ORNITOLOGIA NEOTROPICAL 20: 565–584, 2009

MOLT BIOLOGY OF RESIDENT AND MIGRANT BIRDS OF THE MONSOON REGION OF WEST MEXICO

Vanya G. Rohwer[1,3], Sievert Rohwer[1], & Marco Fabio Ortiz Ramîrez[2]

[1]Department of Biology and Burke Museum, Box 353010, University of Washington, Seattle, WA 98195, USA. *E-mail*: 6vgr@queensu.ca

[2]Museo de Zoología "Alfonso L. Herrera" Facultad de Ciencias, Universidad Nacional Autónoma de México, Apartado postal, 70-399, 04510 México, D.F., México.

Resumen. – Biología de la muda de plumas de aves migratorias y residentes de la región monzónica del oeste de México. – El remplazo anual de las plumas (muda) es el evento clave en el ciclo de vida de las aves. En este trabajo describimos la duración e intensidad de la muda de las plumas primarias de 12 especies de aves del oeste de México. Durante el trabajo de campo encontramos que algunas de éstas especies mudan sus plumas de vuelo en las mismas fechas en que se reproducen (traslapan muda y reproducción) y son el *Pachyramphus aglaiae*, *Auriparus flaviceps*, *Saltator coerulescens* y *Aimophila carpalis*, y probablemente también *Melanerpes uropygialis*. Para comparar la muda entre las especies se hicieron regresiones con 1) Los estimados de la duración de la muda de las plumas primarias contra el tamaño del cuerpo y 2) Los estimados de la intensidad de la muda de las plumas primarias contra el tamaño del cuerpo. La duración de la muda de las primarias se incrementa ligeramente conforme aumenta el tamaño del cuerpo, aunque no es una diferencia significativa. Las especies que traslapan su muda y reproducción, reemplazan aproximadamente 10% menos plumas a la vez (aproximadamente una pluma menos) que las especies que no traslapan la muda y la reproducción. Finalmente, comparamos la intensidad de la muda (el número de plumas primarias reemplazadas simultáneamente) y la duración de la muda de las plumas primarias para mostrar que la duración de la muda fue inversamente proporcional a la intensidad de la muda. De acuerdo a nuestro conocimiento, éste es el primer análisis comparativo que muestra que las especies que reemplazan más plumas simultáneamente requieren menos tiempo para mudar.

Abstract. – The annual replacement of feathers (molt) is a key event in the avian life cycle. We describe the duration and intensity of the primary feather molt in 12 resident birds of west Mexico and eight Neotropical migrant birds that molt in the monsoon region of west Mexico. During our fieldwork, we found evidence of flight feather molt occurring at the same time as reproduction (molt-breeding overlap) in four resident species, Rose-throated Becard (*Pachyramphus aglaiae*), Verdin (*Auriparus flaviceps*), Grayish Saltator (*Saltator coerulescens*), Rufous-winged Sparrow (*Aimophila carpalis*), and likely in Gila Woodpecker (*Melanerpes uropygialis*). To compare molts between species, we regressed 1) estimates of primary molt duration on body size and 2) estimates of primary molt intensity on body size. Duration of primary molt increases slightly, but not significantly, with body size. Birds that overlap primary molt and breeding replace approximately 10% fewer feathers at once (about 1 feather less), than birds that do not overlap molt and breeding. Finally, we compare primary molt intensity (the number of primaries molted simultaneously) and primary molt duration to show that molt duration was inversely related to molt intensity. To our knowledge, this is the first comparative analysis to show that the time required to replace the

---

[3] *Current address:* Department of Biology, Queen's University, Kingston, ON K7L 3N6, Canada.

primaries is inversely related to the number of primaries growing simultaneously in species that fly while molting. *Accepted 19 October 2009.*

Key words: Molt, molt-breeding overlap, molt intensity, molt-migration, monsoon, west Mexico, Pimm regressions.

INTRODUCTION

Molt is an important factor in avian life histories because it is an energetically demanding and time consuming process that birds must undergo annually (Murphy & King 1992, Langston & Rohwer 1996, Voelker & Rohwer 1998). Comparative analyses suggest that constraints on feather growth rate force flight feather replacement to be time demanding and that the evolution of large body size in birds is facilitated by replacing the primaries either simultaneously or in multiple waves (Rohwer *et al.* 2009). While body size is an important factor in molt strategies, comparing the molts of tropical and temperate species is likely to offer further insight into the evolutionary pressures that affect the timing, duration and intensity of molt. For example, we might expect differences in the timing, duration and intensity of molt between temperate and tropical birds because tropical and temperate species represent extremes along a continuum of variation in life history strategies and selective pressures. However, such comparisons will have little generality until the molts of more tropical species are described.

For over a decade, the monsoon region of northwestern Mexico has been recognized as an important molting site for many western Neotropical migrants (Young 1991, Bulter *et al.* 2002, Voelker 2004, Rohwer *et al.* 2005). Forests in this region are exceedingly seasonal with a long dry period lasting most of the year; during this time the deciduous forest is mostly leafless. During July–September the monsoon region of northwestern Mexico receives the bulk of its annual precipitation (Comrie & Glenn 1998). Following these late summer rains, the forest quickly greens and generates a flush of productivity. Species that move to the monsoon region to molt are thought to be attracted to the flush of insects and seeds that provide abundant food for growing new feathers (Rohwer *et al.* 2005). While our understanding of the temperate migrants that move to this region to molt has progressed dramatically in the past decade, little research has been directed at the resident species of the monsoon region, many of which use the seasonal rains both to breed and to molt.

Here we examine the timing, duration and intensity of primary molt in 12 resident species and eight western molt-migrants, all of which molt in the monsoon region of coastal Sinaloa and Baja California Sur, Mexico. We describe the Lark Sparrow (*Chondestes grammacus*) as yet another molt-migrant that breeds in the USA and Canada and moves to this region for its annual molt. We treat each species in a separate account and then synthesize our molt data by: 1) comparing the duration of primary molt to body size, 2) by relating the intensity of primary molt (scored as the percentage of primaries growing simultaneously) to body size and to whether species do or do not overlap molt and breeding, and 3) by relating the peak intensity of primary molt to its duration. For our first comparison, we predicted that larger species should have longer molt durations than smaller species because the summed length of the primary feathers increases with body size almost twice as fast as the growth rate of primary feathers (Rohwer *et al.* 2009). Because primary growth rate fails to increase with body size as fast as primary length, larger birds should require more time to molt. For our second comparison, we predicted that larger species should grow more primaries simultaneously because larger birds typically take longer to molt (Rohwer *et al.* 2009) and because the time during which sufficient food is available to molt is limited in the annual cycle. Growing more primaries simultaneously should minimize the time required to molt (Prevost 1983, Rohwer 1999) and Dawson (2004) has confirmed this prediction experimentally with European Starlings (*Sturnus vulgarius*). For our third comparison, we predicted that species that replace more primaries simultaneously should have shorter molt durations than expected for their body size.

METHODS

Expeditions. In 2005, we surveyed the coastal lowlands of Sinaloa, Mexico during 17–30 July and 10–11 August, and in Baja California Sur from 1–9 August. In 2006, we surveyed in coastal Sinaloa from 8 July–25 August and 5–6 September and in Baja California Sur from 27 August–4 September. In 2007, we made two trips to northern Sinaloa during 4–31 July and 7–25 September. In 2009 we worked in coastal Sinaloa from 25 July–24 August. During these expeditions to west Mexico we focused our surveys in low elevation (100 m) thorn forest and riparian zones and in low elevation (< 500 m) tropical deciduous forest. For all our netting effort, we used 12 m mist nets that were open in the early mornings and closed in late morning or early afternoon during high temperatures; the number of nets setup varied by day and by study site but was usually about 6 nets.

Scoring molt. We used museum specimens and birds that were netted and released to estimate the duration and intensity of primary molt. Molt scoring followed Yuri & Rohwer (1997), wherein old feathers = 0, newly replaced feathers = 1, missing feathers (in a sequence) = 0.01, and growing feathers were assigned fractional estimates of their full length; a feather that was 80% of full length received a score of 0.8. Feathers that were nearly full length, but still retained sheathing at their bases, were scored as 0.95. All species treated here have simple descendent molt, where molt begins with primary one (P1) and proceeds distally to the outer-most primary. Thus a hypothetical bird might read: 1, 1, 0.9, 0.6, 0.3, 0.01, 0, 0, 0; where P1–2 are new, P3–5 are growing, P6 is missing, and P7–9 are old. The summed primary molt score would be 3.81 out of 9. A molt score of 0 indicates that molt has not begun, while a score of 9 indicates completion for a passerine with nine primaries.

When we were unsure of the length that fully grown feathers would achieve, we measured the length of growing feathers and later converted these lengths into appropriate fractions after measuring feather lengths on a wing that was not in molt. While direct measurements of feather length would be more precise than our fractional scores, measuring lengths is impractical in the field and damaging to traditional museum specimens.

Estimating molt duration. We estimated the duration of the primary molt using Pimm (1976) regressions, where date (measured as day of year) is regressed on molt score. The y-intercept represents the mean start date of primary molt and multiplying the regression coefficient by the number of primaries gives the average duration of primary molt for individuals in that population. We provide one regression plot as an example and for other species we summarize molt durations in Table 1.

Pimm (1976) estimates of molt duration have been criticized because this method assumes that all feathers within the wing are equal in size (Underhill & Zucchini 1988). However, Butler *et al.* (2006) accounted for differences in feather lengths of a migrant flycatcher by converting factional estimates of feather length to mm lengths, thus better accounting for differences in feather size. Butler *et al.* (2006) found a difference of only one-day between these two methods of estimating primary molt duration. Further, using Pimm (1976) regressions makes our estimates of molt durations comparable with most duration estimates published for North American passerines.

Two species, Gila Woodpecker and Verdin (see species account for scientific names), have short, vestigial tenth primaries. We treated both species as if they had nine primaries in our duration estimate because P10 achieves it full length prior to P9. Nutting's and Ash-throated Flycatchers look strikingly similar; these species were distinguished from each other by the color of their mouth linings (Lanyon 1961). Because juveniles of these two flycatchers undergo a complete molt of their primaries, we distinguished between age classes by examining for retained juvenal plumage, primary coverts, and by examining wear in the outer primaries (Pyle 1997).

Unless otherwise noted, our estimates of molt duration for each species include adults but exclude hatch-year birds because the latter often molt later than adults and may fail to replace several of their inner primaries in their first molt, if they replace any at all (Pyle 1997). Because molt scheduling may differ between age or sex classes and because we were not always able to distinguish age and sex, the sample composition varied by species and is noted in each species account.

Scoring molt intensity. There is a growing body of evidence suggesting that birds decrease the time required to molt by growing more feathers at once (Hall & Fransson 2000, Ryder & Rimmer 2003, Dawson 2004), rather than increasing the rate at which feathers grow (Prevost 1983, Rohwer 1999, Rohwer *et al.* 2009). Thus the number of feathers growing simultaneously provides an index of the intensity of molt. Following Yuri & Rohwer (1997), we grouped our molt intensity scores according to the outermost growing primary. Because the primaries are replaced in sequence from innermost (P1) to outermost (P9 or P10), intensity typically increases steadily over the first few primaries replaced, reaches a peak or plateaus in the middle primaries and then declines when the outermost primary is nearly grown. To correct for this variation in intensity over the course of molt, we plotted the percentage of primaries growing simultaneously against the outermost growing primary. For each plot, we used STATVIEW 5.0 to fit a loess curve with the tension set to 80. We then used the number of primaries growing simultaneously at the peak or plateau of these loess curves as our measure of molt intensity for each species. This approach has the advantage of making use of all available data, but is inappropriate if birds are not in the middle of their primary molt when intensities peak (often between P4 and P7 for species with intense primary molts). We considered primaries scored as 0.95 as fully grown for our estimates of molt intensity because primary growth rates slow considerably when feathers are nearly fully grown (Dawson 2004). We considered missing feathers to be growing if the missing feather should have been the next feather to be replaced. Feathers lost out of sequence were excluded because they were likely lost adventitiously. We present only a single plot of molt intensity to show how intensity changes throughout the wing and to illustrate how we estimated molt intensity.

Assessing molt-breeding overlap. Molt-breeding overlap was challenging for us to document because we were not recapturing marked individuals and finding their nests. For netted

TABLE 1. Summary of the timing, duration, and intensity of primary molt for the eight molt-migrant and 12 resident species of northwestern Mexico examined in this study. Primary molt duration estimates follow Pimm (1976). Primary molt intensity is scored as the percentage of primaries replaced simultaneously. [1]Primary molt duration likely underestimated see species account for details; [2]used adult males only; [3]preliminary estimate; *age classes combined; "n.a." indicates too few individuals to estimate primary molt duration.

Species	Category	Duration (days)	Average start–end dates	Molt intensity
Ash-throated Flycatcher (*Myiarchus cinerascens*)	Molt-migrant	75 (n = 40)	19 July–27 Sept	25% (n = 40)
Western Kingbird (*Tyrannus verticalis*)	Molt-migrant	70 (n = 58)	19 July–27 Sept	35% (n = 58)
Lucy's Warbler* (*Vermivora luciae*)	Molt-migrant	67 (n = 41)	12 July–7 Sept	26% (n = 41)
Western Tanager (*Piranga ludoviciana*)	Molt-migrant	46 (n = 19)	12 Aug–27 Sept	34% (n = 19)
Black-headed Grosbeak (*Pheucticus melanocephalus*)	Molt-migrant	68[1] (n = 21)		44% (n = 21)
"Western" Painted Bunting[2] (*Passerina ciris pallidior*)	Molt-migrant	43 (n = 58)	13 Aug–25 Sept	40% (n = 43)
Lark Sparrow (*Chondestes grammacus*)	Molt-migrant	62 (n = 14)	2 Aug–1 Oct	35% (n = 14)
Bullock's Oriole (*Icterus bullockii*)	Molt-migrant	47 (n = 20)	22 July–7 Sept	35% (n = 20)
Gila Woodpecker* (*Melanerpes uropygialis*)	Resident Overlap	85 (n = 36)	6 July–29 Sept	25% (n = 36)
Rose-throated Becard (*Pachyramphus aglaiae*)	Resident Overlap	n.a.		26% (n = 3)
Nutting's Flycatcher (*Myiarchus nuttingi*)	Resident	61 (n = 22)	8 July–7 Sept	34% (n = 22)
Bell's Vireo* (*Vireo bellii*)	Resident	n.a.		27% (n = 13)
Verdin (*Auriparus flaviceps*)	Resident Overlap	94 (n = 21)	16 June–18 Sept	28% (n = 21)
Sinaloa Wren (*Thryothorus sinaloa*)	Resident	n.a.		26% (n = 4)
Northern Cardinal (*Cardinalis cardinalis*)	Resident	98[3] (n = 11)	25 July–31 Oct	33% (n = 11)
Grayish Saltator (*Saltator coerulescens*)	Resident Overlap	n.a.		28% (n = 5)
Varied Bunting (*Passerina versicolor*)	Resident	n.a.		42% (n = 14)
Rufous-winged Sparrow (*Aimophila carpalis*)	Resident Overlap	n.a.		18% (n = 5)
Streak-backed Oriole (*Icterus pustulatus*)	Resident	50 (n = 37)	31 July–19 Sept	37% (n = 37)[3]
House Finch (*Carpodacus mexicanus*)	Resident	67 (n = 32)	28 June–3 Sept	33% (n = 32)

birds, we inferred the breeding status of males by assessing cloacal protuberance and the breeding status of females by the condition of their brood patch. For collected males, breeding status was assessed by measurements of the testis and of the seminal vesicles, which create the cloacal protuberance. For collected females, we assessed breeding status from the size of developing follicles or of regressing post-ovulatory follicles, from the size and condition of the oviduct, and from the condition of the brood patch. Females of small to medium-sized passerines that have follicles larger than 3 mm are generally about to lay, and any female with visible ruptured follicles will have just completed laying (Pearson & Rohwer 1998). Females with edematous (watery) brood patches are incubating. These methods underestimate the number of breeding females by at least two-fold because the brood patch dries up shortly after young hatch and postovulatory follicles can only be seen for a few days. Thus females with bare, dry brood patches could be feeding nestlings or fledged young, but they can equally as well have been captured between broods or between breeding attempts.

Given these criteria for assessing breeding condition, molt-breeding overlap is easily recognized in individuals if they are replacing primaries at the same time that they show evidence of active reproduction. Due to the time demands of our fieldwork we could only consider primary replacement in our assessment of molt and breeding overlap.

Synthesis of molt data presented in species accounts. To test our predictions relating the duration and intensity of molt to body size, we regressed each against body mass (masses from Dunning 2007). In our molt duration analysis, we present our findings both with and without Verdin because it was the only species that we found direct evidence of molt and breeding overlap for which we had an estimate of molt duration. For our analysis of molt intensity, we first regressed intensity on mass for all 20 species we studied but included only adult Ash-throated Flycatchers. To see if molt intensity is affected by the life history category, we compared our three groups: molt migrants, residents that do not overlap molt and breeding and residents that do overlap molt and breeding. In this analysis, we included Gila Woodpecker as a species that overlaps molt and breeding. For these analyses, we used both parametric and nonparametric tests because for some comparisons, our data was normally distributed, but for others we had a small sample size with a non-normal distribution; all results are means ± standard error (SE). To test our prediction that the intensity of the primary molt would be inversely related to its duration, we regressed an index of molt duration (residuals from the regression of duration on body size) on molt intensity, using all species for which we had both duration and intensity estimates. We used residual molt durations to control for body size because, when comparing a broad range of body sizes, larger birds have longer molt durations than smaller birds (Rohwer *et al.* 2009).

RESULTS

Summary of netting effort. Figure 1 summarizes our netting effort in low elevation thorn forest of western Mexico during our fieldwork in 2005, 2006, 2007, and 2009. There are two small gaps in our netting effort, the first (mid to late August), when we were working in high elevation sites, and the second (early September), when Hurricane John in 2006 prevented us from working (Fig. 1).

MOLT-MIGRANT SPECIES ACCOUNTS

Ash-throated Flycatcher (Myiarchus cinerascens). Butler *et al.* (2006) described this species as a molt-migrant, where both adults and juveniles

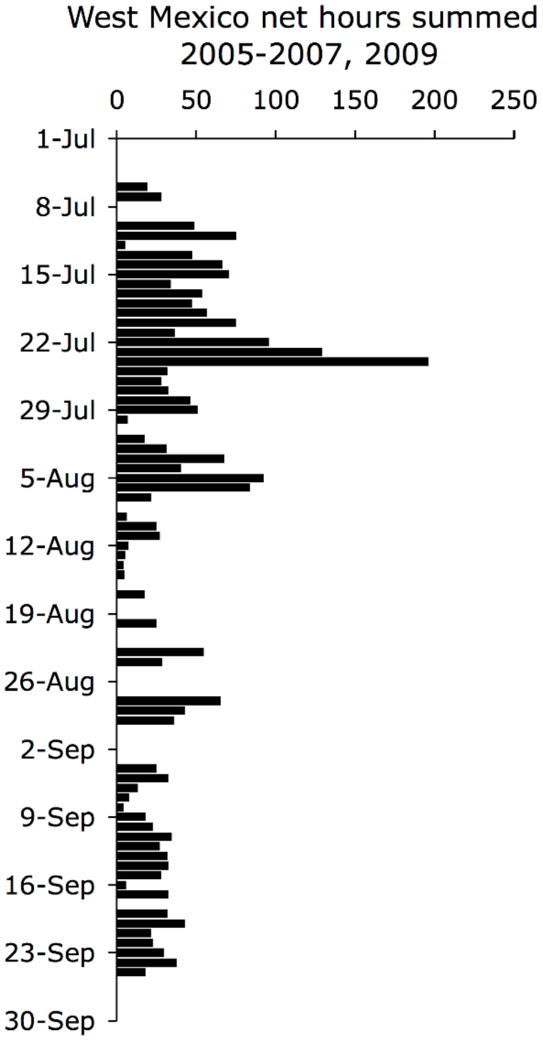

FIG. 1. Summary of net hours from Northwest Mexico from 2005–2007 and 2009. Net hours are for low elevation (< 500 m) sites in Sinaloa, Mexico. The two gaps in netting effort at the end of August and early September are from working in high elevation sites and from Hurricane John in 2006.

depart their northern breeding range to molt in the monsoon region. From our fieldwork, we added 5 molting adults (n = 40 combined) and 1 molting juvenile (n = 37 combined) to Butler *et al.*'s (2006) molt data. Adults require about 75 days ($r^2 = 0.81$) to replace the primaries, with a mean start date of 19 July and mean end date of 27 September (Table 1). In contrast, primary molt in juvenile Ash-throated Flycatchers requires about 47 days ($r^2 = 0.48$), beginning on average on 2 August and finishing 18 September. Surprisingly, juveniles do not grow more primaries at once (Butler *et al.* 2006); both adults and juveniles grow about 25% of their primaries simultaneously (Table 1).

Western Kingbird (Tyrannus verticalis). This species has only recently been recognized as a molt-migrant (Barry *et al.* 2009). Most adults move to the region of the Mexican monsoon to molt in July, while juveniles remain on the breeding grounds for an additional 1–2 months before migrating, without initiating primary replacement. We used 58 molting kingbirds to estimate molt duration. On average primary molt required 70 days ($r^2 = 0.85$), beginning about 19 July and ending 27 September (Table 1). The number of primaries growing simultaneously increased steadily to P4 and then stabilized at about 35% of the primaries growing from P4 through the loss of P10 (Table 1). We used molt data from Western Kingbirds to show examples of our molt duration and molt intensity plots see Fig. 2.

Lucy's Warbler (Vermivora luciae). Lucy's Warbler was originally thought to molt on its breeding grounds (Voelker & McFarland 2002). While some birds do molt in the breeding range, most seem to move to the region of the Mexican monsoon where both adults and juveniles molt (Rohwer *et al.* 2007, Pyle *et al.* in press). We combined molt data from Voelker & McFarland (2002) with 26 molting Lucy's Warblers from our recent fieldwork (n = 41 combined). Both duration and intensity estimates include adults and hatch-year individuals because hatch-years undergo complete molts making them difficult to distinguish from adults (Rohwer *et al.* 2007). Primary molt requires about 67 days ($r^2 = 0.84$), starting about 12 July and finishing about 17 September (Table 1). Molt intensity peaks when P3 or P4 are growing and remains constant until completion, with about 26% of the primaries growing simultaneously (Table 1).

Western Tanager (Piranga ludoviciana). Adult Western Tanagers begin arriving to the monsoon region to molt towards the end of August, while juveniles remain on the breeding grounds to replace their body feathers prior to migration (Butler *et al.* 2002). We found many molting individuals in the thorn forest of Baja California Sur and in low elevation (~ 450 m) tropical deciduous forest in Sinaloa; nearly all tanagers netted in Baja were stained red on their faces from eating columnar cactus fruit. Tanagers seemed absent in low elevation (100 m) thorn forest in Sinaloa, suggesting that they prefer the tropical deciduous forest of slightly higher elevations. We used nine molting adults from our fieldwork and 10 adults from Butler *et al.* (2002) (n = 19 combined); we excluded adults from Bulter *et al.* (2002) that were molting outside of Mexico to control for any difference in the rate and intensity of molt that might be related to molt location. Adults typically require 46 days ($r^2 = 0.53$) to replace their primaries, starting about 12 August and finishing 27 September (Table 1). Western Tanagers typically replace 34% of their primaries simultaneously (Table 1).

Black-headed Grosbeak (*Pheucticus melanocephalus*). Black-headed Grosbeaks breed from the highlands of central Mexico north into western Canada and populations that breed north of Mexico move to the region of the Mexican monsoon for their molt (Froehlich *et al.* unpubl. data). Using 21 molting individuals, we estimate that primary replacement in molt-migrant Black-headed Grosbeaks requires 68 days ($r^2 = 0.68$) (Table 1). Most of these birds were either just beginning or nearing completion of the molt. Two birds with late molt initiation dates pull the regression line to a slightly shallower slope, perhaps artificially decreasing our estimate of molt duration. Excluding these two birds, we estimate primary molt to take 75 days ($r^2 = 0.92$); however, we used our estimate of 68 days for further analyses. Molt is intense in the Black-headed Grosbeak, with more than 40% of the

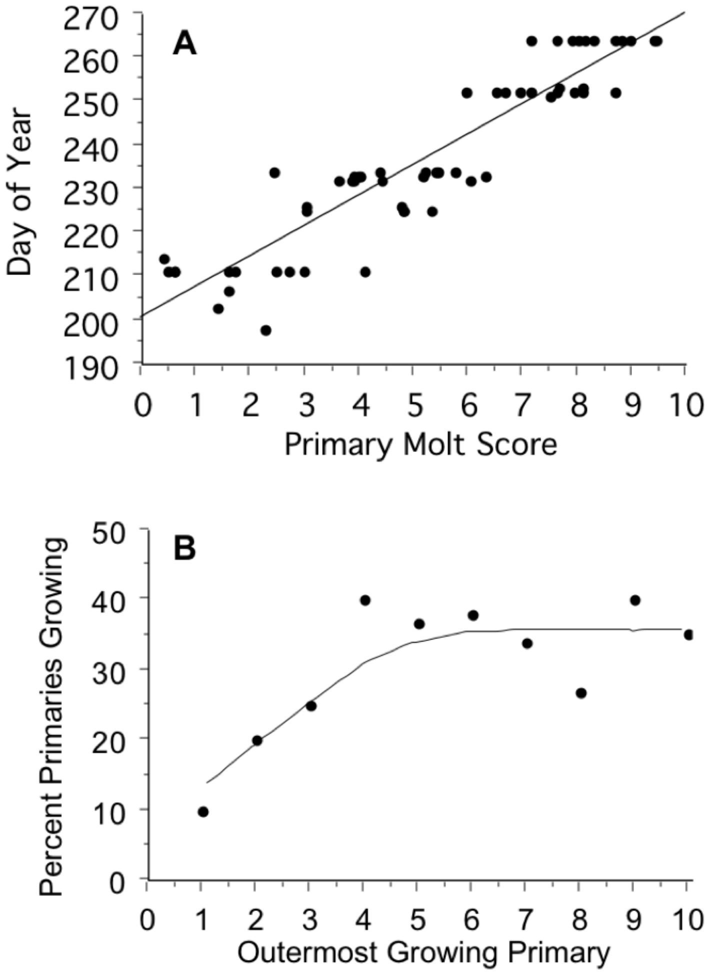

FIG. 2. Estimates of primary molt duration and intensity for adult Western Kingbirds. A) "Pimm" estimate of primary molt duration; molt requires about 70 days and on average begins 19 July and ends 27 September ($Y = 200.2 + 6.99X$, $r^2 = 0.85$). B) Plot of primary molt intensity for adult Western Kingbirds. Intensity increases steadily until about P4 where it stabilizes and remains constant until completion, replacing about 35% of the primaries simultaneously.

primaries growing at peak molt intensities when primary replacement has proceeded to P4 or P5 (Table 1).

"Western" Painted Bunting (*Passerina ciris pallidior*). Painted Buntings that breed in the central USA migrate to the monsoon region for their fall molt (Thompson 1991), congregating in fallow fields and grassy mesquite flats where seeds are abundant. Our estimate of molt duration includes only adult males because females show great variation in the timing of their molt (VGR unpubl. data). We used 58 molting males, all netted or collected in coastal Sinaloa. On average, adult males initiated primary molt on 13 August and finished

on 26 September, requiring 43 days ($r^2 = 0.74$) (Table 1). Molt is intense in adult males, with 40% of the primaries growing simultaneously during peak molt (Table 1). Some males were replacing as many 6 primaries at once while also replacing all rectricies and several secondaries; these individuals were nearly flightless.

Lark Sparrow (Chondestes grammacus). Lark Sparrows have been suspected to migrate to the monsoon region to molt (Rohwer *et al.* 2005, Pyle *et al.* in press) and our recent fieldwork in the Mexican monsoon region clearly shows that they are indeed molt migrants. We frequently encountered flocks of molting birds in August in New Mexico and in late August and September in Sinaloa and we were encountering more than 50 birds per day in the course of running mist nets in open, grassy mesquite flats in early September of 2007. Lark Sparrows did not arrive in coastal Sinaloa until late August and young birds in full juvenile plumage were first encountered in early September. The absence of this species in July shows that molting individuals netted in August and September were not local breeders. Complementing these observations from the monsoon region, not one of seven adults and juveniles collected from breeding sites in Washington State (UWBM collection) in late July and early August had started molting, further suggesting that Lark Sparrows are molt-migrants.

Adults initiate molt earlier than juveniles, so our estimate of molt duration includes only adult birds ($n = 14$). On average, primary molt requires 62 days ($r^2 = 0.85$), beginning 2 August and ending 1 October (Table 1). At peak molt intensity, Lark Sparrows replace about 35% of the primaries simultaneously (Table 1).

Bullock's Oriole (Icterus bullockii). This species was recognized as a molt-migrant almost 20 years ago (Rohwer & Manning 1990), yet, few molting individuals have been recorded or collected. We scored primary molt on a total of 20 molting adult (including second-year) orioles; 17 from our fieldwork in Sinaloa and Arizona, and 3 specimens scored by Rohwer & Manning (1990). On average molt begins 22 July and ends 7 September, requiring 47 days ($r^2 = 0.91$) (Table 1). Molt intensity peaked near P4 with approximately 35% of the primaries growing simultaneously (Table 1).

RESIDENT SPECIES ACCOUNTS

Gila Woodpecker (Melanerpes uropygialis). To estimate molt duration and intensity for Gila Woodpeckers, we used 36 molting birds that were a mix of 6 adults, 24 juveniles and 6 individuals whose ages were not recorded. Juveniles initiate primary molt while in the nest hole (Pyle & Howell 1995) and typically undergo a complete molt of the primaries (Pyle 1997, VGR pers. observ.). Unfortunately, our sample of molting adults is small but we found no difference in the rate or intensity of molt between adults and juveniles, thus we combined age classes for our estimates of duration and intensity. On average primary molt begins 6 July and ends 29 September requiring about 85 days ($r^2 = 0.71$) (Table 1). Molt intensity is low with about 25% of the primaries replaced simultaneously throughout most of the molt (Table 1).

While we caught no individuals for which molt breeding overlap could reliably be assessed, adults likely begin their molt during post-fledgling care. Fledglings first appeared in early July. We frequently caught molting adults and juveniles in the same net that were likely family groups. Because Gila Woodpeckers undergo a long, non-intensive molt and because molting adults were often netted with juveniles, we believe that they overlap molt with at least the final stages of fledgling care and perhaps with nestling care.

Rose-throated Becard (*Pachyramphus aglaiae*). We caught nine molting males and females, all of which were in early stages of primary replacement. During our expeditions, we found no individuals that were advanced in the molt so we provide only a preliminary estimate of primary molt intensity. Our intensity estimate comes from averaging the number of feathers growing simultaneously in three individuals whose growing primaries were flanked by newly replaced inner primaries and old outer primaries. Intensity appears low with approximately 26% of the primaries growing simultaneously (Table 1).

In July of 2006 and 2007, along riparian zones bordering mesquite lowlands and in low elevation tropical deciduous forests, we frequently netted pairs of becards (one male and one female) that presumably were actively breeding. In 2009 we netted a pair (and a possible auxiliary male) associated with a nest containing 6 young that were more than half grown. All three of these adults were molting primaries: the female growing P1–2 and the two males P1–P4 and P1–P5. Two additional females that we collected had watery, vascularized brood patches (suggesting they were incubating or had very small young) and both were in early stages of the molt. The first was replacing both P1 and P2 simultaneously, the second was replacing P1, 2, and 3 simultaneously. In September 2007, when we returned to sites where we had found breeding becards, we neither netted nor observed a single Rose-throated Becard, adult or juvenile.

Nutting's Flycatcher (Myiarchus nuttingi). We examined 22 molting adult Nutting's Flycatchers, collected or netted in low elevation thorn forest of Sinaloa Mexico. For adults, primary molt starts, on average, 8 July and ends 7 September requiring about 61 days (Table 1). At peak molt intensity Nutting's Flycatchers replace about 34% of their primaries simultaneously (Table 1). The initiation of primary molt in adults coincided with the presence of recently produced young, thus adults do not appear to overlap molt and breeding. Shortly after we began to net molting adults, we netted recently fledged young in full juvenal plumage. In 2005, we netted the first fledglings on 23 and 25 July, and in 2007, we netted our first fledgling on 15 July, two more on 17 July and another on 19 July.

Bell's Vireo (Vireo bellii). During our field seasons we encountered few molting Bell's Vireos and thus we could not estimate the duration of primary molt. We used 13 molting individuals to estimate molt intensity; this estimate includes 10 hatch year birds, some of which were in eccentric molt and three birds of unknown age. Molt is most intense when P4 and P5 are growing, with about 27% of the primaries replaced simultaneously (Table 1).

Verdin (Auriparus flaviceps). To estimate molt duration and intensity in Verdins, we combined molt data from Taylor (1970) for 17 adults with our data of four molting adults from recent fieldwork (n = 21 combined). We converted Taylor's (1970) measurements of lengths of growing primaries to fractions as follows: unopened shafts = 0.2; feathers emerging from shaft = 0.3; missing feathers = 0.01; new feathers = 1, and old feathers = 0. We used Taylor's data for the left wing only.

On average, primary molt started on 16 June and ended 18 September requiring 94 days ($r^2 = 0.86$) (Table 1). As tiny passerines, Verdins take an exceedingly long time to molt their primaries and molt intensity is low with about 28% of their primaries growing simultaneously (Table 1).

We netted two female Verdins that were actively overlapping molt and breeding. The first, collected 13 July 2007 (UWBM 84061) was about to lay with a shelled egg in her oviduct and three enlarged ova (8 mm, 5 mm, 3 mm); she had replaced P1 and P2 and was growing P3. The second, collected 15 July 2007 (UWBM 84069) had a watery, vascularized brood patch, indicating that she was incubating; she was also growing P2 and P3. Three other females and a forth bird of unknown sex were actively molting. None of the three females had a watery brood patch, or enlarged ova (or cloacle protuberance in the unknown individual), thus we could not be certain of their breeding condition. In addition to the two individuals overlapping molt and breeding, Short (1974) described a male that was molting primaries and that was collected together with three nestlings in Sonora, Mexico.

Sinaloa Wren (Thryothorus sinaloa). Sinaloa Wrens appear to use the rains first to breed and then to molt; we found no evidence of molt breeding overlap. Breeding appears to begin in early July and extends into mid-September. During our fieldwork, we caught 16 adults, of which 12 were in breeding condition. We found three active nests, the first, found 14 July 2007 had five slightly incubated eggs (UWBM 86494), the second, found 25 July 2007 was nearly complete, and the third, found 21 September 2007 had at least two large feathered young being fed by an adult. Because the breeding season extends into late September, we encountered few molting individuals and those we encountered were not advanced in their primary molt. Our estimate of molt intensity comes from four adult Sinaloa Wrens, all of which had growing feathers flanked between newly replaced inner primaries and old outer primaries. Adult Sinaloa Wrens do not appear to undergo an intensive molt, replacing about 26% of their primaries simultaneously (Table 1).

Northern Cardinal (Cardinalis cardinalis). Primary molt in cardinals from west Mexico appears to extend into October. Most molting individuals that we netted were in early stages of the molt and none had reached P8 or P9. From our sample of 11 molting adults, we estimate that primary molt requires about 98 days ($r^2 = 0.82$) beginning about 25 July and ending about 31 October (Table 1). However, because the most advanced cardinal was replacing P7, this is a preliminary estimate. Molt is not strikingly intense in cardinals. Peak replacement occurred when P5 was growing with about 33% of the primaries growing simultaneously (Table 1). We found no evidence that cardinals overlap molt and breeding, and other researchers have noted individuals that suspended their molt to breed (P. Pyle pers. com.).

Grayish Saltator (Saltator coerulescens). We caught five adult saltators that were molting primaries and none had advanced beyond P6 making an estimate of molt duration unreasonable. Molt must continue at least throughout October. Our sample of molting adults (two males, two females and one bird of unknown sex) suggests that molt intensity is low, with a mean of only 28% of the primaries growing simultaneously (Table 1). The outermost growing primary in these birds ranged from P2–P6 and all but one had completely grown P1.

We collected a single female (16 July 2005, UWBM 81211) that was preparing to lay with two enlarged ova (4 mm, 3 mm), an enlarged ovaduct (5 mm at cloaca) and a brood patch that was bare and dry; this female was growing P1 and P2, clearly overlapping molt and breeding. We observed two other breeding records: an adult carrying material (12 July 2006) and an active nest with 2 moderately incubated eggs collected 14 July 2007 (UWBM 86522). Finally, we failed to net juvenile Grayish Saltators until 12 September 2007. After this date, we frequently netted two hatch-years and at least one adult together in the same net, suggesting that these were family groups (saltators typically lay 2 eggs). All adults that we netted with hatch years were growing primaries (outermost between P4 and P6), suggesting that adults were molting both while nesting and while caring for fledglings. Because all adults were in active molt, Grayish Saltators likely do not suspend primary replacement for reproduction.

Varied Bunting (Passerina versicolor). We caught 14 molting adult Varied Buntings, none of which was advanced in their primary molt making it impossible to estimate molt duration. In our sample of 14 males and females, primary molt was intense with approximately 42% of the primaries growing simultaneously (Table 1). Varied Buntings apparently use the monsoon rains first to breed and then to molt; we found no evidence of overlap. Breeding extends into late August. We found two active nests, the first from previous work in Pima County, Arizona on 6 August 2004 with eggs slightly over half incubated (UWBM 77692), and a second on 21 July 2007 in Sinaloa, Mexico with 3 eggs about half incubated (UWBM 86526). In addition to these nests, we observed males singing during all expeditions to Mexico from early July through the end of September. In our four years of netting in Mexico, we began catching juvenile buntings in late August and early September.

Rufous-winged Sparrow (*Aimophila carpalis*). We netted 10 Rufous-winged Sparrows that were actively molting primaries; all were in early stages of molt making an estimate of molt duration unreasonable. During our latest expedition in September 2007, we found no individuals that had advanced beyond growing P4 (a male netted on 23 September 2007), thus molt likely extends into October and possibly November. To estimate molt intensity, we used five individuals whose growing primaries were flanked between newly replaced inner primaries and worn outer primaries. Mean molt intensity was 18% (Table 1).

We collected seven Rufous-winged Sparrows that showed signs of molt-breeding overlap. All seven were males with enlarged testies (> 5 x 4 mm) and seminal vesicles, or that showed cloacal protuberance. For two addition birds, a male with enlarged testies and seminal vesicles, with newly replaced P1 and P2, and a female with a 3 mm ovum and newly replaced P1 and P2, we could not distinguish a slow, low intensity molt from a suspended molt; we did not count them as overlapping molt and breeding. In addition to the seven individuals overlapping molt and breeding, we observed many males singing and defending territories and found 3 active nests (all with eggs) between 5 July and 17 September 2007. The co-occurrence of active nests, breeding behavior and individuals in primary molt further suggests molt-breeding overlap in Rufous-winged Sparrows.

Streak-backed Oriole (Icterus pustulatus). We examined 37 molting adult and second year Streak-backed Orioles from coastal Sinaloa, Mexico. On average, primary molt began on 31 July and ended 19 September, requiring about 50 days (Table 1). Unfortunately, most molting individuals were starting or finishing molt; we have only one individual that was in the middle of primary molt making our estimate of molt intensity preliminary. Intensity appears high with 37% of the primaries replaced simultaneously (Table 1). Streak-backed Orioles breed at the start of the rains and replace their primaries after their young have fledged; we found no evidence of molt breeding overlap. Throughout the month of July, we observed several active nests and by late July we began observing recently fledge young (27 July 2007, male feeding fledgling; 2 August 2006, first sightings of fledglings). The presence of recently fledged orioles coincides with the start of flight feather molt in adult Streak-backed Orioles.

House Finch (Carpodacus mexicanus). To estimate molt duration and intensity, we used 32 molting birds and combined age classes from 19 adults, 7 juveniles and 6 individuals whose age was not recorded. On average molt required 67 days, starting about 28 June and ending about 3 September (Table 1). Molt appears intense with about 33% of the primaries replaced simultaneously (Table 1). This surprisingly long molt duration is inconsistent for a species that undergoes an intensive primary molt, making us suspect that some source of sample heterogeneity invalidates our Pimm estimate of molt duration.

Synthesis of molt data presented in species accounts. For the 14 species with duration estimates that we examined, we found no effect of mass on molt duration (Fig. 3, with Verdin $r^2 = 0.035$, $P = 0.52$; without Verdin $r^2 = 0.22$, $P = 0.11$), presumably because of the restricted range of masses in our sample (Rohwer *et al.* 2009).

Combining all three life-history strategies (molt migrants and residents that either do or do not overlap molt and breeding), we found no effect of body size on molt intensity (Fig. 4, $r^2 = 0.013$, $P = 0.63$); again, this may be an artifact of the restricted range of masses available to us.

Molt intensity did vary by life-history strategy. Overall, we found no differences in molt intensity between molt migrants (33.2% ± 2.0) and residents that do not overlap molt and breeding (33.1% ± 2.3) (ANOVA $F = 0.0006$, $P = 0.98$). Therefore, we combined these two life history categories (33.2% ± 1.5), which represent species that do not overlap molt and breeding. The five resident species that overlap molt and breeding had a much lower mean molt-intensity (25.0% ± 1.8) (Fig. 4, ANOVA $F = 7.9$, $P = 0.011$; Wilcoxon $P = 0.031$). Residents that overlap molt and breeding grew about 10% fewer primaries (about one feather less) than the non-overlapping species.

Finally, species that grow more primaries simultaneously typically had shorter molt durations than expected for their body size (Fig. 5, overlap species excluded: $r^2 = 0.23$, $P = 0.11$, $n = 12$; overlap species included: $r^2 = 0.30$, $P = 0.044$, $n = 14$).

DISCUSSION

Molt-breeding overlap. We found direct evidence of molt-breeding overlap in four species: Rose-throated Becard, Verdin, Grayish Saltator, and Rufous-winged Sparrow, and evidence that Gila Woodpecker overlaps molt at least with post fledging care. All these species grow few primaries at once presumably allowing them to molt during reproduction. Low intensity molts are thought to reduce the energetic demands of molting while breeding, thus enabling both activities to occur simultaneously (Foster 1975).

For Rose-throated Becards, we encountered both males and females overlapping molt and breeding, and for Verdins and Grayish Saltators, we encountered only females that were in mid stages of molt and early stages of breeding. For Rufous-winged Sparrow, we and Phillips (1951) observed overlap only in males and apparently during the final stages of breeding in September. While our samples are small, the pattern between timing of overlap and sex may be of significance, at least in Rufous-winged Sparrows. Males may be able to overlap molt with the final stages of reproduction because they are able to invest less than females in nestlings and in post fledging care (Svensson & Nilsson 1997, Hemborg & Merilä 1998). In many species of raptors (Accipitridae) females suspend molt for breeding more frequently than males (Pyle

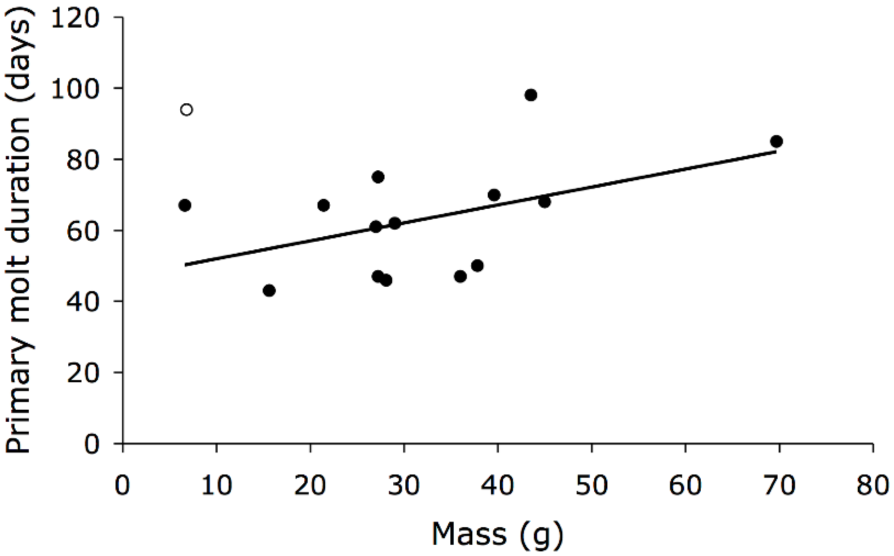

FIG. 3. Relationship between primary molt duration for 14 species regressed on weight, a proxy for body size. Larger species typically take longer to molt than smaller species. The open point in the upper left hand quadrant is Verdin, a small passerine species considered to overlap molt and breeding (with Verdin $r^2 = 0.035$, $P = 0.52$; without Verdin $r^2 = 0.22$, $P = 0.11$). Little of the variation in molt duration is explained by body size.

2005), thus females many initiate then suspend molt to reduce overlap between these two activities.

Why we found molt-breeding overlap in these five species (including Gila Woodpecker) and not others of the 12 resident species we examined remains a mystery. There seems to be no dietary similarity among the five residents that overlap molt and breeding that distinguishes them from the eight residents that did not overlap molt and breeding. Foster (1975) also found no dietary differences between species that did or did not overlap molt and breeding in Costa Rican birds.

Small clutch sizes should characterize species that overlap molt and breeding because raising fewer offspring requires less energy and allows more breeding attempts (Foster 1974). Excluding Gila Woodpecker because it is a non-passerine and nests in cavities, we found little evidence of smaller clutches in our four passerine species that overlap molt and breeding. Mean clutch size was slightly smaller for residents that overlap molt and breeding (3.4 eggs, n = 4) than for residents showing no overlap (3.9 eggs, n = 8) (clutch size data from Howell & Webb 1995; not from individuals we encountered), but not significantly lower (Wilcoxon *P* = 0.079). Further, the becard nest we checked had six young, two more than the largest clutch listed by Howell & Webb (1995) and both parents were molting. We caution that comparing clutch size data for a species may be unreasonable when only some individuals within a species overlap molt and breeding.

Residents of the monsoon region in west Mexico are likely to overlap molt and breeding because resources are limited throughout much of the year (Foster 1975). In the coastal lowlands of Sinaloa where most of our field

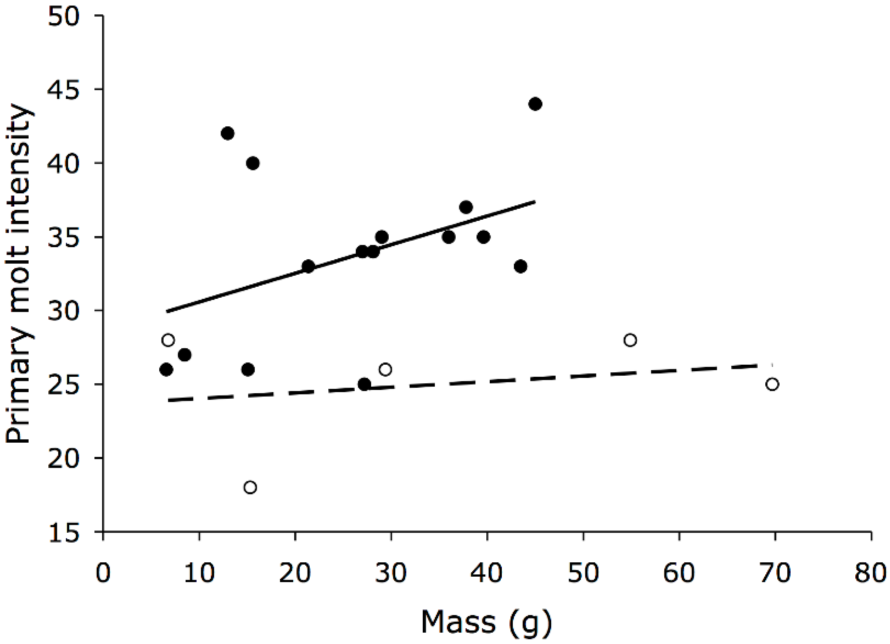

FIG. 4. Relationship between primary molt intensity and life-history category regressed on body size. Open points are residents that overlap molt and breeding, filled points are both molt migrants and residents that do not overlap molt and breeding; in this analysis we included Gila Woodpecker as a species considered to overlap molt and breeding. Residents that overlap molt and breeding replace about 10% fewer primaries than species that do not overlap molt and breeding (ANOVA P = 0.0063, Wilcoxon P = 0.018). This difference is equivalent to growing about one feather less.

sites were located, there are approximately 50 resident species (Howell & Webb 1995). In our study of molt in 12 resident species, we encountered five (42%) that appeared to overlap molt and breeding. This percentage of molt breeding overlap in the seasonal lowlands of west Mexico is higher than those reported by Foster (1975) (20.2%; 47 of 233 species overlap) for birds in Costa Rica and those reported by Payne (1969) (12.6 %; 24 of 190 species overlap) for diverse African birds. We caution that our sample size of 12 resident species is small and that our small sample alone could inflate the percentage of molt and breeding overlap in west Mexico. However, from our field observations of breeding activity and molting, several other species likely overlap these two events (e.g., Rufous-bellied Chachalaca *Ortalis wagleri*, Common Ground Dove *Columbina passerina*, Ruddy Ground Dove *C. talpacoti*, Groove-billed Ani *Crotophaga sulcirostris*, Greater Road Runner *Geococcyx californianus*, Lesser Road Runner *G. velox*, Golden-cheeked Woodpecker *Melanerpes chrysogenys*, Happy Wren *Thyrothorus felix*).

Molt intensity. Larger birds that must overcome the time constraints to complete their molt in a single season have two options to speed-up their molt: 1) increase the growth rates of individual flight feathers or 2) grow more feathers simultaneously. While these methods are not mutually exclusive, growing more primaries at once appears to be the principle

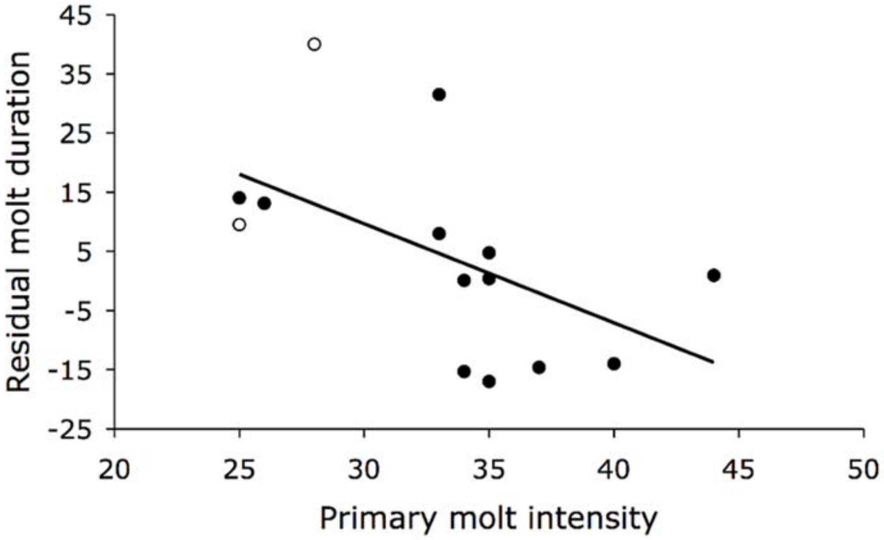

FIG. 5. Residual molt durations regressed on molt intensities. On the Y axis, positive numbers indicate that primary molt takes longer than expected from body size estimates, while negative numbers indicate rapid molts. The two open points (above: Verdin, below: Gila Woodpecker) are species considered to overlap molt and breeding. Growing more primaries simultaneously reduces the time required to molt (overlap species excluded: $r^2 = 0.23$, $P = 0.11$; overlap species included: $r^2 = 0.30$, $P = 0.044$).

strategy for birds to decrease the time required to complete their molt (Hall & Fransson 2000, Ryder & Rimmer 2003, Dawson 2004). However, growing more flight feathers simultaneously creates large gaps in the wings and hinders flight in molting birds (Tucker 1991, Swaddle & Witter 1997). As far as we know this is the first study to show that the duration of the primary molt is inversely related to the intensity of primary molt (Fig. 5). Presumably this inverse relationship will prove to be much more robust when more large species with simple descendent primary molt are added to the analysis. While regression estimates of molt duration are becoming reasonably common in the literature (see Rohwer *et al.* 2008), a large comparative study of the relationship between molt duration and intensity remains impossible because there are virtually no published measures of molt intensity. This is not only unfortunate, but also ironic because much smaller data sets are needed to estimate peak molt intensity than to estimate the duration of the primary molt. We hope this study will inspire others to present data on molt intensities, following the methods of Yuri & Rohwer (1997), and reviewed in Rohwer (2009).

Of all the molt-migrants, Lucy's Warbler has one of the slowest molts requiring about 67 days, with a low peak intensity of just over 25% of the primaries growing simultaneously. Given the abundance of food generated by the monsoon, we suspect this early migrant may molt slowly to grow high quality feathers that are more resistant to wear in the abrasive thorn-scrub habitats where Lucy's Warblers winter and breed. Slow molts have been suggested for palearctic migrants that molt in scrub habitat in sub-Saharan Africa (Rohwer *et al.* 2005). The same is likely true for Verdins that are resident species of thorn-scrub habitats in the American southwest and northwestern Mexico.

For Rufous-winged Sparrows, we encountered one male and one female that we could not distinguish between a low intensity or suspended molt; both had replaced P1 and P2. If individuals we encountered with low intensity molts were artificially lower because molt was about to be suspended, then our estimates of molt duration and intensity could be misleading. Suspended molts would over estimate molt duration and under estimate molt intensity.

Diet and molt rates. Voelker (2004) suggested that the flush of productivity in the monsoon region might permit migrants to undergo rapid molts. In his study of molt in Baird's Sparrow (*Ammodramus bairdii*), Voelker (2004) describes the shortest primary molt duration (39 days) for any molt-migrant species that molts in the monsoon region of west Mexico and that supports its molt with small seeds from ephemeral grasses. While many seedeaters appear to have rapid and intensive molts (e.g., "Western" Painted Bunting, Varied Bunting, Baird's Sparrow) some do not (e.g., Lark Sparrow). A critical question for these seedeaters with short molt durations is whether they benefit from molting rapidly (possibly at the cost of growing lower quality feathers; Dawson 2004), or whether they are forced to molt quickly because the seeds they eat are available only for a short period of time. In contrast to these rapid molts, aerial foragers like swallows and flycatchers typically replace few feathers at once because they rely on flight and high maneuverability to forage (Yuri & Rohwer 1997, Butler *et al.* 2006). Because molt rates vary substantially among these species, we hypothesize that molt intensities have been shaped largely by ecological and life-history variables associated with access to food or escaping predators or to the importance of high quality feathers, rather than to difference in diet.

Molt-related movements. Several resident species appear to undergo a molt-related movement. Rose-throated Becards, Northern Beardless Tyrannulets (*Camptostoma imberbe*) and Sulphur-bellied Flycatchers (*Myiodynastes luteiventris*) bred and were frequently netted in riparian zones and low elevation tropical deciduous forests (~ 400 m) throughout July and August; yet, we neither heard nor saw them when we revisited the same locations in September. The absence of these species suggests that they move (up-slope? further south?) to undergo or complete their molt. Perhaps species that depart these low-elevation deciduous forests move to regions avoided by temperate migrants to reduce competition during their molt (Wolfe *et al.* 2009).

Molt is an essential part of the annual cycle in birds, yet, in comparison to temperate species, we know little about the molts and molt biology of tropical species. Here, we have provided estimates of molt duration and intensity of several tropical species and Neotropical migrants and hope to inspire more research that examines the molts of tropical birds. As more molt studies are published, researchers can examine differences in duration, intensity and timing of molt between temperate and tropical species to better understand differences and similarities in their life histories.

ACKNOWLEDGMENTS

Many thanks to those who helped with fieldwork: Rob Faucett, Chris Wood, Samuel López de Aquino, Erick Alejandro García-Trejo, Jessie Barry, Brigitte Rohwer, Dan Froehlich, Anne Hilborn, Rosa Daniela Tovilla Sierra, POLO, Jamie Castro Navarro, and Diana Thayer. Special thanks to Rob Faucett and Adolfo Navarro for organizing permits. Thanks to Paul Martin, Mark Conboy, Peter Pyle, and an anonymous reviewer for helpful comments on an early version of this manuscript. Our expeditions were supported by the Burke Museum Endowment for Ornithology and by grants from Hugh Ferguson and the U. S. Fish and Wildlife Service. VGR was supported by the Bailie Family Endowment and VGR and several field assistants were supported by the Burke Museum Endowment for Ornithology. We thank the University of Washington Burke Museum (UWBM) and the Museum of Vertebrate Zoology (MVZ) for access to specimens.

REFERENCES

Barry, J. H., L. K. Butler, S. Rohwer, & V. G. Rohwer. 2009. Documenting molt-migration in Western Kingbirds using two measures of collecting effort. Auk 126: 260–267.

Butler, L. K., M. G. Donahue, & S. Rohwer. 2002. Molt-migration in Western Tanagers (*Piranga ludoviciana*): age effects, aerodynamics, and conservation implications. Auk 119: 1010–1023.

Butler, L. K., S. Rohwer, & M. Rogers. 2006. Prebasic molt and molt-related movements in Ash-throated Flycatchers. Condor 108: 647–660.

Comrie, A. C., & E. C. Glenn. 1998. Principal components-based regionalization of precipitation regimes across the southwest United States and northern Mexico, with an application to monsoon precipitation variability. Clim. Res. 10: 201–215.

Dunning, J. B., Jr. 2007. CRC Handbook of avian body masses, 2nd ed. CRC Press/Taylor and Francis Group, Boca Raton, Florida.

Dawson, A. 2004. The effects of delaying the start of moult on the duration of moult, primary feather growth rates and feather mass in Common Starlings *Sturnus vulgaris*. Ibis 146: 493–500.

Foster, M. S. 1974. A model to explain molt-breeding overlap and clutch size in some tropical birds. Evolution 28: 182–190.

Foster, M. S. 1975. The overlap of molting and breeding in some tropical birds. Condor 77: 304–314.

Hall, K. S. S., & T. Fransson. 2000. Lesser Whitethroats under time-constraint moult more rapidly and grow shorter wing feathers. J. Avian Biol. 31: 583–587.

Hemborg, C., & J. Merilä. 1998. A sexual conflict in collared flycatchers, *Ficedula albicollis*: early male moult reduces female fitness. Proc. R. Soc. Lond. B. 265: 2003–2007.

Howell, S. N. G., & S. Webb. 1995. A guide to the birds of Mexico and northern Central America. Oxford Univ. Press, Oxford, UK.

Langston, N. E., & S. Rohwer. 1996. Molt-breeding tradeoffs in albatrosses: life history implications for big birds. Oikos 76: 498–510.

Lanyon, W. E. 1961. Specific limits and distribution of Ash-throated and Nutting Flycatchers. Condor 63: 421–449.

Murphy, M. E., & J. R. King. 1992. Energy and nutrient use during moult by White-crowned Sparrows *Zonotrichia leucophrys gambelii*. Ornis Scand. 23: 304–313.

Payne, R. B. 1969. Overlap of breeding and molting schedules in a collection of African birds. Condor 71: 140–145.

Pearson, S. F., & S. Rohwer. 1998. Determining clutch size and laying dates using ovarian follicles. J. Field Ornithol. 69: 587–594.

Phillips, A. R. 1951. The molts of the Rufous-winged Sparrow. Wilson Bull. 63: 323–326.

Pimm, S. 1976. Estimation of duration of bird molt. Condor 78: 550–550.

Prevost, Y. 1983. The moult of the Osprey *Pandion haliaetus*. Ardea 71: 199–209.

Pyle, P. 1997. Identification guide to North American birds. Slate Creek Press, Bolinas, California.

Pyle, P. 2005. Remigial molt patterns in North American Falconiformes as related to age, sex, breeding status, and life-history strategies. Condor 107: 823–834.

Pyle, P., & S. N. G. Howell. 1995. Flight-feather molt patterns and age in North American woodpeckers. J. Field Ornithol. 66: 564–581.

Pyle, P., W. Leitner, L. Lozano Angulo, F. Avilez Tehran, H. Swanson, E. Gómez Limón, & M. Chambers. *in press*. Temporal, spatial, and interannual variation in the occurrence of molt-migrant passerines in the Mexican monsoon region. Condor.

Rohwer, S. 1999. Time constraints and moult-breeding tradeoffs in large birds. Pp. 568–581 *in*

Adams, N. J., & R. H. Slotow (eds.). Proc. Int. Ornithol. Congr. 22: 568–581.

Rohwer, S. 2009. A primer on summarizing molt data for flight feathers. Condor 110: 799–806.

Rohwer, S., L. K. Butler, & D. R. Froehlich. 2005. Ecology and demography of east-west differences in molt scheduling of Neotropical migrant passerines. Pp. 87–105 *in* Greenberg, R. & P. P. Mara (eds.). Birds of two worlds: The ecology and evolution of migratory birds. John Hopkins Univ. Press, Baltimore, Maryland.

Rohwer, S., & J. Manning. 1990. Differences in timing and number of molts for Baltimore and Bullock's Orioles: Implications to hybrid fitness and theories of delayed plumage maturation. Condor 92: 125–140.

Rohwer, S., A. G. Navarro, & G. Voelker. 2007. Rates versus counts: fall molts of Lucy's Warbler, *Vermivora luciae.* Auk 124: 806–814.

Rohwer, S., R. E. Ricklefs, V. G. Rohwer, & M. M. Copple. 2009. Allometry of the duration of flight feather molt in birds. PLoS Biol. 7(6): e1000132. doi:10.1371/journal.pbio.1000132.

Rohwer, V. G., S. Rohwer, & J. H. Barry. 2008. Molt scheduling of western Neotropical migrants and up-slope movements of Cassin's Vireo. Condor 110: 365–370.

Ryder, T. B., & C. C. Rimmer. 2003. Latitudinal variation in the definitive prebasic molt of Yellow Warblers. Wilson Bull. 115: 325–332.

Short, L. L. 1974. Nesting of southern Sonoran birds during the summer rainy season. Condor 76: 21–32.

Svensson, E., & J. Nilsson. 1997. The trade-off between molt and parental care: a sexual conflict in the blue tit? Behav. Ecol. 8: 92–98.

Swaddle, J. P., & M. S. Witter. 1997. The effects of molt on the flight performance, body mass, and behavior of European Starlings (*Sturnus vulgaris*): an experimental approach. Can. J. Zool. 75: 1135–1146.

Taylor ,W. K. 1970. Molts of the Verdin, *Auriparus flaviceps.* Condor 72: 493–496.

Thompson, C. W. 1991. The sequence of molts and plumages in Painted Buntings and implications for theories of delayed plumage maturation. Condor 93: 209–235.

Tucker, V. A. 1991. The effect of molting on the gliding performance of a Harris' Hawk (*Parabuteo unicinctus*). Auk 108: 108–113.

Underhill, L. G., & W. Zucchini. 1988. A model for avian primary moult. Ibis 130: 358–372.

Voelker, G., & S. Rohwer. 1998. Contrasts in scheduling of molt and migration in eastern and western Warbling Vireos. Auk 115: 142–155.

Voelker, G. 2004. Can migrants do it faster? Accelerated molt of Baird's Sparrows and further insights into southwestern molting grounds. Condor 106: 910–914.

Voelker, G., & S. L. McFarland. 2002. Molt patterns and molting grounds of Lucy's and Virginia's warblers: Similar yet different. Wilson Bull. 114: 255–263.

Wolfe, J. D., P. Pyle, & J. Ralph. 2009. Breeding seasons, molt patterns, and gender and age criteria for selected northeastern Costa Rican resident landbirds. Wilson J. Ornithol. 121: 556-567.

Young, B.E. 1991. Annual molts and interruption of the fall migration for molting in Lazuli Buntings. Condor 93: 236–250.

Yuri, T., & S. Rohwer. 1997. Molt and migration in the Northern Rough-winged Swallow. Auk 114: 249–262.