mangrove. I analyzed stable-carbon isotope ratios (δ^{13}C) from birds' red blood cells to support my understanding of relative habitat quality for the study species. Using the Motus Wildlife Tracking System, I tracked precise dates of migration departure so I could evaluate the influence of habitat quality, body condition, and prealternate moult on departure timing. Moult intensity was generally higher in first-cycle birds but its relationship with body condition varied among species, indicating that body condition may not be the most important driver of prealternate moult phenology. For American Redstarts, the effect of age on moult varied with habitat type, suggesting that birds with the poorest quality feathers, associated with poorer quality, open habitat, require a more intense moult than older birds and those in higher quality habitat. I found the first potential evidence of a carry-over effect from prealternate moult to departure timing in a parulid warbler, the American Redstart. Male American Redstarts with high-intensity moult prior to departure, indicating a later moult, departed later, suggesting that prealternate moult can represent an important seasonal interaction in some birds. Ultimately, this study is an important step in beginning to understand the role

of prealternate moult in nonbreeding period carry-over effects and highlights that moult should not be overlooked when considering a birds' full annual cycle.

INTRODUCTION

To identify the drivers of population decline and ultimately conserve declining migratory bird populations (Rosenberg et al. 2019), it is imperative to understand how birds' life history stages interact across their annual cycle to influence individual performance and population dynamics (Marra et al. 2015). Breeding, migration, and moult, arguably the most important and energy-intensive stages in the annual cycle of migratory birds, are influenced by a combination of interacting endogenous and exogenous factors (Barta et al. 2008). Endogenous factors such as physiology, and exogenous factors such as environmental conditions, vary seasonally as migratory birds track resources from their breeding grounds to stationary nonbreeding (hereafter "nonbreeding") grounds. Both the timing of a life history stage and an individual's physiological state during that event can carry over to influence the timing of subsequent stages, often with fitness consequences (Norris and Marra 2007, Harrison et al. 2011). For example, a bird that occupies xeric nonbreeding habitat (an exogenous factor) may have poorer body condition (an endogenous factor) than birds occupying mesic habitat, resulting in a delayed pre-breeding migration (e.g., Marra et al. 1998, Studds and Marra 2005, Reudink et al. 2009a) or delayed arrival to the breeding grounds culminating in reduced reproductive success (e.g., Norris et al. 2004, Reudink et al. 2009a). In other cases, birds can mitigate carry-over effects from one event through plastic behaviour, for example by adjusting their migration rate (e.g., González et al. 2020) or reducing time spent at stop-over sites (e.g., Stutchbury et al. 2011) to arrive on time despite a late departure. Carry-over effects from the nonbreeding grounds to pre-breeding migration or the breeding period are well documented across bird families from passerines to shorebirds (e.g., Gill et al. 2001, Clements et al. 2022) but the role of moult, particularly the prealternate moult that occurs on the nonbreeding grounds, has largely been overlooked.

Many species of Nearctic-Neotropical and Afro-Palearctic migrants evolved to moult twice in their annual cycle: once post-breeding (prebasic moult) and again prior to breeding (prealternate moult). The evolution of this moult strategy, called a Complex Alternate Strategy (Howell et al. 2003), has been linked to long-distance migration and an associated longer photoperiod (Svensson and Hedenström 1999, Terrill et al. 2020, Pageau et al. 2021, Cuervo et al. 2022). Exposure to ultra-violet radiation (Lennox and Rowlands 1969, Surmacki 2008) degrades the non-renewable keratin structures of wing and body feathers, necessitating the replacement of at least some feathers more than once per year. The feather wear hypothesis proposes that the prealternate moult evolved primarily for birds to renew feathers for maintaining feather function (Terrill et al. 2020). Prealternate moult was likely then co-opted under sexual selection pressures for the evolution of seasonal dichromatism (Pyle and Kayhart 2010, Terrill et al. 2020), as the mechanism through which some species moult from drab basic, or nonbreeding, plumage into usually more colourful alternate, or breeding, plumage. Because the feathers resulting from prealternate moult serve an important structural function, are critical for social and sexual signaling, and come at a high energetic cost, the timing and intensity of prealternate moult have the potential to play a role in birds' migratory performance and subsequent reproductive success.

Moult is in part cued by photoperiod and hormones, but aspects of its phenology including onset, duration, extent, and intensity, can also be influenced by environmental conditions (e.g., Danner et al. 2015, Hutton et al. 2021), individual condition (e.g., Piersma and Jukema 1993, Hutton et al. 2021), or timing constraints imposed by breeding (e.g., Morton and Welton 1973, Borowske et al. 2017) and migration (e.g., Conklin and Battley 2012). The environmental conditions that birds experience during moult can also influence the expression of plumage ornaments (e.g., Saino et al. 2004, Sparrow et al. 2017), which can have a direct impact on fitness (Romano et al. 2017). Despite evidence that nonbreeding conditions such as food availability can influence prealternate moult phenology (e.g., Danner et al. 2015) and that the prebasic and preformative moults can influence both inter- (e.g., Carlisle et al. 2005, Bozó et al. 2017) and intraspecific (e.g., Stutchbury et al. 2011) migration timing, potential carry-over effects from the prealternate moult to pre-breeding migration have received extremely limited attention.

The influence of prealternate moult strategy on the timing of other life stages, including pre-breeding migration, has been subject to some consideration in shorebirds (e.g., Buehler and Piersma 2008, Lourenço and Piersma 2015). However, I am aware of only two studies investigating the potential link between prealternate moult and pre-breeding migration in Nearctic-Neotropical migratory warblers (Family: Parulidae). Those studies found no link between the prealternate moult and timing of arrival to a stopover site (Boone et al. 2010) or the breeding grounds (Jones et al. 2014). However, they did not account for the birds' entire prealternate moult, only focussing on a particular region of contour feathers and/or wing coverts. To better understand how the prealternate moult interacts with pre-breeding migration phenology, it will be important to consider moult across the entire body. Further, carry-over effects from the nonbreeding period to pre-breeding migration vary among species, sexes, age classes, and years (e.g., Rockwell 2013, Akresh et al. 2019), highlighting the need for further study of the prealternate moult in relation to subsequent life stages.

Here, I investigated the relationships between nonbreeding habitat quality, individual body condition, moult intensity, and departure date, in three migratory parulid warblers to understand if prealternate moult carries over to affect pre-breeding migration phenology. First, I assessed the influence of habitat quality and body condition on moult intensity throughout the prealternate moult period. Using the Motus Wildlife Tracking System (Taylor et al. 2017), I tracked precise departure dates from the nonbreeding grounds to assess whether departure was influenced by prealternate moult intensity. I predicted that a combination of exogenous and endogenous factors would influence prealternate moult intensity and departure dates. Specifically, that individuals occupying mesic mangrove habitat would be in better condition and, in turn, would undergo a more intense moult, and individuals who completed moult earlier, indicated by low moult intensity prior to departure, would depart earlier.

METHODS

Study system

I studied nonbreeding populations of the migratory Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), and Northern Waterthrush (*Parkesia noveboracensis*) in Font Hill Nature Preserve (18.0391°N, 77.9411°W, <100 m above sea level), St. Elizabeth Parish, on the southwest coast of Jamaica. I conducted this research from January 13 to April 18, 2023, during the birds' nonbreeding period, in two habitat types: xeric second-growth dry scrub forest and mesic mangrove. A description of vegetation structure and composition in the habitat types is available in Cooper et al. (2021).

Precipitation at this site follows the highly seasonal pattern typical of the neotropics: a wet season from August to November (average monthly precipitation > 100 mm) followed by a dry season from December through May (average monthly precipitation <25 mm) (Powell et al. 2021), though conditions vary annually (Studds and Marra 2011, Brunner et al. 2022, Dossman et al. 2023a). Relatively low levels of precipitation preceded my study period and as a result, mangrove habitat held little and at times no standing water. While similar conditions have been observed in dry years (Cooper et al. 2015), mangrove plots typically hold 0.3 to 2 m of brackish water through the dry season (Cooper et al. 2021). Scrub habitat remained dry without standing water, as expected for a typically water stressed habitat (Cooper et al. 2021). See Chapter 2 for a complete description of the number and size of habitat plots sampled.

Habitat quality and stable-carbon isotope sampling

At this site, a large body of evidence indicates that mangrove is a higher quality habitat than scrub for American Redstarts (Marra et al. 1998, Studds and Marra 2007, Reudink et al. 2009a, Studds and Marra 2011) due to greater water and associated arthropod availability (Studds and Marra 2007, 2011). American Redstarts are highly territorial at this site (Studds and Marra 2005, 2011), so habitat type at capture likely represents the predominant habitat they occupied during the study period and can be used as an explanatory variable in statistical analyses.

The relative quality of mangrove and scrub habitats at the site are not well understood for the Black-and-White Warbler or Northern Waterthrush, though I predict that mangrove will be higher quality given the estimates of greater arthropod availability. A recent study comparing mass change among habitats suggests that mangrove may be higher quality for the Black-and-white Warbler at this site (Cooper et al. 2021), and other research has linked better condition with mesic nonbreeding habitat in the species (Paxton and Moore 2015). Links between habitat quality and individual body condition have not been tested for Northern Waterthrush at this site, but habitat quality increases with moisture (i.e., standing water) for the species in other Caribbean systems (Puerto Rico; Smith et al. 2010). However, through recapture data and re-sighting banded birds, I determined that Black-and-white Warblers and Northern Waterthrushes ranged further and regularly utilize multiple habitat types, thus I deemed capture location an unreliable indicator of the habitat type they occupied. For these two species only, I used stable-carbon (δ^{13}C) isotope ratios from blood to infer habitat use during the stationary nonbreeding period. At the study site, mangrove and scrub habitats tend to have distinct δ^{13}C ratios because of differences in water stress and photosynthetic system in the plants that dominate each habitat type (Marshall et al. 2007), though there is some overlap in isotopic ratios (e.g., Marra et al. 1998, Reudink et al. 2009a). The isotope ratios of the corresponding habitat incorporate into bird tissues through the insectivorous prey they consume (reviewed by Kelly 2000), resulting in depleted stable-carbon ratios in birds foraging in wetter mangrove (e.g., -26 to -20) relative to enriched ratios in birds foraging in drier scrub (e.g., -22 to -20) (Marra et al. 1998, Reudink et al. 2009a).

While the turnover rate for blood plasma can be as quick as a few days, the cellular fraction of blood (i.e., red blood cells) has a turnover rate of a few weeks (Oppel and Powell 2010), making it a suitable indicator of the birds' foraging habitat and diet in the weeks leading up to sampling. I collected blood samples from the brachial vein of 18 Northern Waterthrushes and 26 Black-and-white Warblers on the date that I applied their nanotags (see below for a full description of the tagging procedure). I separated the red blood cells from blood plasma by centrifuging each sample within four hours of collection and immediately froze the separate components. All samples were processed and analyzed by The Cornell Isotope Laboratory of Cornell University (Ithaca, NY) in December 2023 using a Thermo Delta V isotope ratio mass spectrometer (IRMS) interfaced to a NC2500 elemental analyzer. An in-house internal animal standard was run after every ten samples resulting in an overall standard deviation of 0.06%, and two additional in-house standards were used to perform two-point normalization (linear regression) corrections. I report corrected values measured in units of per mil (‰) relative to the international standard Vienna Pee Dee Belemnite.

Stable-nitrogen isotopes (δ^{15}N) can be reliably used within a limited spatial area to infer birds' trophic level from diet items as enriched values indicate higher trophic levels (reviewed by Kelly 2000). δ^{15}N is commonly used to determine the ratio of arthropod to fruits and seeds in a bird's diet (e.g., Contina et al. 2022, Gonzalez et al. 2020). However, δ^{15}N may not be a useful indicator of nonbreeding habitat quality (e.g., Gonzalez et al. 2020), and more work needs to be done to understand how it can be applied in this study system. I sampled δ^{15}N following the same procedure outlined above and present the ratios in Appendix B, Table B.1, so that this information can be applied in future work.

Capture, body condition, and moult intensity

I captured 268 individual warblers (73 Black-and-white Warbler, 100 American Redstart, and 95 Northern Waterthrush) over 47 capture days using a combination of passive mist-netting and target netting with conspecific playback of songs and calls from each species. See Chapter 1 for complete details on capture effort. After capture, I banded all birds with a uniquely numbered United States Geological Survey aluminum band. Using moult and plumage characteristics from Pyle (2022), I assigned each bird to one of two age classes: First Prealternate Moult (FPA, hereafter "first-cycle") or Definitive Prealternate Moult (DPA, hereafter "definitive-cycle") following the WRP classification system (Wolfe et al. 2010) most recently modified by Pyle et al. (2022). I determined sex for Black-and-white Warblers and American Redstarts based on sex-based differences in plumage characteristics (Pyle 2022).

I measured tarsus length (to the nearest mm) and body mass (to the nearest 0.1 g) each time I captured or recaptured a bird and calculated the ratio of body mass divided by tarsus length to estimate the bird's body condition while accounting for structural body size. One of three skilled observers (BCD, IAC, and SAT) took all measurements. At the start of the study period, we repeated tarsus length measurements on the same birds to standardize our measurements and reduce variability associated with the observer. If I captured a bird more than once, I took the average of all tarsus measurements to use in its body condition calculations. I was unable to use a scaled mass index following Peig and

Green (2009) as my body condition metric because tarsus length and mass were not correlated in my species' samples.

Each time I captured a bird I searched for the presence of active prealternate moult in each of 17 feather patches across the head and body (Chapter 2, Figure 2.1) by systematically blowing on the feather patches and scanning for pinfeathers (Mettke-Hoffman et al. 2010; Wright et al. 2018). I assigned a moult intensity score (adapted from Greenwood et al. 1983 and Wright et al. 2018) to each feather patch between 0 and 4 which indicates the percentage by quarters of feathers in active moult: 0 = 0%, 1 = 1–25%, 2 = 26–50%, 3 = 51–75%, and 4 = 76–100%. For each bird, I then summed all patch scores and divided the sum by the total number of patches (17) to calculate a Combined Contour Moult Index (CCMI; adapted from Greenwood et al. 1983 and Wright et al. 2018). Moult scores were collected by one of two skilled observers (SAT and IAC) and repeated across observers at the start of the season to reduce variability associated with the observer. See Chapter 2 for complete details on quantifying moult intensity. I recaptured 47 birds at least once (16 Black-and-white Warbler, 16 American Redstart, and 15 Northern Waterthrush) and repeated their body condition and moult intensity measurements at each recapture, resulting in a total of 408 moult scores (Chapter 2).

Tracking migration departure dates

In March and April 2023, I fitted 20 Northern Waterthrushes, 28 Black-and-white Warblers, and 59 American Redstarts with digitally coded nanotag transmitters (Lotek Wireless, Newmarket, ON) using a leg-loop harness (Rappole and Tipton 1991) of 0.7-mm nylon thread. Transmitters and harnesses combined weighed no more than 4% of a bird's body mass: 0.28 g NTQB2-1 tags on American Redstarts and 0.28 g NTQB2-1 or 0.32 g NTQB2-2 tags on Northern Waterthrushes and Black-and-white Warblers. An array of five automated radio towers passively recorded the dates that birds departed Font Hill Nature Preserve for pre-breeding migration. Each tower comprised a SensorGnome receiver (https://www.sensorgnome.org) with four 3-element directional Yagi antennas (Maple Leaf Communications, Everett, ON) mounted 9 m above ground.

After tag detection data was uploaded to The Motus Wildlife Tracking System network (Taylor et al. 2017), I used R version 4.4.0 (R Core Team 2024), package *Motus*

(Birds Canada 2024), to visualize, clean, and explore the data according to Crewe et al.'s (2018) guidelines for Motus data analysis. I visually inspected each bird's signal strength (dB) over time prior to its last detection to quantify explicit departure dates: a peak in signal strength followed by a sharp decline at the bird's last detection indicated a migratory departure (Mills et al. 2011; Dossman et al. 2016; Taylor et al. 2017). Of the total 107 tagged birds, 80% showed a departure signal (n = 16/20 Northern Waterthrush, 22/28 Black-and-white Warbler, and 48/59 American Redstart). I removed one outlier from the statistical analyses that was three standard deviations (8.47 days) greater than the mean for the species (May 1): a definitive-cycle male Black-and-white Warbler with a departure date of May 27, late for the species and site when compared with general departure timing windows (Fink et al. 2023) and previous data from the site (unpublished Motus dataset 2022).

Statistical analyses

My goal was to evaluate, through statistical modelling, if nonbreeding habitat and body condition predicted prealternate moult intensity and, if prealternate moult intensity predicted pre-breeding migration departure dates. Because I could not use habitat type at capture as an explanatory variable in my analyses for the Black-and-white Warbler and Northern Waterthrush, I followed a three-step process for those two species. The first step was to create a model set for each species to test whether δ^{13}C predicted body condition (Figure 3.1), a relationship which would indicate if the relative quality of mangrove and scrub habitats differ for the species. Then, I evaluated predictors of prealternate moult and departure dates. I followed a two-step process for the American Redstart, simply using habitat type at capture as an explanatory variable in my models predicting prealternate moult intensity and departure dates (Figure 3.1).

Exploratory analyses revealed that CCMI (see Chapter 2) and body condition (due to migratory fattening) tended to increase over time in the study population for all three species. Thus, to account for these trends while excluding the use of correlated explanatory variables, I calculated, for each species, the residuals of CCMI and body condition over time and used the residuals as the dependent or independent variables for body condition and CCMI in my statistical analyses. Because the relationship between

CCMI and Julian date fit a quadratic relationship in the American Redstart (Chapter 2), I calculated the residuals using the regression equation CCMI ~ Julian date + Julian date^2 to account for both linear and quadratic components of the relationship. For the other species' CCMI and all species body condition, I used the linear regression equations CCMI ~ Julian date and body condition ~ Julian date. I performed all analyses herein using R 4.4.0 (R Core Team 2024).

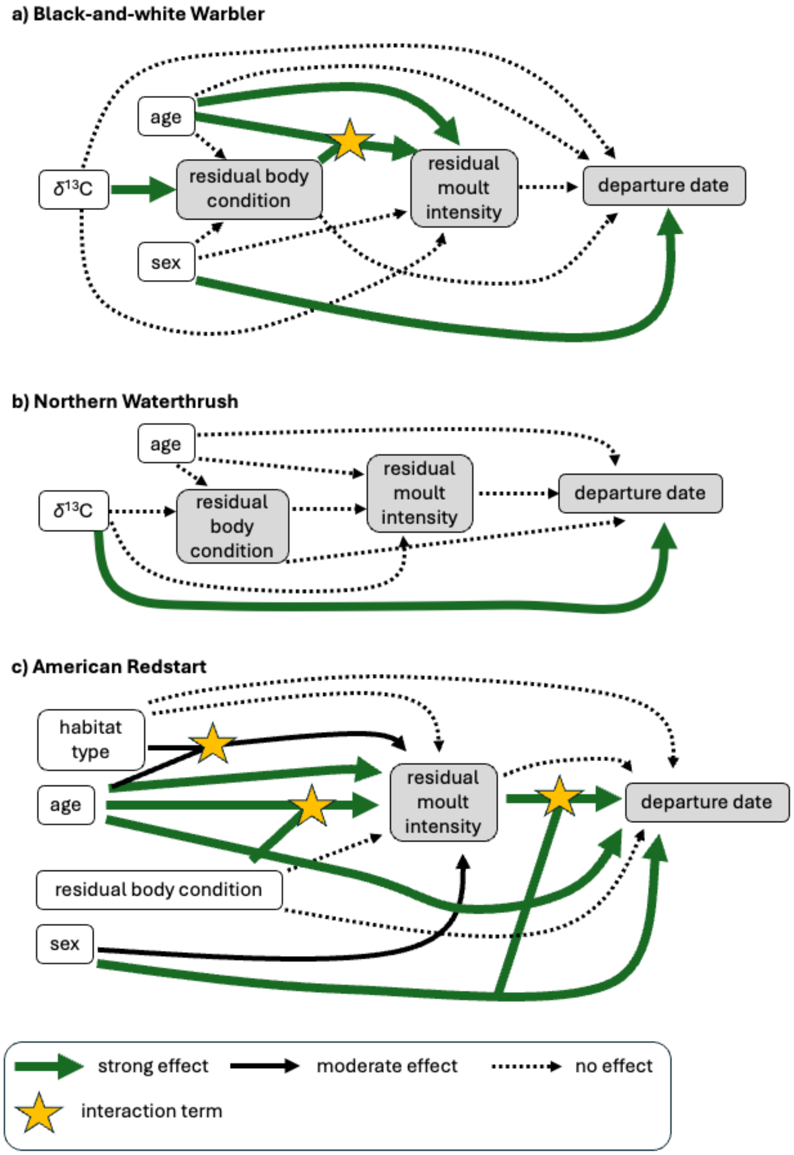

Figure 3.1. Analysis framework and summary of results from evaluating predictors of residual prealternate moult and pre-breeding migration departure dates in a) Black-and-white Warbler, b) Northern Waterthrush, and c) American Redstart. I followed a three-

step process for the Black-and-white Warbler and Northern Waterthrush, adding the first step of testing if δ^{13}C, a proxy for habitat quality, predicted residual body condition. I followed a two-step process for the American Redstart, using habitat type at capture as an explanatory variable for habitat quality. Solid green arrows indicate a strong effect (95% confidence intervals did not overlap zero), solid black arrows indicate a moderate effect (90% confidence intervals did not overlap zero), and dashed arrows indicate a variable with no effect, that was either not retained during model selection or had 85% confidence intervals that overlapped zero. Stars indicate interaction terms with a moderate or strong effect; only statistically meaningful interaction terms are depicted here.

Effect of δ^{13}C on body condition

To examine the influence of δ^{13}C on residual body condition in the Black-and-white Warbler and Northern Waterthrush, I created linear models (function *lm*) and used age as a covariate in both species. I included sex as a second covariate in the Black-and-white Warbler because I could determine sex in the field. When I tested interaction terms associated with δ^{13}C ratios for either species, very high variance inflation factors (> 1,000) indicated multicollinearity and model unreliability. I found patterns of association between δ^{13}C and the covariates age or sex, as well as lower variation in δ^{13}C ratios for some age/sex classes relative to others (see Appendix B, Figure B.1 for boxplots). Further, I had minimal representation for one of four age-sex classes for the Black-and-white Warbler (*n* = 1 first-cycle female). For these reasons, I ran final, simplified models including only the δ^{13}C ratio with age (Northern Waterthrush) or age, sex, plus age*sex (Black-and-white Warbler) as explanatory variables. To evaluate model reliability for these models and all described herein, I confirmed that the variance inflation factor for each explanatory variable was < 7.

Next, I used the *dredge* function (R package *MuMIn*; Bartón 2024) to create the model set including a null model and ranked each model using Akaike's information criterion corrected for small sample sizes (AICc). I considered models with ΔAICc < 1 competitive. This decision was based on my models for the American Redstart, for which a higher ΔAIC resulted in an excess of competitive models with highly variable, and therefore less reliable, β estimates for my continuous explanatory variables. I used ΔAICc < 1 in all analyses for consistency. After averaging the models with ΔAICc < 1, I considered variables to have no effect if their model-averaged 85% confidence intervals overlapped zero. I categorized the magnitude of effects as strong, moderate, and weak, if their 95%, 90%, and 85% confidence intervals did not overlap zero, respectively (following Buler et al. 2007 and Wright et al. 2020). Here, I report the estimates (β) and corresponding confidence intervals only for the explanatory variables from top models with at least a weak effect (see Appendix B, Table B.2 for the explanatory variables with no effect). I followed the same process for all model selection described herein.

Predicting prealternate moult intensity

To examine the influence of residual body condition on residual moult intensity I created global linear mixed-effect models (function *lmer*, R package *lme4*; Bates et al. 2015) with individual as a random effect to account for recaptures in the Black-and-white Warbler and Northern Waterthrush. Again, I added age for both species and sex for the Black-and-white Warbler. I included all possible interaction terms, including those with residual body condition, in each species' global model. Because δ^{13}C was correlated with body condition in the Black-and-white Warbler (Pearson's product-moment correlation: $r_{(24)} = 0.65$, $p < 0.001$) and I found modelling δ^{13}C with additional continuous explanatory variables resulted in very high variance inflation factors (> 1,000) in both species, I created two additional linear models to separately examine the effect of δ^{13}C on residual moult intensity. I included age as a covariate for the Northern Waterthrush and age, sex, plus their interaction term for the Black-and-white Warbler.

For the American Redstart, I did not have sufficient recapture records for all combinations of categorical covariates, making model fitting with a random effect unreliable. To handle the individuals with repeated moult intensity measurements I ran a linear model three ways and compared the results: once including only the first capture record, once including only the second capture record, and finally including all capture records without accounting for the effect of individual. The results of model selection were identical, so here I report the models including only the first capture records (see Appendix B, Table B.3 for the results of all approaches). I included habitat type at capture, age, sex, residual body condition, and all interaction terms as predictors of residual prealternate moult intensity.

Predicting departure date

I next created global linear models to examine the influence of residual body condition, residual moult intensity, age, sex, and their interaction terms on departure dates for each species. Again, I excluded sex from the Northern Waterthrush model and included habitat type for the American Redstart model. Due to a small sample size, I could not include all interaction terms in the Northern Waterthrush model. Because I did not detect a difference in moult intensity between age classes for this species (Chapter 2), I expected age*moult intensity would be less biologically important than residual body condition's interactions with age and moult intensity and excluded it from the model. For birds that I captured more than once, I used their residual body condition and residual moult intensity score from the last capture prior to departure. Again, I created additional models for the Black-and-white Warbler and Northern Waterthrush to separately examine the influence of δ^{13}C on departure date. I included age as a covariate for the Northern Waterthrush and age, sex, plus their interaction term for the Black-and-white Warbler, excluding interactions with δ^{13}C.

To test for differences in departure dates between age classes in the Black-and-white Warbler and Northern Waterthrush, and between male and female American Redstarts within each age class, I used Independent Samples t-tests and evaluated the significance of *p*-values at $\alpha = 0.05$.

RESULTS

Effect of δ^{13}C on body condition

A model that contained only δ^{13}C as a predictor was the only model within ΔAICc <1 that explained body condition in the Black-and-white Warbler (*n* = 26, Table 3.1). δ^{13}C had a strong effect on residual body condition; enriched δ^{13}C ratios, indicating drier habitat, were associated with better condition ($\beta_{\delta 13C} = 0.03$, model-averaged 95%CI = 0.003, 0.048). δ^{13}C did not predict residual body condition in the Northern Waterthrush; the null model was the top model (all other ΔAICc >1; Table 3.1, *n* = 14). The Northern Waterthrushes I sampled had a wider range of δ^{13}C ratios (-27.54 to -22.87‰) when compared with Black-and-white Warblers (-24.60 to -22.63‰) with a lower minimum value (more negative), indicating that some Northern Waterthrushes occupied wetter (i.e., more flooded) habitat than Black-and-white Warblers (Appendix B, Figure B.1).

Table 3.1. Summary of the top ranked models (ΔAICc < 1) that predicted residual body condition in the Black-and-white Warbler (*n* = 26) and Northern Waterthrush (*n* = 14).

Species	**Top ranked models (ΔAICc < 1)**	**AICc**	**ΔAICc**	**AICc weight**
Black-and-white Warbler	δ^{13}C	-106.9	0.00	0.46
Northern Waterthrush	NULL MODEL	-30.0	0.00	0.61

Predicting prealternate moult intensity

After model selection, a single model (ΔAICc < 1) that included age, residual body condition, and their interaction term interaction best explained variation in residual moult intensity, in the Black-and-white Warbler (*n* = 99, Table 3.2). Residual moult intensity was greater in first-cycle Black-and-white Warblers (β_{age} = 0.55, 95% CI = 0.32, 0.77). The interaction between age and residual body condition indicated that when birds were in better condition, first-cycle birds showed a sharper increase in residual moult intensity than definitive-cycle birds ($\beta_{\text{age* residual body condition}}$ = 6.63, 95% CI = 1.53, 11.78; Figure 3.2). When I separately examined the effect of δ^{13}C, I found no effect on residual moult intensity (*n* = 26, Table 3.3); the single top model included age alone. Age had a strong effect on residual moult intensity, with greater residual moult intensity predicted for first-cycle birds (β_{age} = 0.85, 95% CI = 0.30, 1.41).

Neither age nor residual body condition influenced residual moult intensity in the Northern Waterthrush; the top model was the null model (*n* = 106, Table 3.2). When I examined the effect of δ^{13}C residual prealternate moult intensity, I found no effect (*n* = 14, Table 3.3). Model selection resulted in only the null models with ΔAICc < 1.

Four models within ΔAICc < 1 explained residual moult intensity in the American Redstart (*n* = 111, Table 3.2). Age and its interaction with body condition had strong effects on residual moult intensity (Figure 3.3). The interaction between age and body condition indicated that in first-cycle birds, moult intensity decreased with increasing condition, but in definitive-cycle birds, moult intensity varied little with changes in body condition (β_{age} = 0.40, 95% model-averaged CI = 0.16, 0.64; $\beta_{age*residual\ body\ condition}$ = -8.73, 95% model-averaged CI = -17.22, -0.23). Sex had a moderate effect on residual moult intensity, where moult intensity was higher in females than males (β_{sex} = -0.15, 90% model-averaged CI = -0.28, -0.02). The moderate effect of the interaction between age and habitat type indicated that within the first-cycle age class, moult intensity was greater in scrub than in mangrove habitat ($\beta_{age*habitat\ type}$ = -0.36, 90% model-averaged CI = -0.66, -0.05; Figure 3.4).

Table 3.2. Summary of the top ranked models (ΔAICc < 1) that predicted residual prealternate moult intensity in the Black-and-white Warbler (*n* = 99), Northern Waterthrush (*n* = 106), and American Redstart (*n* = 111).

Species	Top ranked models (ΔAICc < 1)	AICc	ΔAICc	AICc weight
Black-and-white Warbler	1. age + residual body condition + age*residual body condition	129.70	0.00	0.68
Northern Waterthrush	1. NULL MODEL	-1.00	0.00	0.69
American Redstart	1. age + sex	111.9	0.00	0.08
	2. age + residual body condition + habitat type + sex + age*residual body condition + age*habitat type	112.0	0.01	0.08
	3. age + residual body condition + habitat type + age*residual body condition + age*habitat type	112.6	0.65	0.06
	4. age + habitat type + sex + age*habitat type	112.6	0.68	0.06

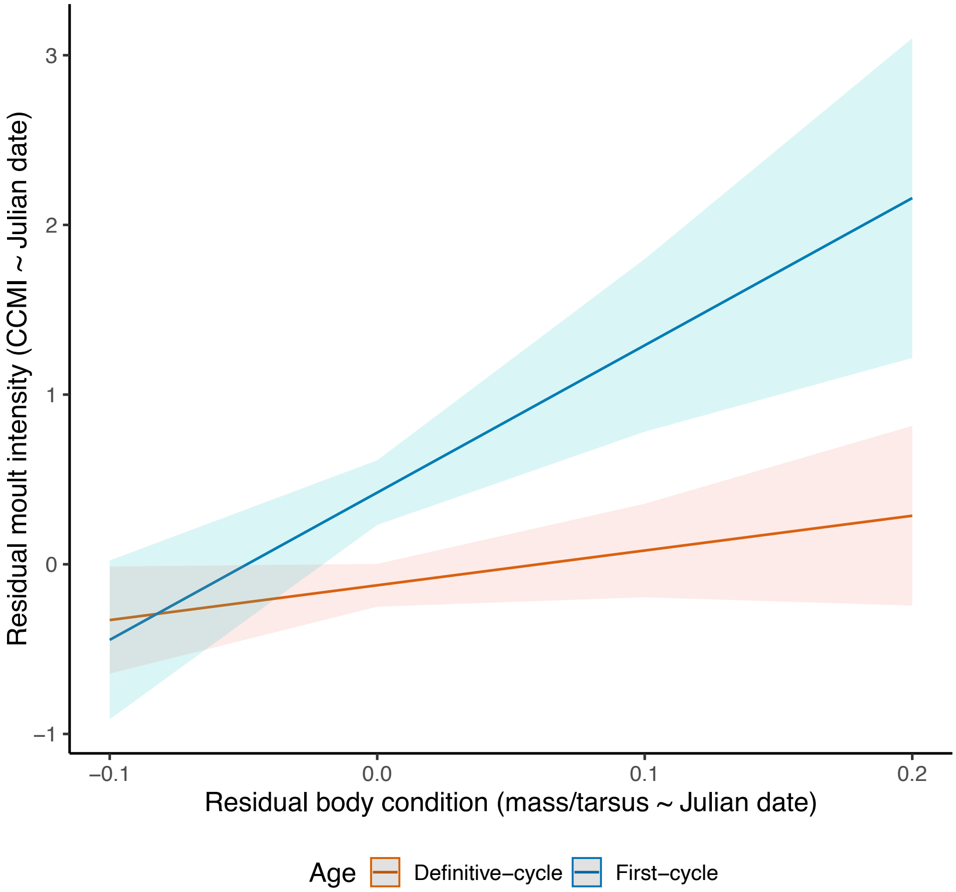

Figure 3.2. Predicted relationship between residual moult intensity and residual body condition by age class in the Black-and-white Warbler (*n* = 99). The residuals in this model were derived from the linear regression equations body condition (mass/tarsus) ~ Julian date and Combined Moult Contour Index (CCMI) ~ Julian date. Shaded areas represent 95% confidence intervals.

Table 3.3. Summary of the top ranked models (ΔAICc < 1) that predicted residual prealternate moult intensity in the Black-and-white Warbler (*n* = 26) and Northern Waterthrush (*n* = 14), using δ^{13}C as an explanatory variable.

Species	**Top ranked models (ΔAICc < 1)**	**AICc**	**ΔAICc**	**AICc weight**
Black-and-white Warbler	1. age	50.3	0.00	0.57
Northern Waterthrush	1. NULL MODEL	20.6	0.00	0.68

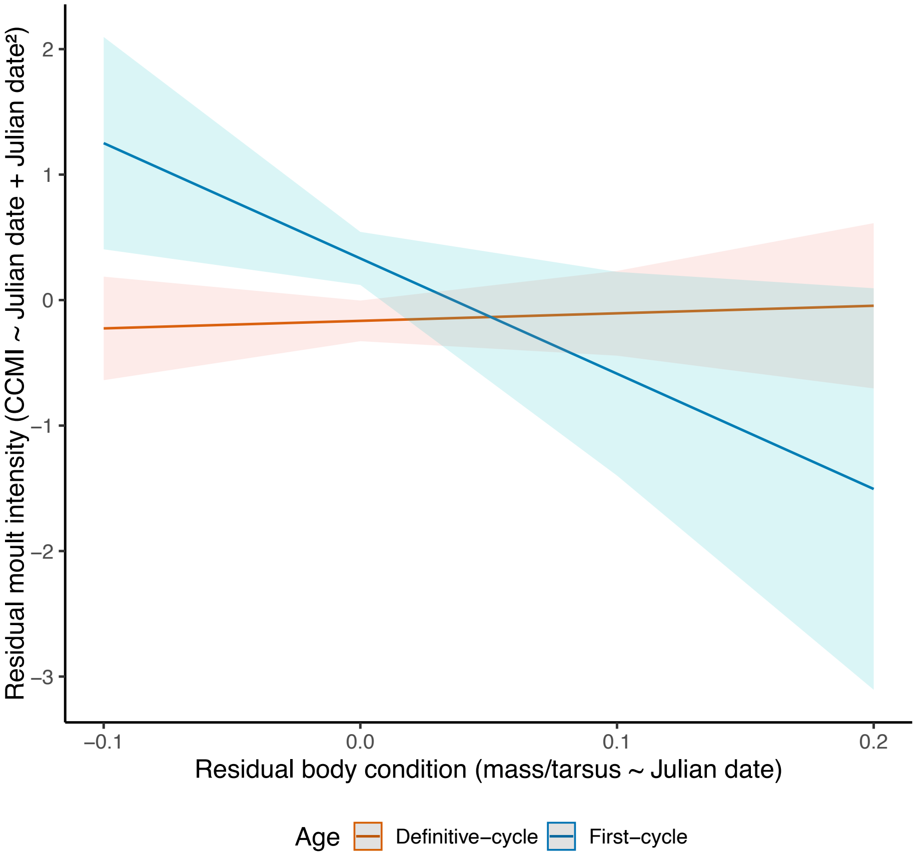

Figure 3.3. Predicted relationship between residual moult intensity and residual body condition by age class in the American Redstart (*n* = 111). The residuals in this model were derived from the linear regression equations body condition (mass/tarsus) ~ Julian date and Combined Moult Contour Index (CCMI) ~ Julian date + Julian date^2. Shaded areas represent 95% confidence intervals.

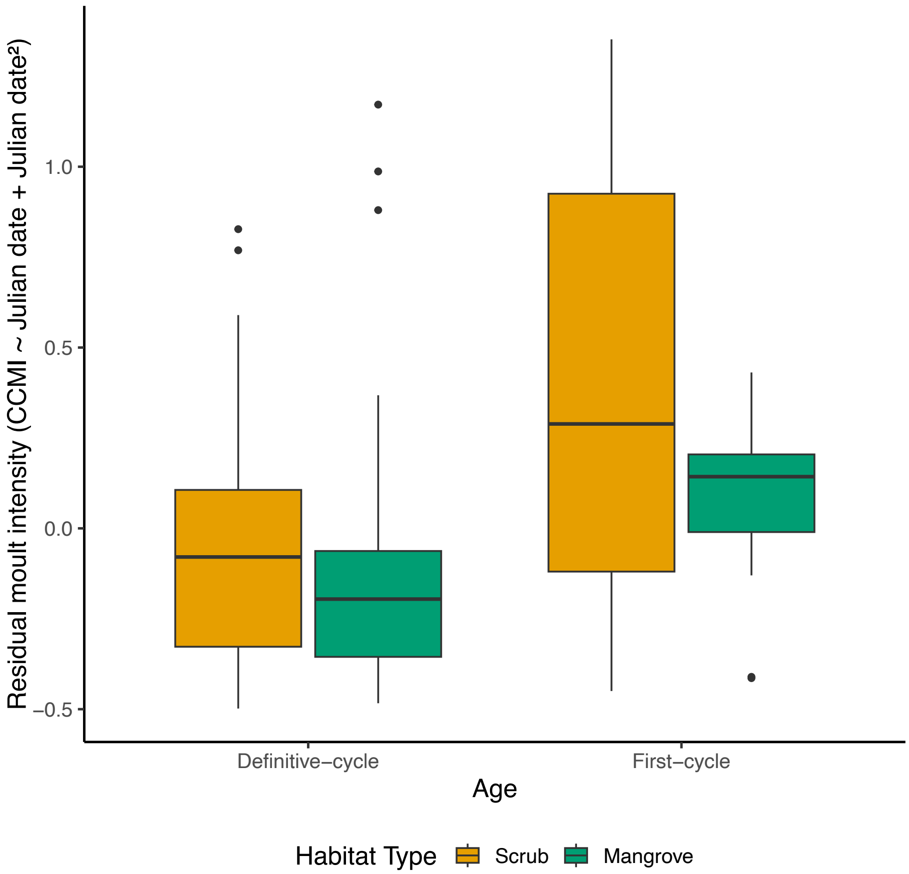

Figure 3.4. Boxplots of residual moult intensity grouped by age class and habitat type in the American Redstart (*n* = 111). Residual moult intensity was derived from the linear regression equation Combined Moult Contour Index (CCMI) ~ Julian date + Julian date^2.

Predicting departure dates

Pre-breeding migration departure dates ranged from April 13 to May 27, with Northern Waterthrushes generally departing earliest (mean ± SD = Apr 26 ± 4.23 days, range = Apr 18 - May 2, *n* = 16), followed by Black-and-white Warblers (mean ± SD = Apr 30 ± 6.43 days, range = April 21 – May 14, *n* = 21) and then American Redstarts (mean ± SD = May 3 ± 8.52 days, range = April 13 – May 27), though American Redstarts showed the widest range in departure dates.

After model selection, a single model (ΔAICc < 1) that included only sex best explained variation in departure dates in the Black-and-white Warbler (*n* = 21, Table 3.4). Males departed earlier than females (β_{sex} = -5.51, 95%CI = -10.93, -0.09). δ^{13}C did not predict departure dates; model selection including δ^{13}C resulted in a top model with sex as the only predictor, followed by the null model (ΔAICc < 1) (*n* = 17, Table 3.5). Consistent with the analysis excluding δ^{13}C, males departed earlier than females, though the relationship was weak (β_{sex} = -2.60, 85% model-averaged CI = -9.62, -0.60). When I examined age-based differences alone, mean departure dates (± SD) were similar for first- (May 1 ± 5.74 days) and definitive-cycle birds (April 30 ± 6.94 days) (Independent Samples t-test: $t_{(14)}$ = -0.23, *p* = 0.82).

I found no association between departure dates and age, residual body condition, residual moult intensity, and the interaction terms age*residual body condition and residual body condition*residual moult intensity for the Northern Waterthrush; the top model (ΔAICc < 1) was the null model (*n* = 16, Table 3.4). However, I found that δ^{13}C was associated with departure date. Model selection resulted in a single model within ΔAICc < 1 that included only δ^{13}C (*n* = 14, Table 3.5). δ^{13}C had a strong effect on departure date, where birds with depleted δ^{13}C ratios, consistent with occupying wetter habitat, departed earlier than birds with enriched ratios ($\beta_{\delta 13C}$ = 2.38, 95%CI = 0.45, 4.30; Figure 3.5). When I compared departure dates between age classes, mean departure dates (± SD) were similar for first- (Apr 25 ± 5.80 days) and definitive-cycle birds (Apr 30 ± 9.65 days) (Independent Samples t-test: $t_{(8)}$ = 0.68, *p* = 0.52).

Three models within ΔAICc <1 best explained the variation in American Redstart departure dates and included combinations of the variables age, residual moult intensity, residual body condition, sex, and its interaction with residual moult intensity (*n* = 48, Table 3.4). All variables included in the top models strongly affected departure dates, except for residual body condition, which had no effect. Definitive-cycle birds departed earlier than first-cycle birds (β_{age} = 5.94, model-averaged 95%CI = 0.49, 11.39; Figure 3.6). Males tended to depart earlier than females (β_{sex} = -5.33, model-averaged 95%CI = -10.20, -0.48), but the influence of sex was modified by residual moult intensity ($\beta_{sex*residual\ moult\ intensity}$ = 8.88, model-averaged 95%CI = 1.75, 22.63; $\beta_{residual\ moult\ intensity}$ = -6.98, model-averaged 95%CI = -18.52, -0.64; Figure 3.7). Residual moult intensity was negatively associated with departure dates in females but positively associated in males.

When I examined sex-based differences within each age class, males departed earlier than females on average in definitive-cycle (Independent Samples t-test: $t_{(16)}$ = 2.33, *p* = 0.03) but not first-cycle birds (Independent Samples t-test: $t_{(9)}$ = 0.56, *p* = 0.59).

Table 3.4. Summary of the top ranked models (ΔAICc < 1) that predicted pre-breeding migration departure dates from Jamaica in the Black-and-white Warbler (*n* = 21), Northern Waterthrush (*n* = 16), and American Redstart (*n* = 48).

Species	**Top models (ΔAICc < 1)**	**AICc**	**ΔAICc**	**AICc weight**
Black-and-white Warbler	1. sex	139.6	0.00	0.31
Northern Waterthrush	1. NULL MODEL	95.4	0.00	0.45
American Redstart	1. age + residual moult intensity + sex	336.9	0.00	0.05
	2. age + residual moult intensity + residual body condition + sex	337.8	0.82	0.04
	3. age + residual body condition + sex	337.9	0.96	0.03

Table 3.5. Summary of the top ranked models (ΔAICc < 1) that predicted pre-breeding migration departure dates from Jamaica in the Black-and-white Warbler (*n* = 17) and Northern Waterthrush (*n* = 14), using $\delta^{13}C$ as an explanatory variable.

Species	**Top ranked models (ΔAICc < 1)**	**AICc**	**ΔAICc**	**AICc weight**
Black-and-white Warbler	1. sex	115.5	0.00	0.31
	2. NULL MODEL	115.6	0.07	0.30
Northern Waterthrush	1. $\delta^{13}C$	82.4	0.00	0.70

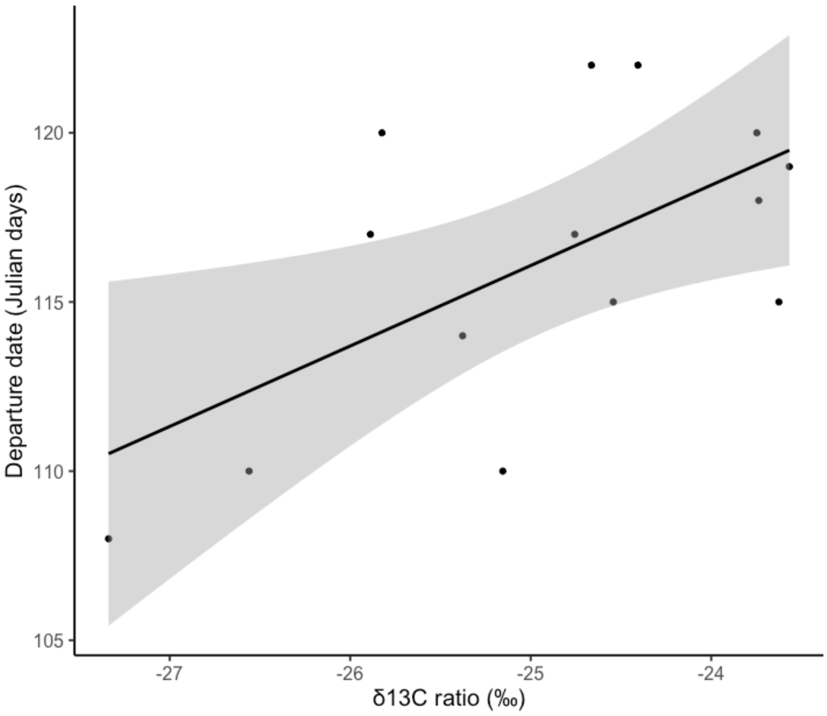

Figure 3.5. δ^{13}C ratios (‰) in the Northern Waterthrush (black circles). The line represents the predicted relationship between pre-breeding departure date from Jamaica and δ^{13}C ratio (‰) in the Northern Waterthrush (*n* = 14). Departure dates are in Julian days; day 105 = April 15, 2023. The shaded area represents the 95% confidence interval.

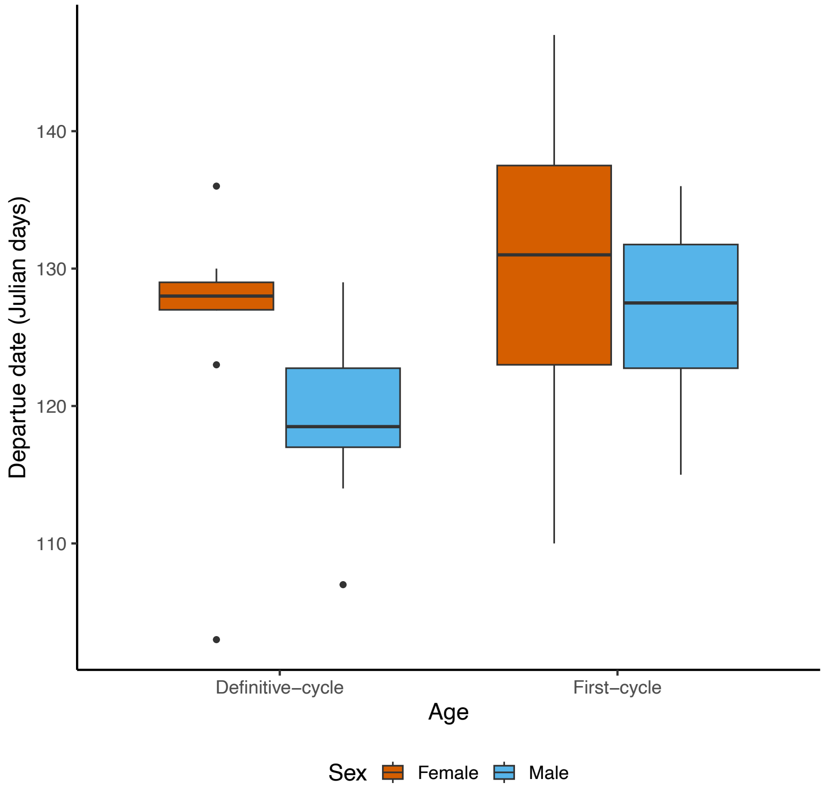

Figure 3.6. Boxplots of pre-breeding migration departure dates from Jamaica grouped by age and sex classes in the American Redstart (*n* = 48). Departure dates are Julian days; day 110 = April 20, 2023.

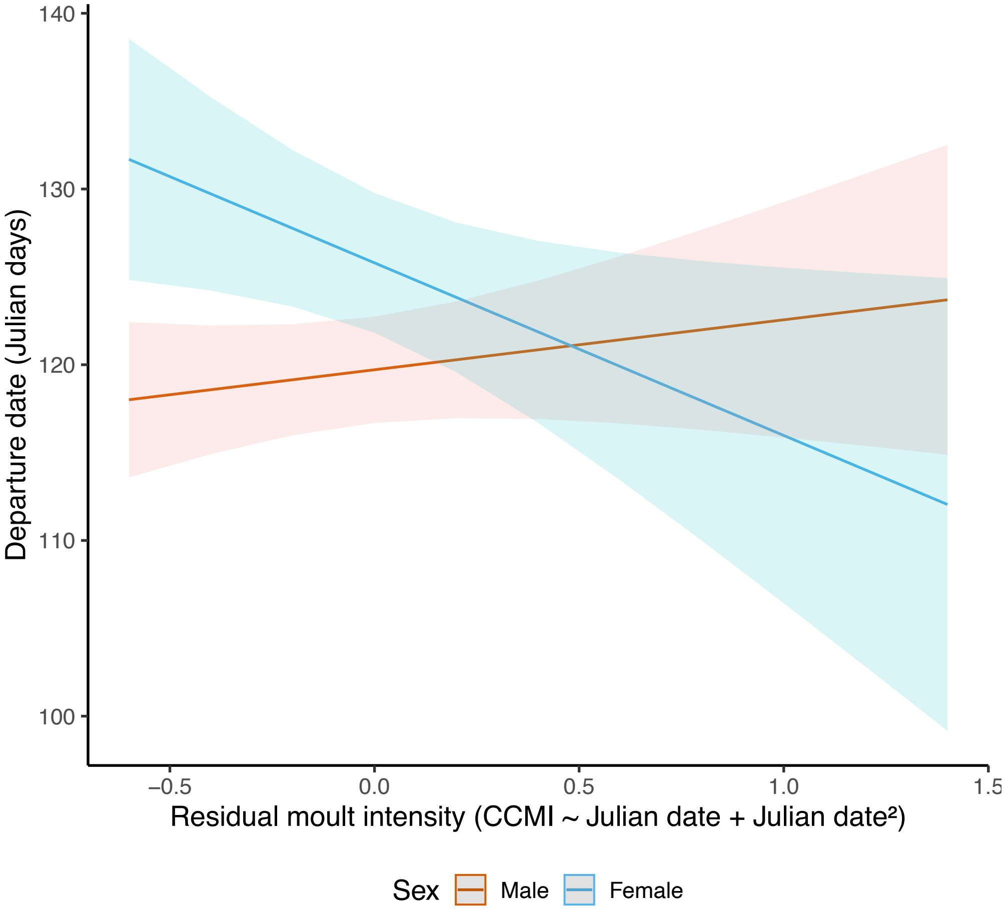

Figure 3.7. Predicted relationship between pre-breeding departure date from Jamaica and residual moult intensity by sex in the American Redstart (*n* = 48). The residuals in this model were derived from the linear regression equation Combined Moult Contour Index (CCMI) ~ Julian date + Julian date^2. Departure dates are in Julian days; day 100 = April 10, 2023. Shaded areas represent 95% confidence intervals.

DISCUSSION

The conditions that warblers experience on the stationary nonbreeding grounds can directly influence the timing of their departure on pre-breeding migration (e.g., American Redstart; Marra et al. 1998, Studds and Marra 2005, Reudink et al. 2009a), yet how the intensity of prealternate moult may modify this seasonal interaction remains largely unknown. Here, I build on a detailed quantification of prealternate moult intensity in three Nearctic-Neotropical migratory songbirds (Chapter 2) to demonstrate that, 1) body condition, mediated by habitat quality, can be associated with moult intensity, and 2) moult intensity can be associated with departure date. These findings provide the first potential evidence of prealternate moult carry-over effects from the nonbreeding period to pre-breeding migration phenology in a parulid warbler and suggest that the timing and intensity of prealternate moult may represent an important seasonal interaction in some species. In addition, the intensity and timing of prealternate moult appears to be flexible and vary in response to nonbreeding conditions. The influence of nonbreeding conditions on moult intensity and their subsequent effects on departure date varied across age and sex classes in addition to species, suggesting that moult and departure phenology are driven by both endogenous and exogenous factors regardless of nonbreeding conditions.

Age was associated with moult intensity in the Black-and-white Warbler and American Redstart, modified by an interaction with body condition. For the Black-and-white Warbler, moult was generally more intense in first-cycle birds and increased with condition. Moult was more intense in some first-cycle American Redstarts, but intensity varied more than in definitive-cycle birds. When compared with Black-and-white Warblers, first-cycle American Redstarts showed the opposite pattern—a negative relationship between moult intensity and body condition. Moult intensity varied less with changes in condition in definitive-cycle birds of both species. First-cycle Black-and-white Warblers and American Redstarts in the study population may moult more intensely than definitive-cycle birds because they can gain a greater benefit from replacing relatively poorer quality contour feathers (as argued in Chapter 1). Birds tend to have poorer quality feathers in their first cycle (Pyle 2022, e.g., Szép et al. 2019) and if territorial, secure poorer quality territories on the nonbreeding grounds than their definitive-cycle counterparts (e.g., Figuerola et al. 2001, Marra and Holmes 2001) which might lead to increased feather wear throughout the nonbreeding period (Reudink et al. 2009b). In birds with a high incentive to moult, such as first-cycle Black-and-white Warblers, being in better condition might facilitate a more intense moult. In contrast, first-cycle American Redstarts in relatively poor condition but showing high intensity moult might indicate the individuals with the poorest quality feathers, hence requiring the most replacement. The differences in the relationships between moult and body condition in these two species demonstrate the importance of future, detailed study on the physiology of prealternate moult and its role within the annual cycle.

In this system, first-cycle American Redstarts tend to occupy nonbreeding territories that are drier and have fewer food resources, resulting in relatively poor body condition (Marra and Holmes 2001). When compared with definitive-cycle American Redstarts, first-cycle territories also tend to be more open (unpublished long-term site dataset 1987—2024), which may result in increased feather wear from solar radiation (Bergman 1982, Froehlich et al. 2005, Reudink et al. 2009b, Terrill et al. 2020, Guallar et al. 2021). In this study, not only did many first-cycle American Redstarts tend to moult more intensely than definitive-cycle American Redstarts, but within first-cycle birds, those occupying poorer quality scrub habitat moulted more intensely than those occupying higher quality mangrove. Ames (2021) observed the same pattern in the Prothonotary Warbler (*Protonotaria critea*), where prealternate moult intensity was higher in first-cycle birds and for birds occupying dry nonbreeding habitat in Panama. The difference in moult intensity among habitats was not as marked in definitive-cycle American Redstarts, possibly because the quality of scrub habitat varies in the study plots and anecdotally, older birds tend to secure higher quality, more closed-canopy scrub territories (unpublished long-term site dataset 1987—2024). However, American Redstarts in this system also have sex-biased habitat occupancy, with females more likely to occupy scrub habitat (Parrish and Sherry 1994, Marra and Holberton 1998). Indeed, I also found a moderate relationship between sex and moult intensity for American Redstarts, where females moulted more intensely than males. The pattern of higher intensity moult associated with more open habitat was found in comparative analyses of the evolution of prealternate moult at the species level (Svensson and Hedenström 1999, Cuervo et al. 2022). Migratory species that occupied open nonbreeding habitats were more likely to evolve a prealternate moult while their congeneric relatives that occupied more closed nonbreeding habitats did not. Further studies should directly measure habitat openness and contour feather quality during the nonbreeding period preceding moult (i.e., October through January) to test this hypothesis for the American Redstart.

As expected, I found inter- and intraspecific variation in the relationship between body condition and moult intensity. In a study of prebasic moult intensity in the House Finch, the influence of body condition on moult intensity varied across the sexes, urban-rural habitat type, and at different stages of moult (i.e., beginning, peak, and end; Hutton et al. 2021). Hutton et al. (2021) concluded that body condition limited feather synthesis during the peak and end stages of moult but did not appear to be an important predictor during the beginning of moult. Because moult intensity often peaks during the middle of the moult period (e.g., Wright et al. 2018, Hutton et al. 2021, Guallar 2024), a relationship I detected for American Redstarts (Chapter 2), I expect body condition to be important mid-moult when energetic demands are high. Unlike the non-migratory House Finch, moult in my study population appears to overlap with migratory fattening (Chapter 2). Therefore, body condition must also be important during the end of moult; though moult intensity is low, energetic demands for migratory fattening are high and birds may be faced with trade-offs for resource allocation (e.g., Bonier et al. 2007, Rubolini et al. 2022, Witkowska et al. 2024). Future study focused on parsing the effect of body condition on moult intensity during different stages of the prealternate moult in this system could improve our understanding of the differing relationships observed in the Black-and-white Warbler and American Redstart, and potentially identify an effect in the Northern Waterthrush. Further, examining habitat use and its relationship to condition during different stages of moult could elucidate why δ^{13}C predicted condition in the Black-and-white Warbler but was not associated with moult intensity.

Moult intensity was strongly associated with departure date in American Redstarts only and modified by an interaction with sex. However, the sexes showed relationships in opposite directions. Because moult intensity followed a parabola in American Redstarts over time (Chapter 2), lower moult intensity prior to departure likely indicates that moult is nearer to completion. Males with higher moult intensity, likely indicating that moult was completed later, departed later. This result suggests that the timing of moult may impose a constraint on male American Redstarts but not females. Because males are under strong selection pressure to arrive earlier to the breeding grounds to secure a high-quality territory and mate(s), a delayed departure has the potential to incur greater reproductive fitness costs (e.g., Lozano et al. 1996, Reudink et al. 2009a, Tonra et al. 2011, Rockwell et al. 2012). While some birds compensate for later departures by increasing their migration speed (e.g., González et al. 2020), previous research shows that when male American Redstarts depart later from Jamaica, they tend to arrive later to the breeding grounds than birds with earlier departure dates (Reudink et al. 2009a).

In this study system, American Redstarts in better condition—typically a result of territory quality—tend to depart the nonbreeding grounds earlier (Marra et al. 1998, Studds and Marra 2005, Reudink et al. 2009a). If better condition, resulting from high quality habitat, can also facilitate a more intense moult (e.g., Hutton et al. 2021), birds in better condition should complete moult earlier via a higher moult intensity (de la Hera et al. 2011, Rohwer and Rohwer 2013), allowing them to depart earlier. However, I did not detect a direct relationship between condition and departure date in American Redstarts or the other species. Contrary to my prediction, enriched δ^{13}C ratios indicating drier habitat were associated with better condition in the Black-and-white Warbler. At Font Hill Nature Reserve, drier habitat was also better quality for the Swainson's Warbler (*Lymnothlypis swainsonii*) because it had more abundant arthropod biomass in the thicker leaf litter found in scrub forest (Brunner et al. 2022). It's possible that xeric scrub habitat can be higher quality for the foliage-gleaning Black-and-white Warbler if their foraging substrate (i.e., tree bark) hosts more abundant resources than trees in mangrove. However, although condition was associated with moult intensity, neither condition nor δ^{13}C were linked to departure date.

Many migratory bird species exhibit age- and sex-based differences in migration timing (reviewed in Newton 2011); males tend to migrate earlier than females (protandry) and older birds tend to migrate earlier than young birds (e.g., passerines; Stewart et al. 2002). In my study population, I would expect earlier departures for males and definitive-cycle birds. I detected two of those expected patterns: male Black-and-white Warblers departed earlier than females, and American Redstarts in their definitive-cycle departed earlier than those in their first-cycle. Given that such patterns of differential migration among age or sex classes can vary interannually in relation to environmental conditions on the nonbreeding grounds (e.g., Prairie Warbler; Akresh et al. 2019), it is not surprising that I did not detect all three patterns among all three study species. Further, nonbreeding populations may breed across a broad latitudinal range, and I was unable to account for the expected differences in intraspecific migration distance (unpublished Motus dataset 2022, Dossman et al. 2023a). Within a nonbreeding population, differences in migration distance can be associated with intraspecific migration timing (e.g., Bar-tailed Godwit (*Limosa lapponica*): Conklin et al. 2010; American Redstart: Dossman et al. 2023b).

Evidence suggests that aspects of migratory behaviour, such as migration timing and direction, are heritable, at least in the Eurasian Blackcap (*Sylvia atricapilla*; Berthold and Helbig 1992, Bearhop et al. 2005; Delmore et al. 2020, Delmore et al. 2023). For pre-breeding migration in particular, the timing of departure from the nonbreeding grounds and arrival to the breeding grounds might be under strong endogenous control (Stanley et al. 2012). Stanley et al. 2012 found that the timing of pre-breeding migration in the Wood Thrush (*Hylocichla mustelina*) was highly repeatable over two or three years of tracking. Males and older birds consistently departed the Neotropical nonbreeding grounds earlier, and in addition, individual departure dates were highly consistent across years. Given that my sample sizes for the departure analysis were relatively small and I could not account for differences in migration distance, innate migration schedules based on the location of breeding grounds likely explain some of the variation in departure dates and confound my ability to fully understand the effect of moult intensity. In this system, a future study that measures body condition, moult intensity, and departure date in the same individuals across multiple years would greatly aid in improving our initial understanding of the potential for prealternate moult carry-over effects in migratory parulid warblers.

In conclusion, my results provide the first potential evidence of a carry-over effect from the prealternate moult to pre-breeding migration phenology in a parulid warbler, the American Redstart. To my knowledge, this study represents only the third of its kind to specifically consider the role of parulid prealternate moult in carry-over effects (see Boone et al. 2010 and Jones et al. 2014), and the first to examine potential prealternate moult carry-over effects in these species. Studies such as this are critical for building our understanding of moult and its role in seasonal interactions among related species, age and sex classes, and can be used in the future to make much needed comparisons across years and nonbreeding populations. Ultimately, this study highlights the importance of considering the role of moult when assessing carry-over effects across the annual cycle.

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CHAPTER 4: CONCLUSION

My goal was to evaluate the potential role of prealternate moult in carry-over effects from the stationary nonbreeding period to pre-breeding migration in Nearctic-Neotropical migratory songbirds. Because there is a large gap in our basic knowledge of prealternate moult (reviewed in Chapter 2), the first step in accomplishing my goal was to quantify patterns, timing, and intensity of prealternate moult on the nonbreeding grounds in Jamaica (Chapter 2). From January to April 2023, I quantified moult in six species of parulid warbler. I demonstrated that head and body feather moult is common for the Northern Waterthrush (*Parkesia noveboracensis*), Black-and-white Warbler (*Mniotilta varia*), American Redstart (*Setophaga ruticilla*), Northern Parula (*Setophaga americana*), and Prairie Warbler (*Setophaga discolor*), and increases in frequency and intensity later in the nonbreeding period for most species. For the Ovenbird (*Seiurus aurocapilla*), I confirmed the occurrence of prealternate moult in at least some individuals. Using this new foundational knowledge of prealternate moult, I then assessed whether nonbreeding habitat quality and body condition influenced the timing and intensity of moult, and, in turn, if moult influenced the timing of departure on pre-breeding migration in three species: Black-and-white Warbler, Northern Waterthrush, and American Redstart (Chapter 3). I found that the intensity and timing of prealternate moult appears to be flexible and vary in response to habitat quality and body condition. Ultimately, I discovered links between nonbreeding conditions, prealternate moult intensity, and departure dates in the American Redstart. I also found inter- and intraspecific variation in the influence of nonbreeding conditions on prealternate moult and their subsequent effects on departure timing, indicating that moult and departure phenology can be driven by both endogenous and exogenous factors regardless of nonbreeding environmental conditions.

Significance to the field of ornithology

The findings of my research fill gaps in our basic understanding of prealternate moult phenology for migratory parulid warblers. To the best of my knowledge, this work represents the first quantification of contour feather moult intensity in all six study species and provide the first detailed description of contour feather moult patterns and timing in the Ovenbird. This study appears to be only the third of its kind to investigate the role of prealternate moult in nonbreeding period carry-over effects in parulid warblers (see Boone et al. 2010 and Jones et al. 2014), and the first to examine it in the species I studied. Thus, finding links between nonbreeding conditions, moult, and departure date in the American Redstart is a meaningful advancement and highlights the importance of considering moult in seasonal interactions across the avian annual cycle. While more work must be done to understand the mechanisms regulating prealternate moult and the variation across species, age and sex classes, my results serve as a jumping off point and can be used for comparison with other nonbreeding populations and years. The data I collected for this research can have long-term impacts through its inclusion in 1) the publicly accessible Motus database of global migration tracking data (www.motus.org), and 2) a long-term site-specific dataset for Font Hill Nature Preserve, Jamaica, which over the past 30 plus years has been instrumental to the scientific community's understanding of the nonbreeding ecology of migratory birds. Further, my research will be widely accessible through the publication of this thesis on an open access repository, and peer-reviewed publication of the data chapters.

Limitations and directions for future study

From previous research the general migratory paths and breeding ranges of my study species are known (i.e., eastern and/or east-central North America), but the locations of breeding grounds vary widely within the study population. For example, American Redstarts migrating from Jamaica likely breed from Alabama in the south to as far north as southern Ontario, resulting in migration distances differing among individuals by 2,000 kilometres or more (Dossman et al. 2023). Innate migration schedules based on breeding latitude and associated migration distance likely explain some of the intraspecific variation in departure dates (e.g., Neufeld et al. 2021) and confound my ability to disentangle the effects of body condition and moult intensity on departure timing. Accounting for migration distance, for example by determining breeding latitude from stable-hydrogen isotopes in feathers grown on the breeding grounds (e.g., Dossman et al. 2023), could clarify the relationships I detected. Further, migration phenology can vary annually with variation in seasonal resources mediated by tropical precipitation (e.g., Studds and Marra 2011, Rockwell et al. 2012, Akresh et al. 2019). Because the timing and intensity of moult appears to be flexible with variable body condition—typically associated with habitat quality—a multi-year study to account for interannual variation would be valuable.

Xeric habitat, which is typically poorer in quality than mesic habitat (Rodríguez Vásquez and Taylor 2024), was associated with Black-and-white Warblers in better condition during my study period, contrary to previous work (Paxton and Moore 2015, Cooper et al. 2021). However, habitat moisture may not be the primary driver of habitat quality for this species, as suggested for the Magnolia Warbler (*Setophaga magnolia*; Boone et al. 2010), but further study is needed. I could not conclusively determine relative habitat quality (i.e., habitat conditions associated with body condition) at my study site for the Northern Waterthrush, potentially due to my small sample size ($n = 14$). For these two species, delineating individual territories (e.g., Marra et al. 2015a, Cooper et al. 2021) and increasing repeated body condition measurements across the season may better indicate habitat use and quality and could improve our ability to determine their combined effects on moult intensity.

To better understand the endogenous and exogenous mechanisms that regulate prealternate moult, future studies should increase the number of repeated measurements of moult intensity across the season in the same individuals, for example every two weeks during the moult period. This approach can facilitate understanding the complete extent of individual moult, which I could not determine from my moult intensity metric. I detected a lower range in moult intensity scores than other studies of contour feather moult in songbirds, during the prealternate (Wright et al. 2018) and prebasic moults (Hutton et al. 2021). However, the biological significance, specifically the physiological costs and benefits, of differing contour feather moult intensities is not known. Increased repeated measurements of moult intensity and body condition across the nonbreeding period, combined with measurements of physiological stress indicated by corticosterone (e.g., Harms et al. 2015), could be used to evaluate if birds make trade-offs between prealternate moult intensity and migratory fattening. Tracking departure dates in those same individuals year-over-year (e.g., Studds and Marra 2011) would allow researchers to evaluate the potential consequences of such trade-offs on migration timing.

Management implications

While the species I studied are currently listed as Least Concern by the International Union for Conservation of Nature (IUCN 2024), Nearctic-Neotropical migrants as a group have declined drastically over the past 50 years (Rosenberg et al. 2019) and continue to face threats such as habitat degradation and loss, exacerbated by global climate change (Albert et al. 2020). My research serves as an important early step in understanding the role of prealternate moult in carry-over effects within the annual cycle. Considering how all life stages interact across the avian annual cycle is critical for identifying the spatial and temporal periods that limit declining populations (Marra et al. 2015b), and then applying this information to prioritize high-quality habitats for conservation.

Understanding if and how life stages that occur on the nonbreeding grounds are limiting has become increasingly important as a long-term drying trend impacts the Caribbean (Neelin et al. 2006). As a result of this trend, precipitation during the tropical dry season in Jamaica has declined and become less predictable (Studds and Marra 2011), and this unpredictable season coincides with the nonbreeding period for Nearctic-Neotropical migrants. Periods of drought, or reduced rainfall, have been linked to reduced annual survival (e.g., Dossman et al. 2023), reduced breeding success (e.g., Rockwell et al. 2017), and shifts in breeding range (e.g., Dossman et al. 2023). Further drying may amplify these effects, leading to further population declines. Projections also suggest that the frequency of North Atlantic hurricanes will increase (Emanuel 2005, reviewed in Knutson et al. 2010). Although their effect on migrant survival appears to be minimal, these storms can alter the quality of habitat, causing migrants to shift toward less damaged and potentially poorer-quality, habitat (Wunderle Jr. and Arendt 2017). In fact, since I conducted my field research, Jamaica was hit by Hurricane Beryl, a category 4 storm (July 2024; NOAA 2024). Hurricane Beryl caused serious damage to the southwest coast of the island (CBC 2024), where the study site is located. In the context of global climate change, managing high quality nonbreeding habitats such as mesic mangrove is now more important for migratory birds than ever (Albert et al. 2020), especially because coastal habitats are under constant threat of degradation or loss associated with unsustainable management and land development (Muñoz Sevilla and La Bail 2017, Guimarais et al. 2021, Gómez et al. 2022).

People of diverse demographics across the Americas and the Caribbean share in the delights, and ecological benefits, of Nearctic-Neotropical migratory birds. International collaboration is essential to achieving the shared goal of reversing the decline in migratory bird populations and safeguarding their habitats (Runge et al. 2015, Albert et al. 2020). To this end, it is crucial that researchers and land managers from the Global North (i.e., the United States and Canada) establish equitable collaborations with Neotropical partners to support locally led work. Improving equity will require those global northerners with current Neotropical projects to critically evaluate how their work has in the past, or present, contributed to the systemic exclusion of Neotropical researchers, much to the detriment of the field of ornithology (Soares et al. 2023). While much work remains on this front, improving equity to emphasize local objectives and leadership can strengthen both science and conservation (de Vos 2022, Soares et al. 2023).

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APPENDIX A

Table A.1. Estimates for significant predictors (*p*-value < 0.05) of moult intensity as measured by the Combined Contour Moult Index, in the American Redstart and Prairie Warbler, modelled three ways using a linear model to handle individuals with repeated measurements (recaptured birds): a) excluding the second capture, b) excluding the first capture, and c) including both captures. Linear modelling followed a stepwise regression (backward elimination), starting with the full initial model including the explanatory variables: Julian date, Julian date^2, age, and sex. For the American Redstart, I considered the interaction term age*Julian date. It was not significantly related to moult intensity, so I removed it from the final model.

Species	**Model**	**Explanatory variable**	**Estimate**	**Residual standard error (degrees of freedom)**	***t*-value**	***p*-value**
American Redstart	a. excluding second capture	Julian date	0.063	0.024 (82)	2.667	0.009
		Julian date^2	-0.0004	0.0002 (82)	-2.710	0.008
		Age	0.377	0.106 (82)	3.545	0.0007
	b. excluding first capture	Julian date	0.061	0.023 (82)	2.683	0.009
		Julian date^2	-0.0004	0.0001 (82)	-2.817	0.006
		Age	0.307	0.103 (82)	2.976	0.004
	c. including both captures	Julian date	0.063	0.022 (90)	2.930	0.004
		Julian date^2	-0.0004	0.0001 (90)	-3.034	0.003
		Age	0.335	0.100 (90)	3.347	0.001
Prairie Warbler	a. excluding second capture	Julian date	0.086	0.029 (17)	2.955	0.009
		Julian date^2	-0.0007	0.0002 (17)	-3.229	0.005
	b. excluding first capture	Julian date	0.056	0.026 (17)	2.141	0.047
		Julian date^2	-0.0005	0.0002 (17)	-2.461	0.025
	c. including both captures	Julian date	0.060	0.027 (18)	2.285	0.035
		Julian date^2	-0.0005	0.0002 (18)	-2.585	0.019

Table A.2. Sample sizes of the numbers of six species moulting and not moulting at capture, after the observed onset of moult, used as input for a Pearson's chi-squared test.

Species	**# moulting**	**# not moulting**
Ovenbird	10	8
Northern Waterthrush	75	36
Black-and-white Warbler	62	8
American Redstart	89	14
Northern Parula	14	5
Prairie Warbler	18	3

APPENDIX B

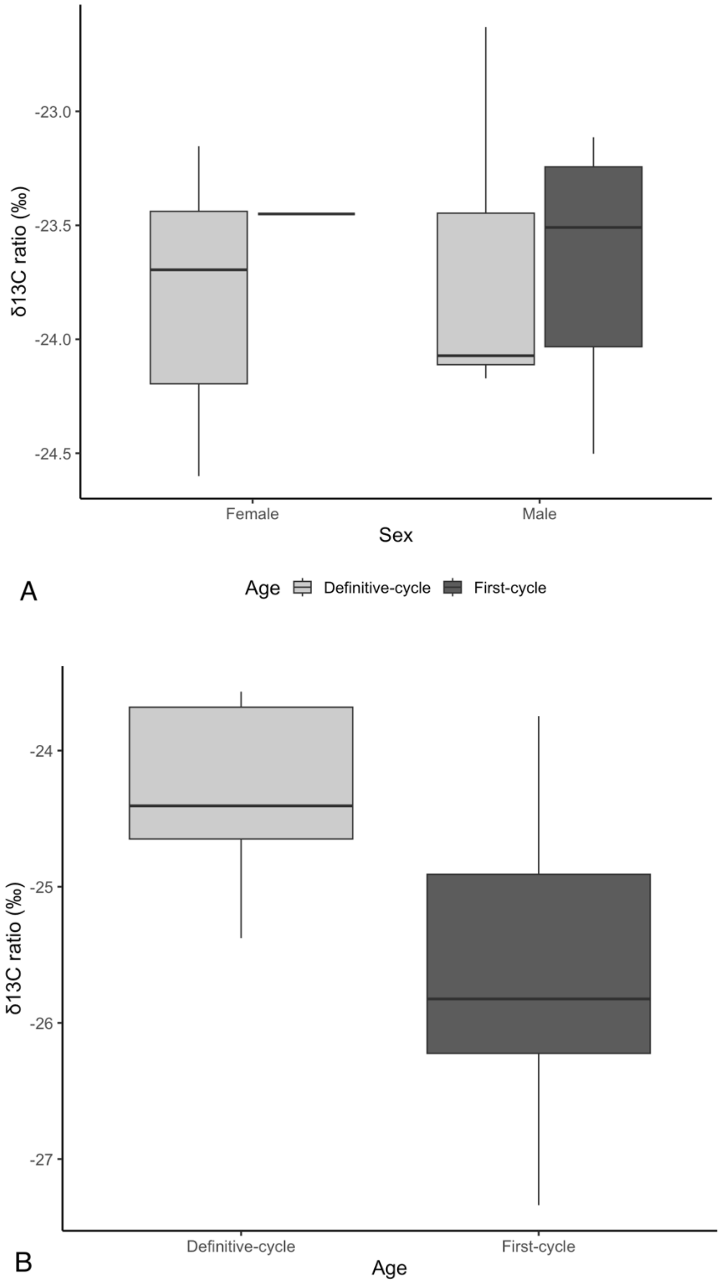

Figure B.1. Boxplots of δ^{13}C ratios (‰) sampled from A) Black-and-white Warbler, and B) Northern Waterthrush, grouped by age class. δ^{13}C ratios for each age class in the Black-and-white Warbler are further grouped by sex because I could determine sex in the field for these species.

Table B.1. Stable-nitrogen ($\delta^{15}N$) ratios (‰) sampled from Black-and-white Warblers and Northern Waterthrushes in March and April, 2023, at Font Hill Nature Preserve, Jamaica. I report corrected values measured in units of per mil (‰) relative to the international standards Atmospheric Air for $\delta^{15}N$.

Species	**Age**	**Sex**	**$\delta^{15}N$ ratio (‰)**
Black-and-white Warbler	*Definitive-cycle*	*Female*	7.65
			7.32
			5.60
			5.68
			5.55
			5.36
			6.30
			5.73
			7.32
			7.00
			6.41
			6.59
			6.66
			6.76
		Male	6.80
			5.88
			5.91
			7.20
			5.50
			6.36
	First-cycle	*Female*	5.98
		Male	2.08
			7.08
			5.26
			6.02
			6.51
Northern Waterthrush	*Definitive-cycle*	*NA*	7.44
			7.69
			7.63
			8.47
			7.87
			7.45
			7.31
	First-cycle		6.46
			6.98
			7.47
			6.53
			7.35
			7.00

Species	Age	Sex	δ^{15}N ratio (‰)
			6.12

Table B.2. Summary of estimates (β) and 85% confidence intervals for explanatory variables from the top-ranked models (ΔAICc < 1) of all analyses that had no effect (85%CIs overlapped zero) on the dependent variable.

Model type	Species	Explanatory variable	β (85%CI)
Predicting prealternate moult intensity	Black-and-white Warbler	residual body condition	2.05 (-0.06, 4.01)
	American Redstart	residual body condition	-0.15 (-2.66, 2.05)
		habitat type	-0.02 (-0.15, 0.11)
Predicting departure date	American Redstart	residual body condition	-37.07 (-132.39, 0.51)

Table B.3. Summary of the top ranked models (ΔAICc < 1) that predicted residual prealternate moult intensity in the American Redstart, modelled three ways using a linear model to handle individuals with repeated measurements (recaptured birds): a) excluding the second capture, b) excluding the first capture, and c) including both captures. All three modelling methods produced the same results.

	Top ranked models (ΔAICc < 1)	AICc	ΔAICc	AICc weight
a	1. age + sex	111.9	0.00	0.08
	2. age + residual body condition + habitat type + sex + age*residual body condition + age*habitat type	112.0	0.01	0.08
	3. age + residual body condition + habitat type + age*residual body condition + age*habitat type	112.6	0.65	0.06
	4. age + habitat type + sex + age*habitat type	112.6	0.68	0.06
b	1. age + sex	111.9	0.00	0.08
	2. age + residual body condition + habitat type + sex + age*residual body condition + age*habitat type	112.0	0.01	0.08
	3. age + residual body condition + habitat type + age*residual body condition + age*habitat type	112.6	0.65	0.06
	4. age + habitat type + sex + age*habitat type	112.6	0.68	0.06

	Top ranked models (ΔAICc < 1)	AICc	ΔAICc	AICc weight
c	1. age + sex	111.9	0.00	0.08
	2. age + residual body condition + habitat type + sex + age*residual body condition + age*habitat type	112.0	0.01	0.08
	3. age + residual body condition + habitat type + age*residual body condition + age*habitat type	112.6	0.65	0.06
	4. age + habitat type + sex + age*habitat type	112.6	0.68	0.06