THE GRASS IS ALWAYS GREENER: DO MONSOON RAINS MATTER FOR MOLT OF THE VERMILION FLYCATCHER (*PYROCEPHALUS RUBINUS*)?

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ABSTRACT.—Millions of migratory and resident passerines molt in southwestern North America each summer, when ecological productivity spikes in response to the North American Monsoon. Although a monsoon-region molt is a critical event in the annual cycle of many species, the benefits of molting in the monsoon region are unclear. I used museum specimens to compare molt dynamics of the Vermilion Flycatcher (*Pyrocephalus rubinus*) in relation to the timing and location of the monsoon rains, and between northern and southern monsoon latitudes. In the north and the south, populations did not vacate arid non-monsoon areas to molt in adjacent monsoon areas, unlike several other lowland western passerines with more northern distributions. Onset, rate, and intensity of molt were similar between populations in and out of the monsoon region at the same latitude. By contrast, molt started significantly later and was significantly faster at northern latitudes than in the south, suggesting a strong, latitude-based temporal influence on molt dynamics, which was correlated with later nesting in the north. Thus, for this insectivorous passerine, the monsoon region may simply provide adequate habitat for molting at a low latitude, rather than abundant resources important for molt, as has often been proposed to explain the evolution of molt-migration to the monsoon region by western migrants. Similarities in foraging ecology of Vermilion Flycatchers and other western passerines may make these results applicable to other species, helping to clarify the role of the monsoon region in the evolution of molt schedules in North American passerines. *Received 19 November 2012, accepted 16 January 2013.*

Key words: life history, migration, molt, North American Monsoon, *Pyrocephalus.*

El Césped es Siempre Más Verde: ¿Son Importantes las Lluvias Monzónicas para la Muda de *Pyrocephalus rubinus*?

RESUMEN.—Millones de aves paserinas migratorias y residentes mudan cada verano en el suroccidente de Norte América, cuando la productividad ecológica alcanza un máximo como respuesta al Monzón Norteamericano. Aunque la muda en la región monzónica es un evento crítico en el ciclo anual de muchas especies, los beneficios de mudar en esta región no han sido aclarados. Usé especímenes de museo para comparar la dinámica de muda de *Pyrocephalus rubinus* en relación con el ritmo y la localización de las lluvias monzónicas, y entre latitudes al norte y al sur de la región monzónica. En el norte y en el sur, las poblaciones no desocuparon las áreas áridas no monzónicas para mudar en las áreas monzónicas adyacentes, a diferencia de muchos otros paserinos de tierras bajas del occidente que se distribuyen más hacia el norte. El comienzo, la tasa, y la intensidad de la muda fueron similares entre poblaciones dentro y fuera de la región monzónica en la misma latitud. En contraste, la muda empezó significativamente más tarde y fue significativamente más rápida en las latitudes septentrionales que en las meridionales, lo que sugiere una influencia temporal fuerte de la latitud en la dinnica da migratoria en la regimente para explicar la evoluciento recurrente ultos, el volumen de la nidada, las fechas de inámica de la muda. Este patrón se correlacionó con una anidación más tardía en el norte. De este modo, la región monzónica podría simplemente proveer un hábitat adecuado para la muda de este paserino insectívoro en latitudes bajas, en vez de proveer abundantes recursos que son importantes para la muda, como ha sido propuesto frecuentemente para explicar la evolución de la muda migratoria en la región monzónica por parte de los migrantes occidentales. Las similitudes de la ecología de forrajeo de *P. rubinus* con la de otras aves paserinas del occidente podría hacer que estos resultados sean aplicables a otras especies, y ayuda a aclarar el papel de la región monzónica en la evolución de los calendarios de muda en las aves paserinas norteamericanas.

EVOLUTION OF THE timing and location of molt is heavily influenced by the energetic and temporal demands of feather and integument renewal (Murphy and King 1992, Svensson and Hedenström 1999, Barta et al. 2008). In temperate-breeding passerines, the postbreeding (prebasic) molt can span a quarter of the annual cycle (Yuri and Rohwer 1997) and can require a daily energy input of about 50–100% of basal metabolic energy (Murphy and King 1992, Lindström et al. 1993, Hoye and Buttemer 2011). Although time constraints and energy demands are important drivers of successful molt on a proximate level, isolating the relative importance of these influences on the evolution of passerine molt scheduling has been challenging (Rohwer et al. 2005, de la

Hera et al. 2010c). Available food resources usually change predictably over time, but so do other factors that depend heavily on latitude, such as climate, day length (hours available for foraging), and the need to migrate.

Contrasts between passerines of eastern and western North America reveal the importance of energy and time in the evolution of passerine molt schedules. Compared with eastern North America, where precipitation and ecosystem productivity are near their annual peaks in summer, much of the lowland west becomes dry and unproductive in late summer (Rohwer et al. 2005). Correspondingly, whereas nearly all eastern migrants molt on the breeding grounds, many western migrants vacate lowland breeding areas, migrating south to molt in the ecologically productive North American Monsoon region ("molt-migration" to the monsoon region; Rohwer et al. 2005). However, in previous studies of molt dynamics in western passerines, it has been impossible to separate the importance of the abundant food resources in the monsoon region from the location of the monsoon region at a southerly latitude (Rohwer et al. 2005, 2007; Butler et al. 2006; Barry et al. 2009). Thus, molt-migrants may gain energetic resources by moving to the monsoon region (Rohwer and Manning 1990, de la Hera et al. 2012), but they may simply gain time necessary to molt by moving south to a place where it is possible to complete molt before ecological conditions decline (Voelker 2000).

I attempted to isolate the influences of latitude and monsoon-based energetic resources on molt dynamics of the Vermilion Flycatcher (*Pyrocephalus rubinus*), an aerial insectivore with a wide distribution in lowland habitats spanning five climatological regions in southwestern North America. The northern breeding range overlaps the northern monsoon region (Comrie and Glenn 1998), where annual precipitation peaks in late summer (Fig. 1A). Resident and migratory populations also breed west of the monsoon region in the Sonoran and Mojave deserts, which are extremely arid in late summer (Fig. 1A), and they breed east of the monsoon

region, in areas of the Chihuahuan Desert and Great Plains that experience a late-summer nadir in precipitation (Fig. 1A). Finally, residents breed in southern Mexico, in and east of the southern monsoon region (Comrie and Glenn 1998, Ellison et al. 2009). Thus, populations of Vermilion Flycatchers from within, east, and west of the monsoon region offer the opportunity to test for short-distance molt-migration to the monsoon region that is not confounded by long-distance southward movement, and they allow comparisons of molt dynamics between monsoon-based molt of resident populations inside the monsoon region, and non-monsoon-based molt of residents outside the monsoon region, but at the same latitude.

Using museum specimens, I first illustrate the extent of pre-molt movements by small migratory populations breeding adjacent to the monsoon region. If migrants take advantage of monsoon rains for molt, then molters should be rare or absent in migratory parts of the range outside the monsoon region, compared with the frequency of individuals found in those areas prior to molt (Butler et al. 2006, Barry et al. 2009, Pyle et al. 2009). I then compare the timing, rate, and intensity of molt among the five climatological regions described above, to examine the possibility that the monsoon region offers special energetic resources for molting passerines (Rohwer et al. 2005, de la Hera et al. 2012), and to examine the possibility that Vermilion Flycatchers are time-constrained to molt rapidly at the northern end of their range. Monsoon-based energetic resources would be suggested if molt in the monsoon region coincides with or follows shortly after the monsoon rains, and monsoon-molters molt faster (Voelker 2000, de la Hera et al. 2012) and/or more intensely (de la Hera et al. 2011) than molters at the same latitude, but in areas with lower rainfall. Finally, latitude-dependent time constraints would be suggested if molt dynamics are similar among climate regions at the same laititude, but different between northern and southern regions, regardless of monsoon effects.
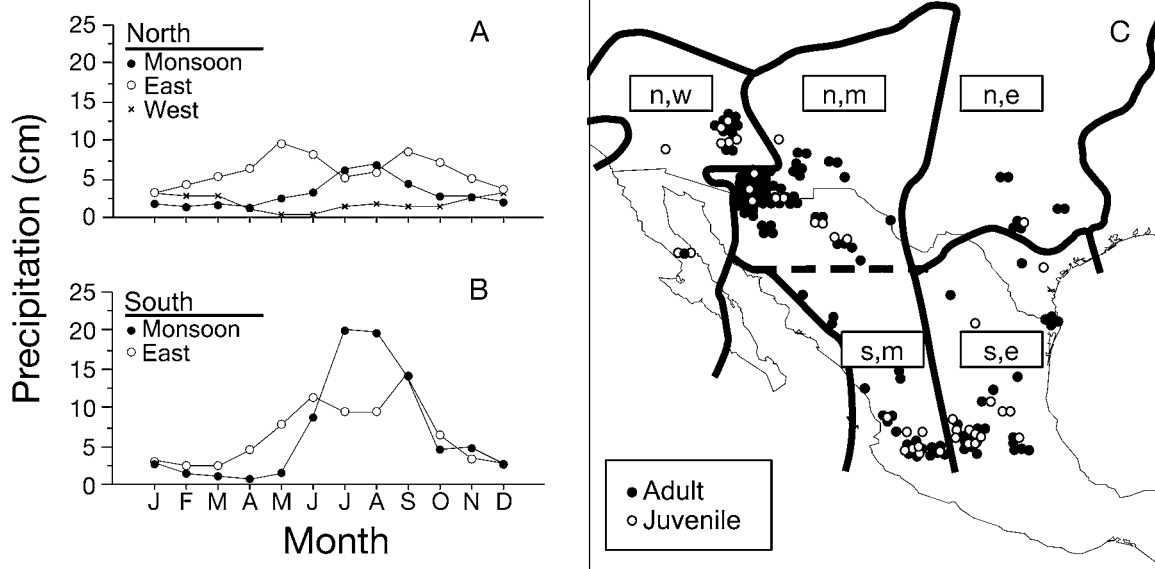

Fig. 1. (A, B) Monthly precipitation in five climatological regions that encompass the breeding and molting ranges of Vermilion Flycatcher populations from this study. (C) Location of Vermilion Flycatchers molting primaries within five latitudinal (n = north, s = south) and climatological (w = west of monsoon, m = monsoon, e = east of monsoon) regions (each dot represents one individual; dashed line indicates 29°N).

METHODS

Specimen data.—Study specimens from Mexico and the United States collected from 1 June to 30 November were initially examined at six ornithological collections (see Acknowledgments). Loans were subsequently requested from eight North American collections (see Acknowledgments) for Vermilion Flycatchers collected in and north of Mexico from 1 June to 31 October. Samples from 1–20 June were used to estimate premolt geographic distributions, and all molters were sampled by late October (see below). In order to relate the onset of molt to the timing of nesting, egg dates were obtained from the Western Foundation of Vertebrate Zoology and downloaded through the ORNIS data portal (www.ornisnet.org) from 10 other collections (see Acknowledgments).

Age, date, and locality criteria.—Individuals hatched in the year they were collected (HYs) were distinguished from after-hatch-year birds (AHYs) on the basis of differences in structure, color, and wear of the body plumage, primary feathers, and wing coverts (Pyle 1997). Hereafter, HYs are referred to as "juveniles" and AHYs are referred to as "adults," and the molts that are described are the preformative molt (juveniles) and the prebasic molt (adults).

Specimens were mapped and dated according to information on the specimen labels. Specimens that lacked complete locality data (~1%) were mapped to the center of their county (United States) or state (Mexico). The study was limited to specimens with complete month-and-day data, from north of 20°N (explained below), that could be assigned unequivocally to one of five defined climatological regions (described below). Altogether, 304 adults and 90 juveniles were included in the study, but sample sizes varied across analyses because not all molt data could be safely collected from all specimens, given the condition of some specimens.

Defining geographic regions.—Specimens were categorized in five climatological regions based on Comrie and Glenn (1998), who used principal component analysis to identify nine climatological regions in southwestern North America between 20°N and 40°N (Comrie and Glenn 1998). Four of these regions, including the North American Monsoon region, overlap the range of the Vermilion Flycatcher (Fig. 1C). The authors also identified four subregions within the monsoon region (Comrie and Glenn 1998: fig. 9), but the three smaller, northern subregions were combined in the present study because they had nearly identical summer rainfall patterns (Comrie and Glenn 1998: fig. 10). The approximate latitudinal boundary (29°N) between this combined northern monsoon region and the southern monsoon region aligned closely with the southern limit of the climatological regions east and west of the northern monsoon region (Fig. 1C). Thus, 29°N was used to delineate northern and southern populations of Vermilion Flycatchers. Relatively few specimens have been collected around 29°N (Fig. 1C), so the position of the north–south boundary at 29°N introduced little sampling bias.

Scoring molt.—Specimens were examined under a lighted magnifier (Dazor MC100; Dazor, St. Louis, Missouri; used for borrowed specimens; various similar models used at collections). The base of each flight feather (primaries [P1–P10], secondaries [S1–S9], and rectrices [R1–R6]) was exposed by lifting or spreading coverts with a needle probe, and then each feather was scored following Rohwer (2008). Old, missing, and new flight feathers were scored as 0, 0.01, and 1.0, respectively, and lengths of growing feathers were estimated to the nearest 5% of their fully grown lengths in order to reflect obvious symmetrical variation in some specimens (e.g., AMNH 56441: R4–R6 = 0.40, 0.45, 0.35).

Molt series, which define the patterns of feather replacement that comprise a given molt, were identified following the iterated method of Rohwer (2008). Molt series start with a "nodal" feather and end with a "terminal" feather, each identified through comparisons to neighboring feathers (e.g., in songbirds, molt of the primaries is usually defined by one series, with P1 = nodal and P10 = terminal). To quantify the progress of molt (molt score) within each flight feather series, the new amount of each feather in the series was summed, divided by the number of feathers in the series, and then multiplied by 100, yielding the percent molt complete (e.g., DMNH 38899: P1–P4 = 1.0, P5 = 0.8, P6 = 0.2, and P7–P10 = 0, percent primary molt complete = 50). The right wing was the major source of wing-molt data, but left wings were examined to ensure that molt was approximately symmetrical. All 12 rectrices were scored on each specimen because adventitious, asymmetrical rectrix loss was common (36% of 285 adults).

Body-molt intensity was estimated in seven body regions (chin, throat, breast, belly, crown, back, and rump; Pyle 1997) following Yuri and Rohwer (1997). A needle probe was used to lift feather tips and expose incoming feathers at three to five places in each body region, and the percentage of feathers growing was categorized as follows: 10% (<20% growing), 30% (21–40%), 50% (41–60%), 70% (61–80%), or 90% (>80%). The 10% category was further split into 1% (1–2 growing feathers) and 5% (about 2–8%), but in order to avoid including adventitious replacement in molt analyses, only birds with scores ≥1% in three areas, or ≥5% in one area, were considered body molters.

Statistical analyses.—Molt of the primaries encompassed molt in the other tracts (see below), so primary molt was used to estimate overall molt dynamics. Adult primary molt scores were initially length-corrected using mean feather lengths of three specimens in fresh plumage (Rohwer 2008). However, compared with raw scores, length-corrected scores changed individual estimates of percent molt complete by <1%, had no effect on statistical significance ($\alpha = 0.05$) of any test, and changed all regional molt-duration estimates by <2 days (<2%). Thus, raw scores were used in analyses because comparable feather lengths for juveniles were unavailable.

Onset and rate of primary molt were estimated using Pimm's regression method (Pimm 1976), treating percent molt complete as the independent variable and day of year as the dependent variable. This method can slightly overestimate absolute molt duration compared with other methods (e.g., Underhill and Zucchini 1988), but Pimm's method (1) is readily applied to test for the kinds of relative population and age class differences that were the focus of the present study (e.g., Heise and Rimmer 2000) and (2) has been widely applied to studies of passerine molt, making estimates from the present study directly comparable to other relevant studies (e.g., Young 1991, Voelker 2000). To test for group-wise differences in molt dynamics, climatological region (e.g., north–east, south–monsoon), latitude group (north or south), or age class (adult or juvenile) were included in the regression model as covariates. A significant covariate indicates a difference in molt onset (elevation of the regression line), and a significant interaction between covariate and percent molt complete indicates a difference in molt duration (slope of the regression line).

Differences in the number of simultaneously growing primaries between northern and southern populations were tested in analyses of variance with independent factors "latitude group" and "most distal growing primary" (because number of growing primaries varies with molt progression; Rohwer 2008). A Mann-Whitney test was used to compare numbers of primaries replaced by juveniles in the north and south. Fisher's exact test was used to analyze differences in the frequency of Vermilion Flycatchers in and out of migratory areas and the monsoon region before and during molt. A chi-square test was used to compare distribution of eggs in bimonthly periods. Molt series details are presented in the Appendix and are summarized below. Two adults from the northern monsoon region ($n = 58$) were omitted from molt dynamics estimates because their residuals were ± >3 SD from the best-fit regression line.

<center>**RESULTS**</center>

Molt series.—In adults, primaries constituted a single molt series, from P1 to P10 (Appendix: Table A1). Secondaries were replaced in three series: S1 to S6, S8 to S7, and S8 to S9 (Table A1). Rectrix molt started at R5 and progressed medially (Appendix: Table A2). R6 appeared to constitute a separate, concurrent molt series (Table A2).

Molt of the secondaries and tail started during growth of P5, when primary molt was 40–50% complete (Fig. 2). Of 11 adults with P5 as the most distal growing primary, only two had started secondary molt, and only one had started tail molt. By contrast, of eight adults molting P6, seven were molting secondaries and all were molting the tail. Tail molt finished slightly before molt of primaries (Fig. 2). All eight adults with primary molt ≥98% complete had finished tail molt but only two had finished outer secondary molt.

Molt series were the same in juveniles, but juveniles replaced a variable number of primaries, often starting at P2 (16% of nodal primaries, $n = 49$), P3 (22%), or P4 (14%), and always proceeding distally (Table A1). Molt started significantly more distally in
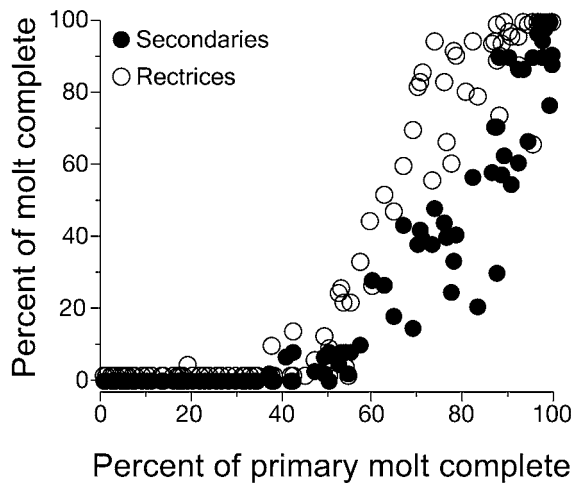
FIG. 2. Progression of molt in the secondaries (S1–S6) and rectrices (R1–R6) in relation to progression of molt in the primaries (P1–P10) of Vermilion Flycatchers. Each dot represents one adult molting in at least one of the flight feather tracts, with all climate and latitude regions combined.

juveniles from the south ($n = 26$) than in those from the north ($n = 23$; $U = 174$, $P = 0.01$; Fig. 3A). Juveniles also replaced a variable number of secondaries 1–6 (Table A2), and nodal secondary was positively correlated with nodal primary ($r_S = 0.68$, $n = 15$, $P = 0.009$; Fig. 3B), which indicates that juveniles that replaced fewer primaries also replaced fewer secondaries.

Body molt overlapped primary molt, with 70% of adults molting at least one body region when P2 was the most distal growing primary ($n = 20$), and all adults molting all body regions when primary molt had progressed to P5 ($n = 11$; Table 1). Comparable juveniles in which molt had progressed to P6 ($n = 5$) were molting in all body regions.

Geographic location of molt.—Vermilion Flycatchers did not appear to undertake premolt movements away from arid, non-monsoon areas. First, contrary to a pattern of premolt movement,
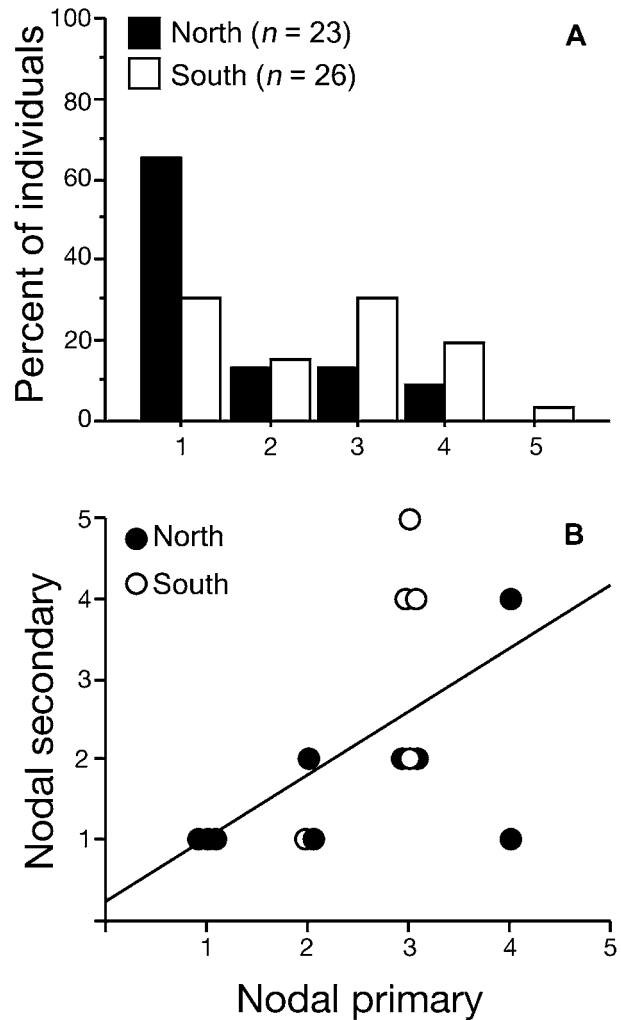
FIG. 3. Variation in the feather that initiated the molt of the primaries or secondaries (nodal feather) among juvenile Vermilion Flycatchers according to latitude group (north or south of 29°N). (A) Proportion of juveniles initiating primary molt among the five inner primaries. (B) Relationship between nodal primary and nodal secondary in juveniles (some points offset horizontally for illustration, but not offset in best-fit line estimate).

TABLE 1. Frequency of adults molting seven body regions in relation to the progression of molt in the primaries of Vermilion Flycatchers (0% values not shown). A few individuals completed molt in some body regions before primary molt (P8–P10 values < 100).

Body region	Most distal growing primary feather							
	1	2	3	4	5	6	7	8–10
Chin	33	55	67	77	100	90	100	98
Throat	33	40	67	92	100	100	100	98
Back		35	56	85	100	100	100	93
Breast		15	67	92	100	100	100	100
Crown	33	10	11	69	100	100	100	100
Rump		10		54	100	100	100	75
Belly		5	22	54	100	100	100	89
n	3	20	9	13	11	10	8	44

adults were slightly more common in migratory, non-monsoon areas of Arizona, New Mexico, and Texas during molt (17% of 122 adults molting primaries, 26 June–4 October) than before molt (10% of 90 adults from 1–20 June; Fisher's exact $P = 0.16$). Second, adults and juveniles were similarly common in the monsoon region before and during molt (71% of 90 premolt adults [1–20 June], 66% of 122 molters, Fisher's exact $P = 0.46$; 67% of 15 premolt juveniles, 44% of 41 molters, Fisher's exact $P = 0.23$). Only one juvenile (7%) was collected in migratory areas before molt ($n = 15$), but two (4.9%) were collected there during molt ($n = 41$).

Geography of molt dynamics.—Onset and rate of molt in adults within the northern monsoon region were intermediate to arid, non-monsoon regions to the east and west (Table 2), and differences among regions were not significant (analysis of covariance [ANCOVA] with region as covariate, factor region: $F = 0.75$, df = 2 and 67, $P = 0.47$; region × percent molt complete: $F = 1.6$, df = 2 and 67, $P = 0.20$; Fig. 4A). Likewise, molt dynamics did not differ between southern adults in and east of the monsoon region (factor

region: $F = 0.27$, df = 1 and 40, $P = 0.61$; region × percent molt complete: $F = 0.10$, df = 1 and 40, $P = 0.75$; Table 2 and Fig. 4B). Sample size of molting adults from east of the northern monsoon region was small ($n = 7$; Table 2), but molt was highly synchronized among individuals ($r^2 = 0.97$; Table 2). Similarly, molt was highly synchronized between adults from migratory and resident areas (Fig. 4A and Table 2).

Adults from the north (three regions pooled) started molt significantly later and completed molt significantly faster than adults from the south (two regions pooled; ANCOVA with latitude group as covariate, factor latitude group: $F = 15.7$, df = 1 and 113, $P < 0.001$; group * percent molt complete: $F = 15.1$, df = 1 and 113, $P < 0.001$; Table 2). Population variation in overall duration was a function of both start and end dates (Fig. 5). Late onset of molt in the north was associated with later nesting in the north than in the south ($\chi^2 = 24.7$, df = 7, $P < 0.001$; Fig. 6).

Northern adults did not appear to complete molt faster than southern adults by growing more feathers simultaneously. The mean number of simultaneously growing primaries was similar between latitude groups (factor latitude group: $F = 0.4$, df = 1 and 80, $P = 0.51$; factor most distal growing primary: $F = 13.9$, df = 1 and 80, $P < 0.001$; Table 2). Overall, the intensity of body and flight feather molt was very similar in southern and northern adults (Fig. 7).

Among the subset of juveniles that initiated primary molt at P1 (and, thus, were comparable to adults), onset and rate of primary replacement were similar between northern and southern regions (factor latitude group: $F = 0.02$, df = 1 and 14, $P = 0.88$; group × percent molt complete: $F = 0.2$, df = 1 and 14, $P < 0.65$; Table 2 and Fig. 4C, D). Molt dynamics were also similar between juveniles and adults within northern and southern regions (ANCOVA with age as covariate, northern region, factor age: $F = 1.8$, df = 1 and 82, $P = 0.19$; factor age × percent molt complete: $F = 0.7$, df = 1 and 82, $P = 0.41$; Fig. 4C; southern region, factor age: $F = 0.05$, df = 1 and 45, $P = 0.82$; factor age × percent molt complete: $F = 0.01$,

TABLE 2. Estimates of the onset, duration, and intensity of molt for Vermilion Flycatchers according to latitude group (north or south of 29°N), climatological region, and age (values ± SE). Onset and duration were estimated using Pimm's (1976) regression method (day of year regressed on percent primary molt complete). Only juveniles that replaced all primaries (as in adults) were included, and only individuals in which molt had not progressed to P10 were included in growing primaries estimates.

| Latitude group Region or age class	Onset (date)	Onset (day of year)	Duration (days)	r^2	n	Mean number of growing primaries (n)
North adults						
West (desert)	17 July	198 ± 3.2	51 ± 0.07	0.88	10	2.4 ± 0.2 (8)
Central (monsoon)	14 July	195 ± 1.5	63 ± 0.03	0.91	56	2.6 ± 0.2 (41)
East (desert–plains)	10 July	191 ± 3.3	68 ± 0.05	0.97	7	2.6 ± 0.3 (5)
South adults						
Central (monsoon)	2 July	183 ± 4.4	78 ± 0.07	0.87	21	2.7 ± 0.2 (16)
East (desert–plains)	5 July	186 ± 2.7	80 ± 0.05	0.94	23	2.5 ± 0.2 (18)
North (regions combined)						
Juveniles	8 July	189 ± 6.3	69 ± 0.11	0.77	13	2.3 ± 0.2 (11)
Adults	14 July	195 ± 1.3	62 ± 0.02	0.91	73	2.6 ± 0.1 (54)
Adults (residents only)	13 July	194 ± 1.6	63 ± 0.03	0.91	54	2.5 ± 0.2 (39)
South (regions combined)						
Juveniles	6 July	187 ± 17.4	80 ± 0.28	0.73	5	2.0 ± 0.0 (4)
Adults	4 July	185 ± 2.5	79 ± 0.04	0.90	44	2.6 ± 0.1 (34)
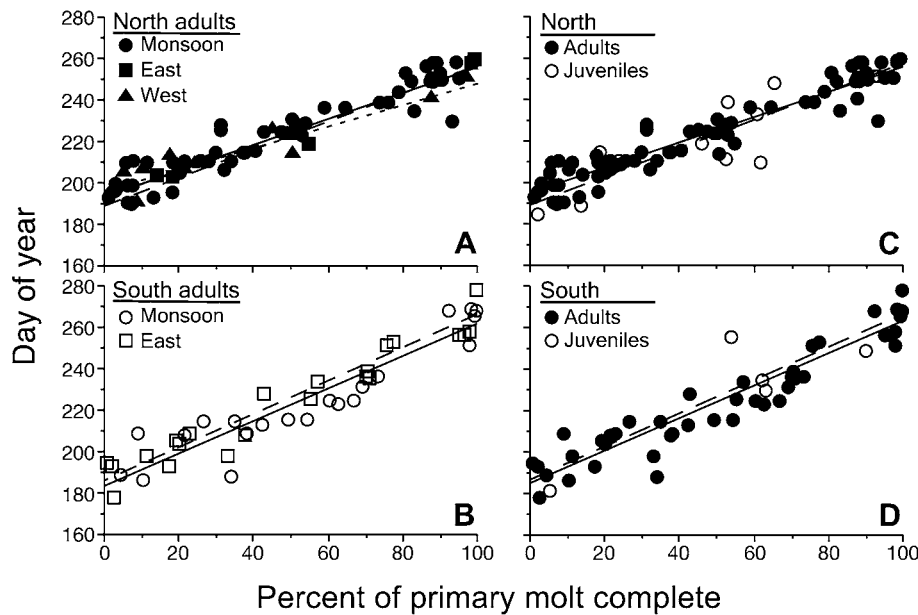
FIG. 4. Pimm's regressions for adult Vermilion Flycatcher according to climatological region within the (A) northern and (B) southern latitudinal regions, and for adults and juveniles in all climatological regions within the (C) northern and (D) southern latitudinal regions (long dash line = east or juveniles, short dash = west).

df = 1 and 45, $P = 0.95$; Table 2 and Fig. 4D), although sample sizes of juveniles were small.

Northern juveniles that initiated molt distal to P1 appeared to be "behind" in molt (i.e., further from completing primary molt at a given day of year) than juveniles that initiated molt at P1. Molt scores of juveniles that initiated molt distal to P1 fell near or beyond the upper 95% confidence limit of the mean of the Pimm's regression of northern juveniles that initiated molt at P1 (Fig. 8), which suggests that distal initiation was characteristic of late-molting juveniles.

DISCUSSION

Population differences in molt dynamics suggest that time is a more important influence than monsoon-related energetic resources for prebasic molt in the Vermilion Flycatcher. The monsoon region did not appear to offer energetic resources that are important for molt but limited elsewhere, because adults from arid breeding grounds east and west of the monsoon region did not appear to vacate those areas to molt; and within the same latitudinal region, molt dynamics were similar between the monsoon region and much drier regions, and between migratory and resident populations. By contrast, molt started later and ended earlier in the north than in the south, both in and out of the monsoon
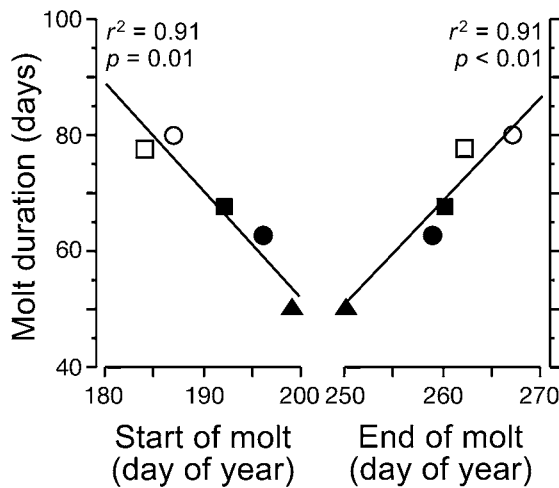

FIG. 5. Estimated duration of adult primary molt in relation to the (A) start and (B) end dates of adult primary molt within the five climate–latitude regions (see Table 2), showing that molt duration is correlated with both a late start and and early finish to molt. Symbol fill indicates latitude group (open = south, closed = north), and symbol shape indicates climate group (circle = monsoon, square = east of monsoon, triangle = west of monsoon).
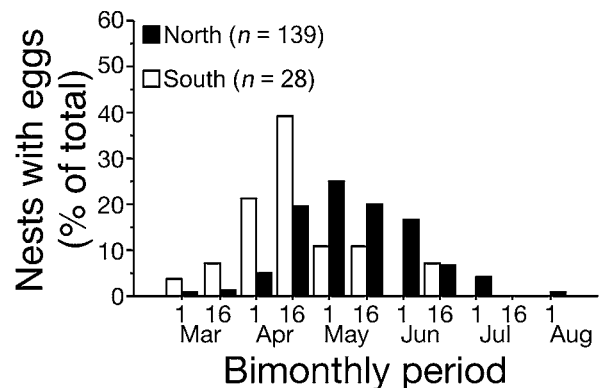

FIG. 6. Frequency of Vermilion Flycatcher nests with eggs according to bimonthly period and latitude group (north or south of 29°N).
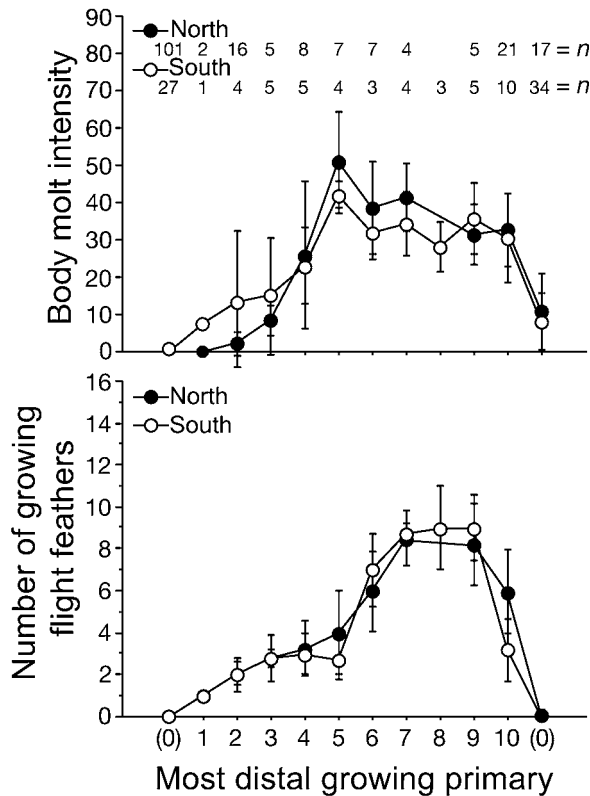
FIG. 7. Variation in body molt intensity (average of seven body regions) and the number of growing flight feathers (wing and tail) of Vermilion Flycatchers in relation to the progress of molt (most distal growing primary) in adults according to latitudinal region (means ± SD; "(0)" indicates birds that had not yet started [<1] or had completed [>10] primary molt).
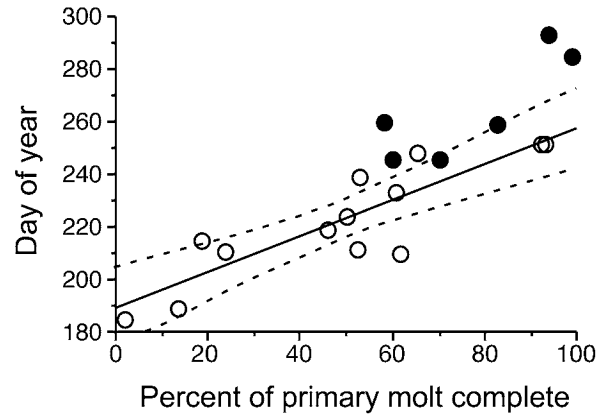

FIG. 8. Pimm's (1976) regression and 95% confidence interval of the mean for juvenile Vermilion Flycatchers from the northern latitudinal region that initiated primary molt at P1 (open circles). Not included in the regression estimates are northern juveniles that started molt distal to P1 (closed circles).

region, which suggests that latitude-based temporal constraints, driven in part by later nesting in the north, influenced molt dynamics in Vermilion Flycatchers.

Clearly, energetic and nutritional resources are important for molt in birds (Murphy and King 1992, Lindström et al. 1993, Barta et al. 2008), and resource availability changes over time. However, both energy and time have often been proposed to explain the evolution of molt-migration to the Mexican monsoon region, and it has previously been difficult to separate possible benefit(s) of molting in the monsoon region. If there is an energetic benefit to Vermilion Flycatchers molting in the monsoon region, the benefit does not take the form of faster molt (Voelker 2000, 2004; Butler et al. 2002; de la Hera et al. 2012). Alternatively, perhaps monsoon-molters produce higher-quality feathers than non-monsoon-molters (Butler et al. 2006). If so, it is hard to explain why flycatchers from outside the monson region did not appear to move there for that benefit, because molt scheduling seems to be evolutionarily labile (Rohwer and Irwin 2011), and several other flycatchers molt after migration (Rohwer et al. 2005, Butler et al. 2006, Barry et al. 2009). Carlisle et al. (2012) found no relationship between food abundance and the energetic condition of western migrants during stopover farther north, and the monsoon region may function similarly, by providing food resources that are sufficient for molt and in a convenient location.

The idea that time is an important factor in the Vermilion Flycatcher's molt scheduling agrees with evidence from other migrant tyrannids of North America. Approximately 75% of all northern tyrannids molt only after moving south to stopover or wintering areas (Rohwer et al. 2005), with notable exceptions. The foraging habits of Say's Phoebes (*Sayornis saya*) and Eastern Phoebes (*S. phoebe*) allow them to arrive in the north earlier in the spring and depart later in the fall than all other tyrannids and many other passerines (Schukman and Wolf 1998, Weeks 2011). Hammond's Flycatcher (*Empidonax hammondii*) overlaps breeding and molt (Johnson 1963), and the Acadian Flycatcher (*E. virescens*) has an intense molt (Mengel 1952), perhaps supported by leaf-gleaning (Whitehead and Taylor 2002) when missing feathers make flycatching inefficient.

The results of the present study may help to understand the molt schedules of other western migrants. Most adult Ash-throated Flycatchers (*Myiarchus cinerascens*; Butler et al. 2006) and Western Kingbirds (*Tyrannus verticalis*; Barry et al. 2009) vacate northern breeding grounds and migrate south to the monsoon region to molt. Ash-throated Flycatchers require ~75 days to molt in western Mexico (approximately 20–32°N; Butler et al. 2006), and Western Kingbirds require ~70 days to molt in southern Arizona (~32°N; Barry et al. 2009). These estimates are similar to estimates for Vemilion Flycatcher populations (62–79 days), but all three are much longer than other monsoon-molters that forage by gleaning or ground-picking (49-day average of four species with published Pimm estimates; Butler et al. 2006). Molt duration in Ash-throated Flycatchers was hard to explain because it was the longest molt reported for any monsoon molt-migrant at the time, contradicting the hypothesis (Voelker 2004) that abundant resources in the monsoon region allowed for a rapid molt (Butler et al. 2006). However, previous studies of monsoon molters were unable to isolate the benefits of moving south from the benefits of moving into the monsoon region. Assuming that molt scheduling in Vermilion Flycatchers is influenced by factors similar to those found in other flycatchers, the results of the present study suggest that, for aerial insectivores that move south to molt in the monsoon region, gaining time may be more important than gaining monsoon resources. Time may also explain why, within some other western migrant species, small numbers of early-molting

adults are able to molt in the north, whereas most later-molting individuals molt in the south (Young 1991, Butler et al. 2002, Barry et al. 2009).

Consequences of molting too rapidly may underlie the evolution of molt-related movements by migrant passerines (Nilsson and Svensson 1996, Dawson et al. 2000, Hall and Fransson 2000). Rapid molt can be achieved by growing many feathers simultaneously (Dawson 2004), but gaps in the wings reduce flight performance (Swaddle and Witter 1997, Hedenström and Sunada 1999), and rapid molt yields low-quality feathers (Dawson 2004, de la Hera et al. 2010a). Slow molt in the south may allow for more efficient flight during molt, and the production of higher-quality feathers, than a faster northern molt. The feather-quality hypothesis could be tested by comparing feathers from birds that molted in and out of the monsoon region, recognizing that investment in feathers can be allocated differently among (de la Hera et al. 2010b) and within (Dawson 2003) feather tracts.

More extensive molt in northern juveniles seems to contradict time-based explanations for molt dynamics in adult flycatchers, but this pattern seems to be common to multiple flycatcher species (Johnson 1974). Johnson (1974) proposed that longer migration of northern juveniles favored replacement of more juvenal feathers. Mulvihill and Winstead (1997) suggested that the extent of molt in juveniles depends on the degree of wear of the feathers in the first year. Both possibilities could be explained if juvenal feathers are of lower quality than adult feathers, because of a tradeoff made by nestlings between investing in juvenal feather quality and investing in structures that promote rapid fledging (Butler et al. 2008). Juvenile Vermilion Flycatchers that start molt more distally appear to be behind in molt compared with other juveniles at the same molt stage (Fig. 3B), so the extent of wing molt appears to depend on when the molt started.

Molt of the tyrannid flycatchers may be more completely described than any other large family of North American passerines (Hussell 1980, 1991, and other references herein). As a group, flycatchers represent a foraging guild somewhat intermediate to substrate-based gleaners (e.g., warblers and sparrows) and coursing aerial insectivores (swallows). Ignoring phylogenetic constraints on the evolution of molt scheduling (which appear to be weak; Rohwer and Irwin 2011), interspecific and interpopulation variation in flycatcher molt dynamics suggest that flycatching favors slow molt, which means that breeding at northern latitudes requires moving before molting, or another specialized strategy (e.g., molting while nesting, as in Hammond's Flycatchers). The results of the present study suggest that flycatchers, and perhaps other western migrant passerines, may benefit primarily from extra time, and not extra energetic resources, provided by moving south to molt in the Mexican monsoon region.

Acknowledgments

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Appendix: Identifying Molt Series

In adults, P1 was dropped before S1 in 98% of informative pairs (n = 50), and molt had progressed through at least P2 in all birds with growing S1, so S1 was inferred to be the nodal secondary of a secondary molt series that progressed proximally, typically terminating at S6 (80% of 20 terminal assignments in S5 or S6; Table A1). S6 was inferred to terminate the S1–S6 series because of the strong directionality from S5 to S6 (83% of 23 directional assignments; Table A1), and because S7 molted before S6 in all 37 informative neighbor pairs. S8 was the node for two series in the wing, terminating at S9 and S7 (Table A1). Similar reasoning applied to juveniles (Table A1).

Juveniles usually started primary molt distal to P1. Of 44 juveniles in active primary molt, 6 (14%) had an actively growing nodal primary between P2 and P4 (Table A1), and 10 (23%) had a new, fully grown P2, P3, P4, or P5 with a juvenal, proximal neighbor, indicating nodes distal to P1. Altogether, 55% of juveniles (n = 49, including those that had completed molt) started primary molt distal to P1. Once started, primary molt only proceeded distally: of the 26 juveniles that initiated molt distal to P1, only one (a P2) had a proximal nodal neighbor (P1) that was newer and actively growing, but the difference was small (0.1), indicating near-simultaneous replacement. By contrast, 9 of these 26 juveniles had a distal nodal neighbor that was newer and actively growing.

Replacement of the tail was intense, with 42% of adult tail molters replacing >6 rectrices simultaneously (n = 52). This resulted in nodal assignments at multiple follicles, with R5 and R6 as dominant nodes (Table A2). Although R6 was nodal in 22% of adult nodal scores (n = 18), R6 was terminal with similar frequency (27% of terminal scores; n = 48), and replacement from R5 to R1 was strongly centripetal between R5 and R1 (Table A2). Therefore, one tail series was inferred to start at R5 and end at R1, and R6 was inferred to constitute a second, separate series in the tail, because replacement of R6 started before or at the same time as replacement of R5 with high frequency (43% of 23 informative individuals; Table A2). Similar reasoning applied to juveniles (Table A2).

Table A1. Number of feathers (below feather numbers) and feather pairs (between feather numbers) used to infer replacement series in the primary and secondary feathers of adult and juvenile Vermilion Flycatchers. Shaded columns mark inferred locations of breaks between replacement series. Nodes were inferred in juveniles if the focal feather was new and the proximal (P1–P4) or distal (S1–S3) feathers were juvenal.

Assignment	Primary										Secondary								
	10	9	8	7	6	5	4	3	2	1	1	2	3	4	5	6	7	8	9
Adults																			
Nodal	2									35	23							24	2
Directional →		2										23	23	20	25	19		1	28
Directional ←		38	39	40	35	37	37	41	44	35					4			34	2
Nondirectional		1								5					1				2
Terminal	38	2													4	16	34		
Number growing	31	36	30	24	22	28	29	28	36	36	13	16	17	12	17	20	17	21	23
Juveniles																			
Nodal							2	2	2	3	2			2	1		2	10	
Nodal (inferred)						1	5	9	6	19	6	4		1					
Directional →												8	6	7	9	6		3	12
Directional ←		14	15	21	19	20	16	7	5	3			2	1				16	
Nondirectional																			
Terminal	14															5			12
Number growing	12	12	15	11	15	13	8	5	4	4	5	5	2	8	6	5	11	12	8

TABLE A2. Number of feathers (below feather numbers) and feather pairs (between feather numbers) used to infer replacement series in the rectrices of adult and juvenile Vermilion Flycatchers. Shaded columns mark inferred locations of breaks between replacement series.

Assignment	Rectrix										
	1		2		3		4		5		6
Adults											
Nodal	3				1		1		9		4
Directional ←		33		31		24		16			
Directional →		3				1		2			
Nondirectional		2		4		4		6			
Terminal	33		1[a]				1[b]				13
Number growing	32		31		27		25		24		23
Juveniles											
Nodal									3		3
Directional ←		14		12		8		6			
Directional →				1				1			
Nondirectional		1				1		1			
Terminal	14								1		3
Number growing	11		10		10		8		8		10

[a] 0.1 < R1.
[b] 0.05 < neighbors.