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Demographic variation in timing and intensity of feather molt in migratory Fork-tailed Flycatchers (*Tyrannus s. savana*)

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ABSTRACT. Understanding the annual cycle of migratory birds is imperative for evaluating the evolution of life-history strategies and developing effective conservation strategies. Yet, we still know little about the annual cycle of migratory birds that breed at south-temperate latitudes of South America. We aged, sexed, and determined the progression and intensity of body, remige, and rectrix molt of migratory Fork-tailed Flycatchers (*Tyrannus s. savana*) at breeding sites in southern South America and at wintering sites in northern South America. Molt of both body and flight feathers occurred primarily during the winter. In early winter, a similar proportion of young and adult flycatchers molted remiges and rectrices, but remige molt intensity (number of remiges molting) was greater and primary molt progression (mean primary feather molting) more advanced in adults. In late winter, remige molt intensity and primary molt progression did not differ between age groups. We found no difference between males and females either in the proportion of individuals molting in winter or in the intensity or progress of remige molt. Our results suggest that the nominate subspecies of Fork-tailed Flycatcher undergoes one complete, annual molt on the wintering grounds, and represents the first comprehensive evaluation of molt timing of a migratory New World flycatcher that overwinters in the tropics. Given that breeding, molt, and migration represent three key events in the annual cycle of migratory birds, knowledge of the timing of these events is the first step toward understanding the possible tradeoffs migratory birds face throughout the year.

RESUMEN. **Variación demográfica en el calendario e intensidad de muda de plumas en Atrapamoscas Tijereta (*Tyrannus s. savana*) migratorias**

La comprensión del ciclo anual de las aves migratorias es fundamental para evaluar la evolución de las estrategias del ciclo vital y el desarrollo de estrategias efectivas de conservación. Sin embargo, todavía sabemos poco sobre el ciclo anual de las aves migratorias que se reproducen en zonas templadas del sur de Sudamérica. Determinamos el año de edad, el sexo, y la progresión y la intensidad de muda de plumas del cuerpo, las remeras y las rectrices en las Atrapamoscas Tijereta (*Tyrannus s. savana*) en los sitios de cría en el sur de Sudamérica y en sitios de invernada en el norte de Sudamérica. La muda de plumas del cuerpo y plumas de vuelo ocurrió principalmente durante el invierno. En el comienzo del invierno, una proporción similar de jóvenes y adultos mudaron las plumas remeras y rectrices, pero la intensidad de la muda de remeras (número de remeras en muda) fue mayor y la progresión de la muda de remeras primarias (media de remeras primarias en muda) fue más avanzado en adultos. A finales del invierno, la intensidad y la progresión de la muda de las remeras primaria no difirió entre los grupos de edad. No se encontraron diferencias entre machos y hembras, tampoco en la proporción de individuos en muda en invierno o en la intensidad o el progreso de la muda de remeras. Nuestros resultados sugieren que la subespecie nominal de

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Atrapamoscas Tijereta se somete a una muda completa cada año en las zonas de invernada, y representan la primera evaluación integral del calendario de muda de una atrapamosca migratoria del nuevo mundo que pasa la invernada en los trópicos. Teniendo en cuenta que la cría, la muda y la migración representan tres etapas claves en el ciclo anual de las aves migratorias, el conocimiento del calendario de estos eventos es un primer paso a la comprensión del intercambio de ventajas y desventajas que enfrentan las aves migratorias durante el año.

Key words: Argentina, Colombia, feather, llanos, rectrix, remige

Feather molt is a key event in the annual cycle of migratory birds, essential for maintaining plumage functionality, which in turn is necessary for efficient flight (Hedenström and Sunada 1999) and thermoregulation (Dawson and Maloney 2004). However, feather molt is both energy-limited (Murphy and King 1992, Lindström et al. 1993, Murphy 1996) and time-limited (Rohwer et al. 2011). Additionally, flight performance during molt may be reduced (Swaddle and Witter 1997) and stress experienced during molt can carry over to other parts of the annual cycle, potentially affecting reproduction and survival (Harms et al. 2015) and delaying migration (Stutchbury et al. 2011). As a result, molt needs to be timed to take advantage of access to adequate resources (e.g., food availability), while not interfering with reproduction and migration (Leu and Thompson 2002). Thus, knowing the timing of molt can help provide a better understanding of how birds minimize tradeoffs between major life-history events, including potential seasonal carry-over effects. Knowledge of molt timing and location of molt of different feather tracts among ages and sexes also precludes the use of stable isotope analysis of feathers to determine migratory connectivity (Szép et al. 2009).

The timing of molt by migrant songbirds can vary with age and sex (Siikamäki et al. 1994, Hemborg et al. 2001, Heise and Moore 2003); thus, age-dependent tradeoffs may exist between the timing of migration and molt. For example, Carlisle et al. (2005) found that adults migrated earlier than hatch-year birds in species where adults molt flight feathers after initiating fall migration, whereas hatch-year birds almost always migrated earlier than adults in species where adults molt on or near breeding areas.

We have a good understanding of the molt cycles of many species that molt after breeding and before initiating fall migration (e.g., Svensson and Hedenström 1999, Rohwer et al. 2005). However, with the exception of several species that undertake a late summer molt migration (e.g., Butler et al. 2002, Rohwer et al. 2005, Rohwer 2013, Barry et al. 2009), we know little about demographic variation in the timing of molt for most species that molt after leaving breeding areas, even though such a molt strategy occurs in such widespread Nearctic-Neotropical migrants as Eastern Kingbirds (*Tyrannus tyrannus*; Pyle 1997, Jahn et al. 2013a), Alder Flycatchers (*Empidonax alnorum*; Pyle 1997), and Purple Martins (*Progne subis*; Pyle 1997, but see Niles 1972). Among Nearctic-Neotropical migrant songbirds, almost half (46%) molt at least some remiges and rectrices after leaving breeding areas (Leu and Thompson 2002). Some of these apparently molt during fall migration (at least seven species from five families), others at late summer/fall stopover sites, and yet others molt almost entirely after arriving in wintering areas (Leu and Thompson 2002). Most of these species are rarely collected or banded in their tropical wintering areas, either because those areas are inaccessible (e.g., Amazonia for Purple Martins, and the eastern slope of the Andes for Alder Flycatchers; Ridgely and Tudor 2009) or because migrants are often difficult to collect or capture during the winter because, for example, they perch and fly high most of the time rather than nesting or defending territories (e.g., Eastern Kingbirds; AEJ, pers. obs.).

Likewise, few details are known about the winter molt of Neotropical austral migrants that migrate between south-temperate breeding grounds and tropical wintering grounds in South America (Chesser 1994, Jahn et al. 2004, Cueto and Jahn 2008, Faaborg et al. 2010). One of the most ubiquitous of these is the nominate subspecies of Fork-tailed Flycatcher (*Tyrannus s. savana*; Tyrannidae) that breeds during the austral summer (September–January) from central Brazil to central Argentina (Fitzpatrick et al. 2004, Marini et al. 2009, Jahn and Tuero 2013, Jahn et al. 2014). These populations overwinter in northern South America from April to August (primarily in the Orinoco and northern Amazon River basins; Chesser 1994, Jahn et al. 2013b), where they undergo an annual winter molt (Zimmer 1937, Pyle 1997; Fig. 1), though the

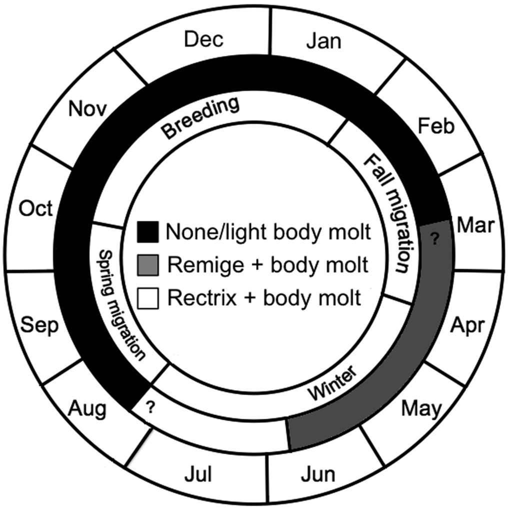

Fig. 1. Annual cycle of the nominate subspecies of Fork-tailed Flycatchers that breed in south-temperate South America, based on measurements taken on captured birds during the breeding season, winter, and from the literature. Timing of breeding may vary slightly, depending on breeding latitude, and some individuals may move during the winter, whereas others remain sedentary. Question marks reflect uncertainty about the exact dates when winter molt begins and ends.

details of their annual molt schedule are still poorly understood (Pyle 1997).

With the goal of improving our understanding of the molt cycle of species in the Neotropical austral migrant system, we studied the molt cycle of the nominate (migratory) subspecies of Fork-tailed Flycatcher. Specifically, we explored the relationship between age, sex, and the timing and intensity of body feather, remige, and rectrix molt of Fork-tailed Flycatchers (hereafter, flycatchers) at two breeding sites, from where flycatchers migrate to overwinter in northwestern South America (Jahn et al. 2013b, AEJ, unpubl. data), where we measured wintering flycatchers.

METHODS

We captured flycatchers during the breeding season (October–January) at Reserva Natural El Destino, Buenos Aires Province, Argentina (35°08′S, 57°24′W), and at La Pampa Province, Argentina (36°48′S, 64°18′W). The Reserva Natural El Destino site is composed of temperate grasslands and seasonal marshes grazed by cattle, intersected by tracts of woodland dominated by *Celtis ehrenbergiana* and *Scutia buxifolia*. We banded flycatchers here during the periods from 9 December 2010 to 11 January 2011, 5 November 2011 to 7 January 2012, 4 November 2012 to 14 January 2013, 8 December 2013 to 25 January 2014, and 3 December 2014 to 14 January 2015. At the La Pampa Province site, we worked on private and public lands south of the city of Santa Rosa, and in Parque Provincial Luro, a public nature reserve. All sites were composed primarily of tracts of *Prosopis caldenia* trees and grasslands with scattered bushes. We banded flycatchers here from 15 to 31 December 2013 and from 29 October 2014 to 21 January 2015.

During the wintering period, we captured flycatchers at Reserva Indigena Wakoyo, Meta Department, Colombia (4°22′N, 71°59′W), and at Arrocera Carimata, Meta Department, Colombia (4°04′N, 73°08′W). At Reserva Indigena Wakoyo, flycatchers roosted in a bamboo grove located in tropical grassland with scattered human dwellings nearby. We banded flycatchers at this roost in early winter (16–18 May 2010 and 30 May 2012). Arrocera Carimata is a rice farm with a roost of several thousand flycatchers. The surrounding landscape was mostly rice fields intersected by windbreaks consisting of low bushes and trees. We banded flycatchers here in early winter from 9 to 12 May 2010 and on 20 May 2010, on 27 May 2012, and during late winter from 28 to 30 July 2009.

Data collection. During the breeding season, flycatchers were captured either by placing a predator model (e.g., Chimango Caracara, *Milvago chimango*, or Striped Owl, *Asio clamator*) or a speaker playing back conspecific calls within 2 m of one or two polyester nets (3 × 12 m or 3 × 18 m, 38-mm mesh size) placed 2–4 m from an active flycatcher nest (i.e., containing eggs or nestlings). During winter, up to six 3 × 12 or 3 × 18 m polyester or nylon nets (38-mm mesh size) were placed from 17:00 to sundown (when flycatchers arrived to roost) 2–6 m from trees used by flycatchers to roost.

Captured flycatchers were banded with an individually numbered metal band or Darvic color bands and processed using techniques described in Ralph et al. (1993) before being released. The winter range of the nominate (migratory) subspecies of Fork-tailed Flycatcher overlaps with that of the resident subspecies *T.*

s. monachus (Fitzpatrick et al. 2004), and we distinguished between the two based on the shape of the primary notch and coloration of the flanks (Pyle 1997). Adults were sexed using the shape of the notch of primary numbers 8–10 (Pyle 1997). Flycatchers were aged based on the presence of juvenile plumage, including lack of yellow crown patch, underparts washed brownish, buff (i.e., juvenile) primary coverts, and the shape of primary feather tips (Pyle 1997, 1998, Jahn and Tuero 2013). The nominate subspecies of Fork-tailed Flycatcher may retain rounded juvenile primaries until the second molt (Pyle 1997). Nevertheless, on the breeding grounds, we rarely captured any birds in their second year that had retained flight feathers, suggesting that juveniles of the nominate subspecies generally molt into complete adult plumage during their first winter. At times, the first primary feather appears older than primaries 2 or 3 in birds in juvenile plumage. Hatch-year birds possibly retain this first primary until their second molt, or young flycatchers may molt the first primary feather at the breeding area, then suspend molt until arriving to the wintering area. To account for our lack of knowledge of the first molt cycle, we conservatively categorized flycatchers with any juvenile plumage as "young" (i.e., those that had not yet completed their second molt), and those without juvenile plumage and with notched primary feathers as "adults" (i.e., those that had already completed their second molt).

Body molt was scored on a 5-point scale: none = no feathers molting, trace = few molting feathers, light = involving more than one feather tract, medium = half of body feathers molting, and heavy = most/all body feathers molting (Ralph et al. 1993). Remige molt was measured by noting which primary (10 per wing in flycatchers; Pyle 1997) and secondary (6 per wing) feathers were molting on each wing. Tail feather molt (12 rectrices) was measured by noting which rectrices were molting (Ralph et al. 1993). Primary feather wear was classified on a 6-point scale: none = no wear, slight = feather edges slightly worn and no fraying/nicks, light = feathers definitely worn with little fraying and few nicks, moderate = considerable wear, definite fraying, and nicks/chips obvious, heavy = very heavily worn/frayed and tips often worn completely off, and excessive = feathers extremely ragged/torn, shafts usually exposed well beyond vane and tips usually completely worn/broken. To estimate the duration of the breeding season (to account for capture rate during the breeding season, see next), we monitored nesting activity during the 2010–2014 breeding seasons at Reserva El Destino, and during the 2013 and 2014 seasons in La Pampa, using methods described in Jahn et al. (2014).

Analyses. To maintain data independence, our analyses were based on initial captures only. To avoid including birds in adventitious molt, we followed Wolfe et al. (2010) and considered flycatchers to be in remige molt when they were actively molting at least one primary on each wing, and in rectrix molt when actively molting at least one rectrix on each side of the tail. Because we sampled flycatchers during early and late winter in different years (see "Methods"), we avoided comparisons between early and late winter, and combined early and late winter data when comparing breeding versus winter seasons.

We evaluated molt timing using chi-square tests to evaluate the proportion of flycatchers with or without remige and rectrix molt in each season (breeding vs. winter), and to compare the proportion of each age and sex with different levels of body molt on a 4-point scale (i.e., combining trace and light categories because there is little difference between the two) in each season (breeding vs. winter).

We compared the progression of remige and rectrix molt among age classes by first calculating the mean primary, secondary, and/or rectrix feather that each bird was actively molting (i.e., in individuals molting at least one primary feather on each wing, and/or at least one rectrix on each side of the tail). Because passerines molt remiges and rectrices from a lower to higher feather number (Ralph et al. 1993), a higher mean molt score indicates a more advanced molt (e.g., a bird molting primaries 8–10 on each wing would have a mean primary molt progression score of 9). We tested for effect of age on the mean primary, secondary, or rectrix molt score in early and late winter using a Mann–Whitney *U*-test in Program R (R Core Team 2013).

We examined possible differences between young and adult flycatchers and between males and females in the intensity of remige and rectrix molt by comparing the mean of the total number of primaries, secondaries, and rectrices actively molting on each individual (e.g., a bird molting primaries 9 and 10 on each wing would have

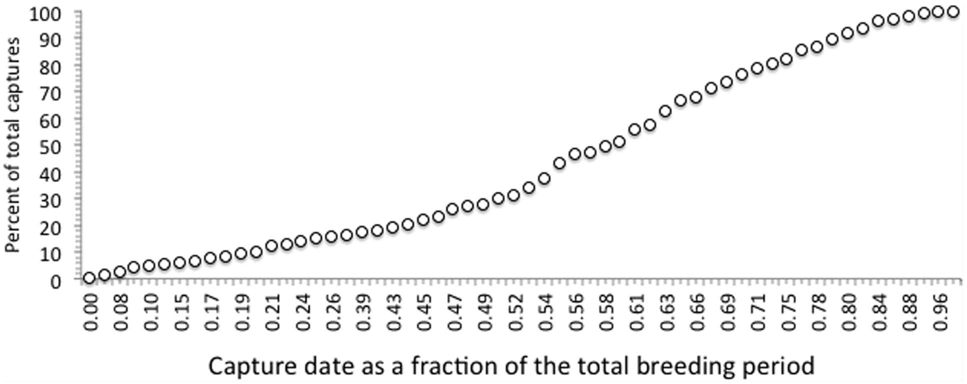

Fig. 2. Cumulative captures during the breeding season expressed as the percentage of total flycatchers captured as a function of the fraction of the breeding season, from the earliest date of capture to the last date on which nestlings fledged, across five breeding seasons (2010–2014) in Argentina.

a primary molt intensity score of 4). We then tested for effect of age on the mean total number of primary, secondary, or rectrix feathers molting using a Mann–Whitney *U*-test in Program R (R Core Team 2013).

Finally, because molt levels could vary throughout the breeding season, uneven temporal sampling of breeding flycatchers (e.g., catching more at the beginning vs. the end of the breeding season) could lead to bias in estimates of molt-breeding overlap. We therefore accounted for capture rate during the breeding season by first calculating the number of days between the earliest capture date in Argentina during our study (29 October) to the capture date of each flycatcher during the breeding season. We divided this number by the duration of the breeding season, defined as the total number of days between 29 October and the latest date on which nestlings fledged during the study (25 January; captures after 25 January were not included in our analysis). This produced a capture date as a fraction of the total breeding season. Finally, we plotted the number of cumulative captures as a function of the fraction of the breeding season (Fig. 2). All values (except percentages) represent means ± SE.

RESULTS

During the breeding season, we captured 129 adult flycatchers at Reserva Natural El Destino and 84 in La Pampa Province, Argentina. Captures throughout the breeding season were constant, with 50% of captures by capture date 0.58 (Fig. 2). We captured 63 young and 72 adults during early winter, and 24 young and 20 adults in late winter in eastern Colombia.

Flycatcher flight molt cycle. We first provide a comprehensive description of the flight molt cycle and molt limits of the nominate subspecies of Fork-tailed Flycatcher, based on our sampling of flycatchers and from the literature. After migrating to northern South America, Fork-tailed Flycatchers begin their annual flight feather molt (flycatchers do not molt flight feathers during the breeding season; Pyle 1997, and data next). By May (early winter), young flycatchers typically sequentially molt P1-3 and adults sequentially molt P1-7. All adults not molting remiges have moderate to heavy levels of primary feather wear. Most (59%) young flycatchers that are not molting remiges in early winter have none to light levels of primary wear. They exhibit lower levels of wear than adults in early winter because this group includes hatch-year birds whose primary feathers are about 4- to 8-mo-old. A few young have begun molting S1 or S2 in early winter and most adults are sequentially molting secondaries up to S6. Some adults and young have begun rectrix molt in early winter, all sequentially. Those not molting rectrices have highly worn tails.

In July (late winter), young flycatchers sequentially molt P8-10, and are also molting secondaries (typically S3-6) sequentially at that time of year. Most adults have finished secondary feather molt by late winter. All young and adults not molting remiges in late winter have no to light levels of primary wear, indicating that

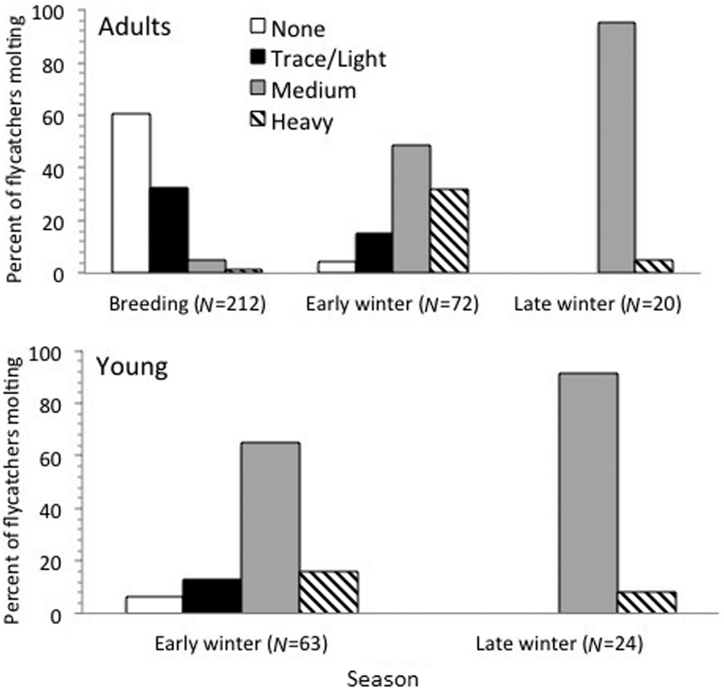

Fig. 3. Proportion of young and adult Fork-tailed Flycatchers molting body feathers during breeding, early winter, and late winter (none = no feathers molting, trace/light = few molting feathers/involving more than one feather tract, medium = half of body feathers molting, and heavy = most or all of body feathers molting).

they have finished primary molt. Rectrix molt is common in late winter, with young sequentially molting R1-6 and adults molting R5 and R6.

Throughout the winter, more proximal primaries and more distal secondaries have less wear than more distal primaries and more proximal secondaries, respectively, with molting feathers in between. Outer rectrices are more worn than central rectrices, with actively molting feathers in between. Combined, these results indicate that this subspecies undergoes one complete annual molt (Fig. 1) in a basic flight molt sequence typical of many passerines where molt proceeds distally in the primaries, proximally in the secondaries, and centrifugally in the rectrices (Jenni and Winkler 1994). Although eccentric molt is common among Tyrannid flycatchers (Pyle 1998), including at least one congener (Western Kingbirds, *Tyrannus verticalis*; Pyle 1998, Barry et al. 2009), our results support Pyle's (1997) preliminary conclusion that Fork-tailed Flycatchers undergo a typical molt after the first year. We cannot rule out the possibility that the wing coverts of the subspecies we studied undergo an eccentric molt, which is common among flycatchers (Pyle 1998), because we did not measure the molt of those feathers. Therefore, our results hereafter focus on the primaries, secondaries, rectrices, and body feathers, excluding primary and secondary coverts.

Proportion of flycatchers molting body feathers. Overall, >60% of breeding flycatchers exhibited no body molt, and >30% had only trace/light levels (Fig. 3). However, during winter, ≥85% of both young and adult flycatchers had at least a medium level of body molt (Fig. 3). Thus, season had a significant effect on body molt ($\chi_3^2 = 268.3$, $P < 0.0001$), but we found no relationship between age and level of body molt during either early ($\chi_3^2 = 5.6$, $P = 0.13$) or late ($\chi_1^2 = 0.0$, $P = 1.0$; Fig. 3) winter.

We found a significant difference in the proportion of adult males and females with different levels of body molt during the breeding season

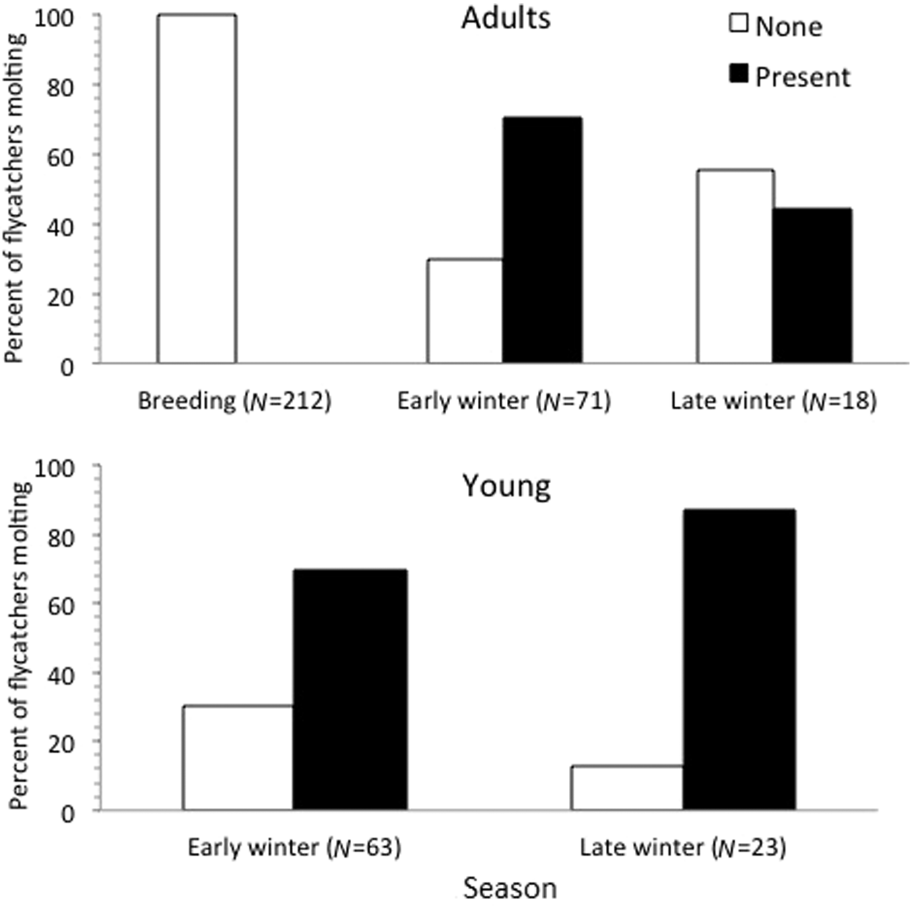

Fig. 4. Proportion of young and adult Fork-tailed Flycatchers molting remiges during breeding, early winter, and late winter.

($\chi^2_3 = 16.1$, $P = 0.001$), with 51% of males exhibiting at least a trace/light level of body molt compared to only 24% of females. This was not due to uneven sampling of each sex throughout the breeding season ($W = 5744.5$, $P = 0.56$). In contrast, we found no difference in the proportion of adults of each sex exhibiting different levels of body molt during winter ($\chi^2_3 = 4.3$, $P = 0.23$).

Proportion of flycatchers molting flight feathers. Neither adult males nor females molted remiges during the breeding season, and we found no difference in the proportion of adult males and females undergoing remige molt in winter ($\chi^2_1 = 0.1$, $P = 0.77$). Similarly, there was no difference in the proportion of each sex molting rectrices during either the breeding season ($\chi^2_1 = 0.9$, $P = 0.35$) or winter ($\chi^2_1 = 1.7$, $P = 0.20$). We therefore combined the sexes into a single category (adult) for further comparisons of remige and rectrix molt between age classes.

Although no adult flycatchers exhibited remige molt during the breeding season (Fig. 4), at least 70% of both young and adult flycatchers molted remiges during the winter (Fig. 4), resulting in a strong effect of season on remige molt ($\chi^2_1 = 227.6$, $P < 0.0001$). In early winter, 70% of each age class molted remiges. However, by late winter, 87% of young, but only 44% of adults, molted remiges, a significant difference ($\chi^2_1 = 6.6$, $P = 0.010$; Fig. 4).

During the breeding season, only 1% of adult flycatchers exhibited rectrix molt, but up to

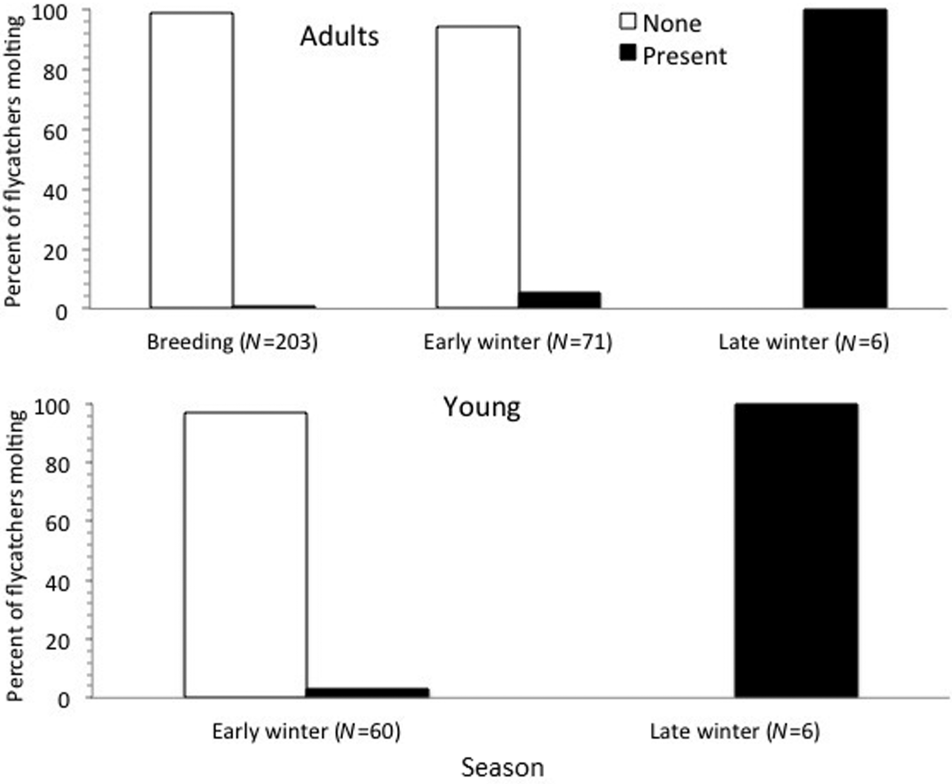

Fig. 5. Proportion of young and adult Fork-tailed Flycatchers molting rectrices during breeding, early winter, and late winter.

100% of young and 86% of adult flycatchers molted rectrices during the winter (primarily late winter; Fig. 5), so there was a significant effect of season on rectrix molt ($\chi_1^2 = 20.9$, $P < 0.0001$). We found no difference in the proportion of each age class molting rectrices in early winter ($\chi_1^2 = 0.04$, $P = 0.84$), when <10% of young or adults molted rectrices. Although late winter sample sizes were small ($N = 6$), 100% of young and adults molted rectrices during that season (Fig. 5).

Intensity and progression of molt. Because ≤1% of flycatchers molted flight feathers during the breeding season (see above), we limited analysis of the progression and intensity of flight feather molt to early and late winter. Sex had no effect on either the intensity of remige molt ($W = 298.0$, $P = 0.59$) or the progression of primary ($W = 300.0$, $P = 0.57$) or secondary ($W = 150.5$, $P = 0.21$) molt during winter, so we combined males and females into one category (adult) for further comparisons of intensity and progression of winter molt. The number of flycatchers molting rectrices in early or late winter was not large enough ($N < 8$) to test for age differences in the intensity and progression of rectrix molt.

We found a significant effect of age on the intensity of remige molt during early winter, with adults ($N = 50$) molting more remiges (mean = 5.0 ± 0.23) than young (mean = 3.5 ± 0.16, $N = 43$; $W = 1635.5$, $P < 0.0001$). However, during late winter, adults ($N = 8$) and young ($N = 20$) molted a similar number of remiges (young mean = 6.1 ± 0.5, adult mean = 5.6 ± 0.46; $W = 73.5$, $P = 0.75$).

Age had a significant effect on the progression of primary feather molt during early winter ($W = 1657.5$, $P < 0.0001$), with adults molting a higher mean primary number (mean = 4.7 ± 0.22, $N = 50$) than young (mean = 3.3 ± 0.26, $N = 44$). During late winter, the progression of primary molt for adults ($N = 8$) and young ($N = 20$) did not differ (young mean = 8.9 ± 0.3, adult mean = 9.6 ± 0.1; $W = 103.0$, $P = 0.21$).

During early winter, the progression of secondary feather molt of adults (mean secondary molting = 2.1 ± 0.2, $N = 29$) and young (1.6 ± 0.3, $N = 9$) did not differ ($W = 165.5$, $P = 0.22$). Sample sizes for late winter were not large enough ($N < 8$) to test for possible age differences in the progression of secondary molt.

DISCUSSION

Overall, our results suggest that body and flight feather molt of migratory Fork-tailed Flycatchers occurs primarily in wintering areas, although we cannot rule out the possibility that young flycatchers may begin molting in breeding areas because we did not sample flycatchers just prior to fall migration. During early winter, the intensity of remige molt was higher and the progression of primary molt was more advanced in adults than young, but, by late winter, there was little difference between age groups.

During both breeding season and winter, we found few differences between males and females in molt timing and intensity. During the breeding season, however, females exhibited less body molt than males. One possible explanation for this is that there is a difference between male and female Fork-tailed Flycatchers in how much they invest in reproduction relative to initiating molt. However, additional studies of the timing of molt by males and females in species that breed in the Southern Hemisphere are needed. Such studies may lend novel insights concerning investment in reproduction by males and females because species that breed at south-temperate latitudes face a different set of biotic (e.g., diet and predation) and abiotic (e.g., climatic) challenges, and also exhibit different life-history traits (e.g., clutch size) than bird species that breed at north-temperate latitudes (Wiersma et al. 2007, Jetz et al. 2008, Robinson et al. 2010, Jahn and Cueto 2012).

The progression of primary molt and intensity of remige molt was more advanced for adults than for young Fork-tailed Flycatchers during early winter, but not late winter. Because the early and late stages of remige molt likely involve different numbers of flight feathers growing simultaneously, adults may have been molting more remiges in early winter because they were at a later stage in the remige molt sequence, whereas young were just beginning remige molt. In contrast, by late winter, the progression and intensity of primary and remige molt were similar for adults and young, likely because young were entering the middle portion of the sequence when molt intensity increases and approaches that of adults. The difference in primary molt of adult and young Fork-tailed Flycatchers in early winter may also explain why more young were still molting remiges in late winter, prior to spring migration. Young Fork-tailed Flycatchers may have to invest more in molting all feather tracts (body feathers, rectrices, and remiges) during late winter to make up for their slower progression of molt earlier in the winter.

Few studies of age-dependent timing of winter molt of migratory songbirds that overwinter in the tropics have been conducted, but the results of those studies have been similar to those in our study. For example, Niles (1972) found that adult Purple Martins (*P. subis*) likely complete winter molt before first-year individuals, and Møller et al. (1995) found that adult remige and rectrix molt was more advanced in adult than juvenile Barn Swallows (*Hirundo rustica*) wintering in Namibia.

Most adult Fork-tailed Flycatchers make a mid-winter movement to a second wintering site (Jahn et al. 2013b), moving through eastern Colombia throughout much of winter (AEJ, unpubl. data). Such movements may track rainfall and food availability (Jahn et al. 2013b) as suggested for other migrants, including Red-backed Shrikes (*Lanius collurio*; Tøttrup et al. 2012), Bobolinks (*Dolichonyx oryzivorus*; Renfrew et al. 2013), and Thrush Nightingales (*Luscinia luscinia*; Stach et al. 2012). Of the adult and young Fork-tailed Flycatchers we sampled, 70% were molting remiges in early winter, so they may undertake mid-winter movements with newly molted remiges, similar to the strategy of Great Reed Warblers (*Acrocephalus arundinaceus*) in Africa (Hedenström et al. 1993, Lemke et al. 2013).

Although based on a small sample size, our results suggest that both young and adults molt tail feathers primarily during late winter. In support of this conclusion, no flycatchers molted rectrices during the breeding season, <10% of young and adult flycatchers molted rectrices during early winter, and tail feathers were highly worn and ragged prior to late winter (AEJ, pers. obs.). In contrast to the heavy investment in body and tail feather molt by Fork-tailed Flycatchers during late winter in our study, congeneric Western Kingbirds begin molting rectrices in late summer and fall (Barry et al. 2009). The timing of tail feather molt by Fork-tailed Flycatchers may be similar to that of Eastern Kingbirds, another congener, which also use two different wintering areas, the first in central South America and, beginning in January, a second area in northwestern South America (Jahn et al. 2013a). Eastern Kingbirds molt flight feathers at the first winter site (Jahn et al. 2013a), but, given that they begin tail feather molt in December (Zimmer 1937), they likely invest in tail feather molt at the second winter site. A potentially fruitful line of research would be to test the hypothesis that timing of winter molt in these species is related to the timing of their winter movements, which, given the energetically expensive nature of molt, may ultimately be driven by spatio-temporal variability in food resources throughout their winter ranges.

For migratory birds that molt during the winter like Fork-tailed Flycatchers, the timing and progress of winter molt might affect other aspects of their annual cycle, such as the timing of spring migration and their reproductive success. As such, a better understanding of the factors that might influence the timing and progress of winter molt, such as food availability, is needed (Danner et al. 2014). Saino et al. (2004) noted a possible relationship between food availability and molt, with Barn Swallows that molted in wintering areas in Africa having longer tail feathers and more advanced breeding schedules after winters with a relatively high normalized difference vegetation index (NDVI). In addition, age-dependent timing of spring arrival in breeding areas has been reported in species that molt during winter, with adults generally arriving earlier than younger birds (e.g., Eastern Kingbirds, Cooper et al. 2009). Such results suggest that the age-dependent differences in timing of winter molt by Fork-tailed Flycatchers in our study, as well as the age-dependent timing of arrival in breeding areas reported for Eastern Kingbirds (Cooper et al. 2009), might be due, at least in part, to age-related differences in winter ecology, such as diet and habitat use (e.g., Sherry and Holmes 1996). Clearly, additional studies of possible age-related differences in the winter ecology of birds that molt during the winter, including possible differences in habitats used and food availability in those habitats and how such differences might influence the timing and progression of molt, are needed.

Given the importance of understanding the annual cycle of migratory birds, we echo previous calls for full life-cycle analysis (Marra et al. 2015), including the duration, extent, and progression of molt (Ryder and Wolfe 2009, Silveira and Marini 2012), with comparisons of such patterns among age classes, populations, and species (e.g., Dietz et al. 2015).

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