PREBASIC MOLT OF BLACK-CAPPED AND WHITE-EYED VIREOS: EFFECTS OF BREEDING SITE AND THE EL NIÑO–SOUTHERN OSCILLATION

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Abstract. Ecological factors on the breeding grounds are expected to have a relatively large effect on the timing of molt in migratory birds breeding at middle latitudes (e.g., southern North America), because constraints on the time available to molt are probably weak. We investigated the timing of prebasic molt in adults of two migratory passerines, the endangered Black-capped Vireo (*Vireo atricapilla*) and the common White-eyed Vireo (*V. griseus*), on their breeding grounds in Texas. We compared the onset and rate of molt between sites differing in habitat and between years differing greatly in precipitation due to the El Niño–Southern Oscillation (ENSO). Black-capped Vireos began molting 13 days later (8 July) and completed molt 12 days faster (50 days) in low quality, clumped habitat than in more typical, contiguous shrubby habitat (62-day molt starting 25 June). Long-term estimates of onset and duration of molt based on study skins were intermediate. White-eyed Vireos in the site with clumped habitat also started molting significantly later (13 July), but did not molt significantly faster (56 days), than those in the shrubby site (63-day molt starting 2 July). Both species started molting significantly later in the wet La Niña year than in the year with dry El Niño conditions. Body condition did not differ between sites or years. Our molt duration estimates of ~55 days for Black-capped Vireos and ~60 days for White-eyed Vireos suggest weak time constraints on molt in these populations. This study highlights the sensitivity of molt dynamics to events and conditions during the preceding breeding season.

Key words: *El Niño, life history, migration, molt,* Molothrus ater, Vireo atricapilla, Vireo griseus.

Muda Prebásica de *Vireo atricapilla* y *V. griseus*: Efectos del Sitio de Cría y de la Oscilación del Sur de El Niño

Resumen. Se espera que los factores ecológicos en las áreas de cría tengan un efecto relativamente grande sobre la estacionalidad de la muda de las aves migratorias que crían a latitudes intermedias (e.g., sur de América del Norte), ya que las restricciones del período de tiempo disponible para mudar son probablemente moderadas. Investigamos la temporalidad de la muda prebásica en adultos de dos aves paserinas migratorias, la especie en peligro *Vireo atricapilla* y la especie común *V. griseus*, en sus sitios de cría en Texas. Comparamos el comienzo de la muda y la tasa de muda tanto entre sitios que difieren en hábitat como también entre años que difieren enormemente en la cantidad de precipitación debido a la Oscilación del Sur de El Niño. *Vireo atricapilla* comenzó a mudar 13 días más tarde (8 de julio) y completó la muda 12 días antes (50 días de muda) en el ambiente agregado de baja calidad, que en el ambiente más típico arbustivo y continuo (62 días de muda comenzando el 25 de junio). Las estimaciones realizadas para períodos prolongados de tiempo sobre el comienzo y la duración de la muda basadas en el estudio de pieles fueron intermedias. *Vireo griseus* también comenzó a mudar significativamente más tarde en el hábitat agregado (13 de julio), pero no la muda no fue significativamente más rápida (56 días) que la de individuos en el sitio arbustivo (63 días de muda comenzando el 2 de junio). Ambas especies comenzaron a mudar significativamente más tarde en el año húmedo de La Niña que en el año con condiciones secas de El Niño. La condición corporal no varió entre sitios ni entre años. Nuestras estimaciones de la duración de la muda de ~55 días para *V. atricapilla* y de ~60 días para *V. griseus* sugieren que las restricciones de tiempo sobre la muda en estas poblaciones son moderadas. Este estudio resalta la sensibilidad de la dinámica de la muda a eventos y condiciones ocurridas durante la estación precedente a la cría.

INTRODUCTION

Breeding activities and ecological forces on the breeding grounds exert important effects on the timing and location of molt in birds breeding in temperate climates. On the proximate level, individuals that extend reproductive activities later into the summer often delay the onset of molt and then molt rapidly, presumably to finish molting before weather deteriorates (Rimmer 1988, Rivera et al. 1998). However, molting later negatively affects survival (Nilsson and Svensson 1996),
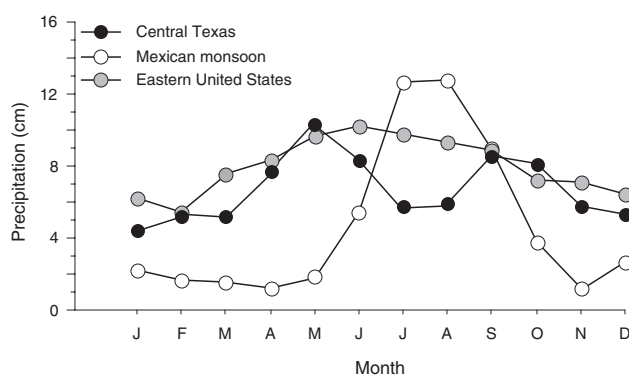

FIGURE 1.   Monthly precipitation in three areas that differ greatly in July and August, when most migratory passerines in North America molt. In June, precipitation starts to decrease in central Texas but increase greatly to the west in the Mexican monsoon region (Comrie and Glenn 1998), and precipitation is at the annual peak in the northeast. Monsoon region values were taken from 30-year averages in Comrie and Glenn (1998:fig. 5.1). Other values are 110-year averages from the online database of the National Oceanic and Atmospheric Administration (<http://www1.ncdc.noaa.gov/pub/data/cirs>; northeastern U.S. values are based on Central, East North Central, and Northeast regions; central Texas values are based on Texas climatological divisions 3, 6, and 7).

likely due to reduced feather quality (Dawson et al. 2000). On the ultimate level, ecological conditions appear to be an important selective factor in the multiple independent evolutionary origins of premolt departure from the breeding grounds. Premolt movements are common in migrants that breed in lowland western North America where conditions become dry and unproductive in late summer, but uncommon in related migrants to the east where precipitation is near the annual peak in summer (Fig. 1; Rohwer et al. 2005, Butler et al. 2006). The benefits to an individual of periodically paying the costs of molt and producing high quality feathers are probably substantial (Nilsson and Svensson 1996). Thus, understanding breeding-season influences on where and when molt happens is important for the conservation of species and populations (Butler et al. 2002, Leu and Thompson 2002), and for understanding life-history evolution.

Here, we report a study of molt in two insectivorous migrants, the Black-capped Vireo (*Vireo atricapilla*) and the White-eyed Vireo (*V. griseus*). We studied populations in central Texas, near the latitudinal center of the historic Black-capped Vireo range, which extended north to Kansas and south to northern Mexico (Grzybowski 1995), and near the southwestern corner of migrant White-eyed Vireo range, which extends north to Iowa and east to Massachusetts and Florida (Hopp et al. 1995). No detailed molt studies exist for either species (Pyle 1997), so two of our goals were to document the timing and location of molt of the endangered Black-capped Vireo, and to make comparisons of molt in this species to molt in a common sympatric congener.

Our wider purpose was to isolate temporal and ecological forces that might influence the evolution of molt strategies in temperate migrants generally. For species or populations that breed in the far north (e.g., *Zonotrichia* sparrows breeding at ~60°N; Mewaldt and King 1978), weather and foraging conditions deteriorate rapidly after breeding (Bonier et al. 2007). This short time window may favor the evolution of rapid molt on the breeding grounds (Rimmer 1988), or partial molt on the breeding grounds followed by additional molt on the wintering grounds (Mulvihill and Rimmer 1997), or departure from the breeding grounds before any molt (Rohwer et al. 2005). Birds breeding farther south, such as the vireos in our study in Texas (31°N), probably have a longer postbreeding window in which to molt, and thus might be predicted to complete all molt on the breeding grounds and to molt relatively slowly.

Although time constraints may be weaker in the south than in the north, ecological conditions may nevertheless be an important selective pressure in the evolution of molt scheduling in birds breeding farther south. The substantial food resources required for molt (Murphy and King 1992, Lindström et al. 1993, Bonier et al. 2007) may not be available to insectivores if their breeding grounds become dry in response to a sharp decline in rainfall (Rohwer et al. 2005), as happens in the breeding habitat of the vireos in this study (Fig. 1). Accordingly, Texas populations of the Painted Bunting (*Passerina ciris*; Thompson 1991) and the Ash-throated Flycatcher (*Myiarchus cinerascens*; Butler et al. 2006) depart their breeding grounds prior to molting and move to the Mexican monsoon region (Douglas et al. 1993), which experiences a large increase in rainfall in late summer (Fig. 1). Moving to the Mexican monsoon region to molt would also take Black-capped Vireos to their wintering grounds (Graber 1961). Thus, vireos breeding in Texas offered an opportunity to test these opposing predictions (latitude predicting complete, slow molt and ecology predicting premolt migration) and, in the absence of any published molt data, we predicted that both species would depart the study area before completing molt. However, both species replaced all flight and body feathers prior to migration (see Results), which allowed us to test three predictions about molt dynamics in relation to breeding-season effects.

First, Black-capped Vireos in our study area have recently been shown to experience higher nest failure rates, due to nest predation and parasitism by the Brown-headed Cowbird (*Molothrus ater*), in highly clumped, grassy scrub than in more contiguous shrubby habitat (Noa et al. 2007). White-eyed Vireos are also susceptible to cowbird parasitism and nest predation (Hopp et al. 1995; LKB and TJH, pers. obs.), and they breed in every area in which Black-capped Vireos breed in our study area. Both species also renest in response to nest failure (Grzybowski 1995, Hopp et al. 1995), so we predicted that as a result of renesting, adults at the low nest success site would begin molting later than adults at the other site.

Second, in 2006, values of the standardized Southern Oscillation Index changed from positive (La Niña) to negative (El Niño), resulting in exceptionally hot and dry weather in Texas, typical of an El Niño year (Kiladis and Diaz 1989). In 2007, conditions reversed, and Texas experienced wet weather typical of La Niña (Kiladis and Diaz 1989). Conditions reversed again in 2008. We took advantage of these alternations to test the prediction that the dramatic increase in primary productivity we observed in 2007 would, by increasing abundance of leaf-eating insects (e.g., Lepidopteran larvae), support a longer breeding season and thus delay molt compared to dry years.

Third, we compared our field estimates of the onset and rate of molt to estimates obtained from museum specimens for Black-capped Vireos collected in central Texas, to test the common assumption that field data are comparable to specimen-based averages for North American passerines (Rohwer et al. 2005, Butler et al. 2006).

METHODS

STUDY AREA

We conducted fieldwork at Fort Hood, Texas (31°08′N, 97°46′W), an 88 000 ha military training area divided into east and west sides by a 15 km wide, north–south oriented, restricted-access live fire area (Cimprich and Kostecke 2006). About 7000 ha of Black-capped Vireo breeding habitat, typified by early successional scrub with deciduous vegetation extending to the ground (Grzybowski et al. 1994, Cimprich and Kostecke 2006), are scattered throughout Fort Hood (Cimprich and Kostecke 2006). White-eyed Vireos breed in a wider variety of scrubby and woody habitat than Black-capped Vireos (Hopp et al. 1995), and are common in almost every shrubby and wooded area on Fort Hood during the breeding season (LKB and TJH, pers. obs.). Common trees and bushes in our sampling areas were shin oak (*Quercus sinuata*), Ashe juniper (*Juniperus ashei*), redbud (*Cercis canadensis*), and, to a lesser extent, Texas ash (*Fraxinus texensis*) and Texas live oak (*Q. fusiformis*).

SITE CONTRASTS IN HABITAT AND NEST SUCCESS

In 2006 we compared molt of vireos on the east and west sides of Fort Hood. West Fort Hood has much more extensive areas of small (<20 m wide) deciduous clumps surrounded by grass and bare ground ("donuts"; Cimprich and Kostecke 2006) than east Fort Hood (Noa et al. 2007). Black-capped Vireo males are half as common and daily nest survival probability is significantly lower in donut habitat (~94%) than in the shrubby habitat (~97%) that typifies east Fort Hood (Noa et al. 2007). We also compared vireo body condition (see below) to test whether any site differences in molt could be attributed to site differences in condition-dependent habitat quality (Grubb and Yosef 1994, Johnson 2007).

INTERANNUAL CONTRASTS IN WEATHER

The Southern Oscillation Index changed from positive (La Niña) to negative (El Niño) in 2006 (all weather data from National Climatic Data Center online databases, <http://lwf.ncdc.noaa.gov/oa/ncdc.html>), resulting in extremely dry conditions in central Texas (Kiladis and Diaz 1989). Of the first six months of 2006, four had below normal precipitation and five had above or much above normal temperatures, including the warmest April on record (111 years of data). With a shift from El Niño to La Niña in fall 2006, conditions in Texas started changing. Of the first six months of 2007, four had much above normal precipitation, including the wettest March on record, and three had below normal temperatures. This shift in weather changed moisture conditions from "extreme drought" in 2006 (according to the Palmer drought severity index; Heddinghause and Sabol 1991) to "extremely moist" in June of 2007. In 2008 conditions reversed again, with the 23rd-driest January–May period in Texas on record (113 years of data), resulting in drought.

FIELD DATA ON MOLT AND CONDITION

Birds were captured from 20 June to 29 August 2006, 20 June to 9 July 2007, and (White-eyed Vireos only) 20 June to 1 July 2008, by attracting them to mist nets with playback of male songs (Bradley 1980, Gryzbowski 1995), chatter calls (Bradley 1980), and screech owl (*Megascops asio*) calls. Males of both species were more likely to be caught than females, so females comprised only 20% of all molting Black-capped Vireos ($n = 40$ including one individual of unknown sex) and 17% of all molting White-eyed Vireos ($n = 82$ including 10 individuals of unknown sex) that we examined. Sex was determined by a combination of singing behavior during playback (Bradley 1980, Grzybowski 1995), incubation patch development (Grzybowski 1995, Hopp et al. 1995), and plumage traits (Black-capped Vireos; Pyle 1997).

We treated all molt scores as independent samples from different individuals. Nearly all birds were fitted with U.S. Fish and Wildlife Service aluminum leg bands before release, and no banded bird was used twice in any analysis. A few birds escaped or were released for other reasons before bands were applied, but both sexes are very difficult to recapture using our playback method, and we avoided netting in the same area twice. Thus, it is very unlikely that any unbanded birds were sampled more than once.

Progression and intensity of wing and tail molt were estimated by scoring each growing feather on a scale from 0.0 to 1.0, in increments of 0.05, with 0.0 = missing, 1.0 = newly grown or with sheathing at the base, and, for example, 0.75 = 75% of fully grown length. Small pin feathers were scored as 0.05 and feathers more than 95% grown with swollen, vascularized follicles were scored as 0.99. For each individual, progression of molt was calculated by summing the individual

scores for each molt series, then dividing by the number of feathers in the tract (10 primaries, six outer secondaries, and six rectrices per side), to yield percent molt completed.

We described the sequence of replacement of flight feathers following the method of Yuri and Rohwer (1997), with modifications suggested by S. Rohwer (University of Washington, unpubl. data), by comparing the length of each growing feather to the length of adjacent growing feathers. Nodal feathers start molt series, and are distinguished by being more advanced in growth than neighboring feathers. Terminal feathers end molt series, and are distinguished by being less advanced in growth than both neighbors. The direction of replacement is indicated when a growing feather is longer than one neighbor but shorter than the other neighbor. For example, if P2 = 0.8, P3 = 0.6, and P4 = 0.3, then P3 indicates proximal to distal replacement. The outermost feathers of the wing (P10) and tail (R6) can only be nodal or terminal because they have only one neighbor. We did not compare neighbors if both scored >0.95, because growth of individual feathers slows as they near their full length, making comparisons of neighboring feathers unreliable (S. Rohwer, pers. comm.).

Body molt was examined by blowing on different body regions to expose feather bases, and then estimating the percentage of developing feathers in each region (following Rohwer 1986) on the following scale: 0 = none (or an asymmetrical patch, which indicates accidental loss), 1 = <5% growing, 2 = 5%–30% growing, 3 = 30%–60% growing, and 4 = >60% growing. The ventral tract was divided into the chin, throat, breast, and belly, and the dorsal tracts were divided into the crown, nape, back, and rump (Pyle 1997). Total body molt intensity was calculated by summing the scores for each region and then diving by the maximum possible molt score (8 regions × molt score of 4 = 32).

Body mass was measured using a 30 g Pesola Micro-Line spring scale graduated to 0.25 g (accuracy ±0.3%). Tarsus length was measured using a pair of calipers (model SPI 2000, Swiss Precision Instruments, Switzerland) graduated to 0.1 mm (accuracy ± 0.0015 mm), following the method of Pyle (1997).

MOLT DATA FROM STUDY SKINS

We examined all Black-capped and White-eyed Vireos collected between 15 June and 31 August in central Texas in the collections of the American Museum of Natural History, Field Museum of Natural History, Museum of Comparative Zoology (Harvard University), National Museum of Natural History (Smithsonian), Texas Wildlife Cooperative (Texas A&M University), and Texas Technical University. We found 11 molting Black-capped Vireos collected from ~100 km south to ~200 km southwest of Fort Hood. Unfortunately, only one molting White-eyed Vireo specimen was discovered within 200 km of Fort Hood, and an internet search of the ORNIS database (<http://olla.berkeley.edu/ornisnet/>) of other large

collections suggested that very few additional specimens were available from this area at this time, so we only compared field and museum data for Black-capped Vireos. Primary molt was scored on these specimens by lifting the underwing coverts with a probe, inspecting the base of each primary under bright light, and estimating the percent of fully grown length as described above.

STATISTICAL ANALYSES

To test for site differences in the rate and timing of primary molt in 2006, we regressed day of year on the percentage of primary molt completed (Pimm 1976), with study site (east or west Fort Hood) as a covariate. In the model, a significant effect of site means that birds at one site reached a given percentage of molt completed earlier than birds at the other site. A significant interaction between study site and percent molt completed means that sites differed in the duration of primary molt. We planned a Mann-Whitney U-test of the prediction that a faster-molting population would have more primary feathers growing simultaneously, indicating more intense molt, than a slower-molting population.

We tested for differences in the onset of primary molt between the dry El Niño years (2006 and 2008) and the wet La Niña year (2007) by comparing the frequency of molting birds near the onset of molt in late spring (comparing Pimm's regressions was not possible because sampling ended on 9 July in 2007.) We controlled for sampling effort (Rohwer et al. 2007) by comparing the frequency of molting adults over time periods with similar sampling distributions each year within each species.

We used graphical and tabular methods to describe the relative timing of molt among the body and flight feathers, which appears to vary across species (Butler et al. 2002, Newton and Rothery 2005) and thus is probably the result of selection on replacement patterns. For illustrative purposes we fit quadratic curves to plots illustrating change in molt intensity over time in 2006, because molt intensity has been shown to increase as more tracts start to molt, and then decline as the different tracts complete replacement (Morton and Welton 1973, DeGraw and Kern 1990). To test for differences in body condition during molt, we used ANCOVA with body mass as the dependent variable, and tarsus length and study site, or tarsus length and year, as independent variables (García-Berthou 2001). Data are presented as means ± SD, and statistical significance was accepted at $P < 0.05$.

RESULTS

MOLT SEQUENCES

Molt in both species began with replacement of P1 and proceeded distally in one series, terminating with P10 (Table 1). The next two series began with S8, after primary molt reached P2 or P3 in Black-capped Vireos (one each with growing

TABLE 1. Number of primary feathers (columns directly below feather numbers) and pairs of neighbors (columns between feather numbers) illustrating identical series of primary replacement in Black-capped Vireos and White-eyed Vireos, and the number of growing feathers examined (n). No pair of feathers indicated distal to proximal replacement.

Species Assignment	Primary									
	1	2	3	4	5	6	7	8	9	10
Black-capped Vireo										
Nodal	14									
Proximal to distal		14	11	7	2	1	3	10	14	17
Terminal										17
n	22	21	12	8	3	3	10	14	20	18
White-eyed Vireo										
Nodal	32									
Proximal to distal		32	17	14	16	15	10	8	12	8
Terminal										8
n	49	44	25	20	22	18	13	13	12	8

S8 ≤0.2) and P3 or P4 in White-eyed Vireos (two and one birds, respectively, with S8 ≤0.2), and proceeded proximally to S9, and then distally to S7 (Table 2).

Molt of the outer secondaries began with S1 (Table 2), after primary molt reached at least P5 in White-eyed Vireos (n = 2 with S1 <20% grown; Fig. 2A). Unfortunately, no Black-capped Vireos were captured with growing S1 <99%, but S1 was old in birds with P4 = 0 (n = 3) or P5 = 0.15 (n = 1). In one Black-capped Vireo specimen with S1 = 0.6 (SNMNH 184838), molt had progressed to P7 = 0.1. In both species, secondary was molt completed about the same time as primary molt (Fig. 2A, 2B).

Among flight feathers, tail molt (Table 3) started last in White-eyed Vireos and finished first in both species (Fig 2C, 2D). In White-eyed Vireos with overall tail molt <10% complete, molt had already progressed to P6 (n = 5) or P7 (n = 3). No Black-capped Vireos were sampled in early tail molt, but in two individuals with the tail about 40% replaced, primary molt had progressed to P9 (Fig. 2C). Tail molt was intense in both species, as indicated by the simultaneous replacement of the inner rectrices: among birds in which the tail was not yet fully grown (all R1–4 ≤0.95), R1–4 scores differed by ≤0.20 in all six Black-capped Vireos and 11 of 15 White-eyed Vireos. Furthermore, among the seven White-eyed Vireos with R1 ≤0.10 (i.e., birds in very early tail molt), R2–5 were ≤0.10 in five birds, and the entire tail was ≤0.10 in four of those five.

Body molt started after P1 was dropped but before P1 was fully grown (three of six Black-capped and 11 of 19 White-eyed Vireos with growing P1 ≤0.3 had no body molt), with nearly simultaneous start of replacement on the breast and back, followed by the rump, crown, belly, nape, throat, and chin (Table 4). Molt in some body regions was completed before primary molt in some individuals (Table 4), and the surface of the plumage of all individuals appeared completely

TABLE 2. Number of secondary feathers (columns directly below feather numbers) and pairs of neighbors (columns between feather numbers) illustrating sequence of replacement in Black-capped Vireos and White-eyed Vireos, and the number of growing feathers examined (n).

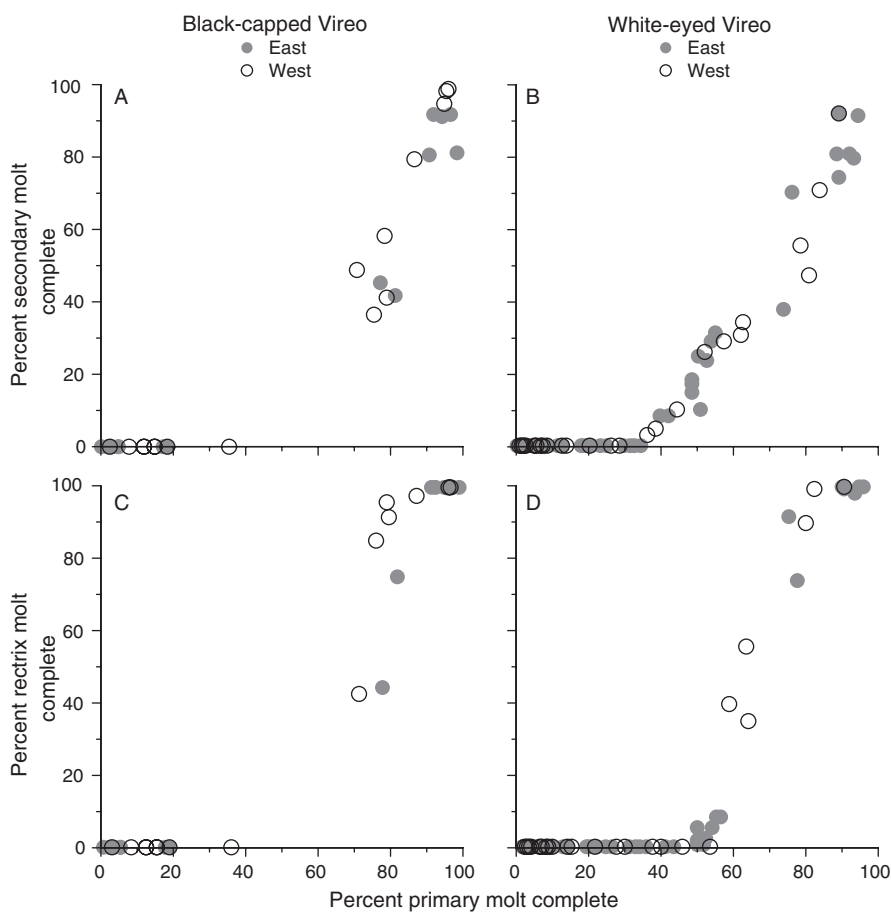| Species Assignment	Secondary								
	1	2	3	4	5	6	7	8	9
Black-capped Vireo									
Nodal	2							1	
Distal to proximal		2	10	13	15	11		5	
Proximal to distal							3		5
Terminal					3	8			4
n	4	11	13	20	17	17	4	7	10
White-eyed Vireo									
Nodal	17							4	
Distal to proximal		12	6	5	8	6		5	
Proximal to distal							1	1	8
Terminal					1	6			12
n	17	17	11	12	9	10	17	13	16

FIGURE 2.   Relationship between progression of molt in the flight feathers of Black-capped Vireos and White-eyed Vireos on the east and west sides of Fort Hood, Texas (~20 km apart). Secondary molt (A, B) starts after but completes at approximately the same time as primary molt. Rectrix molt (C, D) starts after but completes before primary molt in both species, and appears to start after secondary molt in White-eyed Vireos.

TABLE 3.   Number of rectrices (columns directly below rectrix numbers) and neighboring pairs of rectrices (columns between rectrix numbers) illustrating replacement sequence of the tail in Black-capped Vireos and White-eyed Vireos, and the number of growing feathers examined (n).

Species	Rectrix					
Assignment	1	2	3	4	5	6
Black-capped Vireo						
Nodal	1					
Proximal to distal		1	1	2	8	9
Distal to proximal		1				
Terminal	1					9
n	8	6	7	6	11	14
White-eyed Vireo						
Nodal	1	3	2		1	
Proximal to distal		1	6	6	12	13
Distal to proximal		8	3		1	
Terminal	8			1		13
n	16	16	16	16	14	14

new, with no old body feathers remaining, before primary molt was complete.

SITE CONTRASTS

Onset and rate of molt. Black-capped Vireos started molting 13 days later (8 July) in the west site than the east site (25 June) in 2006 (ANCOVA, main factor = site: $F_{1,30} = 21.3$, $P < 0.001$). After starting later, west-site Black-capped Vireos completed primary replacement 12 days faster (50 days) than east-site birds (62 days; interaction term = site∗percent molt complete: $F_{1,30} = 6.5$, $P = 0.02$; Fig. 3). The specimen-based estimate was intermediate: 54-day molt starting 6 July ($y = 188.2 + 0.54x$, $r^2 = 0.85$, $n = 11$). An adult (SNMNH 109494) collected on 1 September in San Angelo, Texas (31°27′N, 100°26′W), had all new body feathers, with only remnants of sheathing at the base of P9 on both wings, P10 = 0.95 on one wing, and P10 fully grown with no sheathing at the base on the other wing.

White-eyed Vireos also started molting later in the west site (13 July) than the east site (2 July) in 2006 (ANCOVA,

TABLE 4. Percentage of vireos replacing feathers in eight body regions relative to the progression of primary feather molt. Percentages <100% during molt of primaries 7–10 indicate individuals that had completed molt in those regions. Dashes indicate no data.

| Species | Most distal growing primary feather | | | | | | |
Body region	1	2	3	4	5	6	7–10
Black-capped Vireo							
Breast		63	100	—	100	—	100
Back		50	85	—	100	—	100
Rump		13	83	—	100	—	100
Crown		13	50	—	100	—	94
Belly		67		—	100	—	100
Nape		50		—		—	100
Throat		17		—	100	—	100
Chin				—	100	—	94
n	2	8	6	0	1	0	16
White-eyed Vireo							
Breast	20	54	91	100	100	100	100
Back	20	58	73	100	100	100	89
Rump		8	9	100	100	100	100
Crown		4	30	100	100	100	94
Belly		12	20	50	43	100	100
Nape		8	36	25	43	86	100
Throat			10	25	71	71	94
Chin			20	25	71	71	100
n	5	26	11	4	7	7	18

main factor = site: $F_{1,64} = 13.3$, $P = 0.001$). However, White-eyed Vireos did not complete primary replacement significantly faster in the west than the east site (west = 56 days, east = 63 days; ANCOVA, interaction term = site*percent molt complete: $F_{1,64} = 1.0$, $P = 0.33$; Fig. 3). We caught enough female White-eyed Vireos in the east site to test the prediction that females molt later than males, as in other passerines, but no significant difference was found (ANCOVA among individuals of known sex, female: $n = 8$, male: $n = 33$, interaction term = sex*percent molt complete: $F_{1,37} = 1.1$, $P = 0.30$).

Molt intensity. Black-capped Vireos averaged 2.9 ± 0.7 ($n = 10$) simultaneously growing primaries in the west site and 2.5 ± 1.2 ($n = 10$) in the east site, but this difference was not significant ($U = 38.5$, $P = 0.38$; analysis only includes birds in which molt had not progressed to P10). Peak molt intensity, estimated by the combined percentage of all flight feathers molting (on one side, $n = 22$) and maximum possible body molt score (32, see Methods), was also similar between sites within each species (Fig. 4). West-site populations of both species reached peak molt intensity in a shorter time than east-site populations, and that difference was more distinct in Black-capped Vireos, paralleling species and population differences in primary molt onset and duration (Fig. 4).

Body condition. Site differences in molt dynamics in 2006 were not correlated with body condition differences in either species (Black-capped Vireos: body mass, east = 9.1 ± 0.6 g, $n = 7$, dates = 4 July–29 August; west = 9.1 ± 0.4 g, $n = 13$, dates = 8 July–28 August; ANCOVA with body mass as dependent variable, interaction term = tarsus length*population: $F_{1,16} = 0.7$, $P = 0.41$; White-eyed Vireos: east = 11.7 ± 0.8 g, $n = 41$, dates = 1 July–29 August; west: 11.6 ± 0.6 g, $n = 28$, dates = 7 July–28 August, $F_{1,65} = 2.2$, $P = 0.14$; Fig. 5).

CONTRASTS BETWEEN DRY AND WET YEARS

Onset of molt. Molt started significantly earlier in both species under the drought conditions of 2006 than the wet conditions of 2007, as reflected by the proportion of molting birds near the onset of molt (Table 5). Among Black-capped Vireos sampled in the east site from 21 June to 5 July, significantly more were molting in 2006 (82%, $n = 17$) than in 2007 (29%, $n = 7$; $\chi^2_1 = 6.5$, $P = 0.01$). Likewise, significantly more White-eyed Vireos sampled in the east site from 21 June to 10 July were molting in 2006 (56%, $n = 32$) than in 2007 (21%, $n = 29$; $\chi^2_1 = 8.1$, $P = 0.01$). Because sampling effort was biased later in the wet year in White-eyed Vireos (Table 5), they were probably delayed even longer in 2007 than this analysis suggests. Only
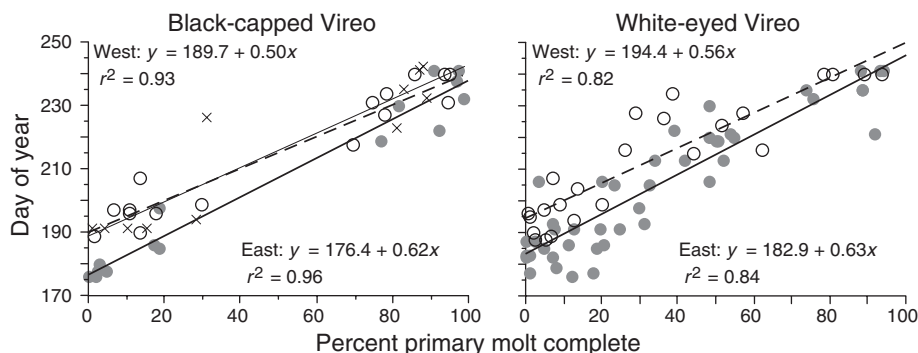

FIGURE 3. Regression of day of year on the percentage of primary molt completed, to estimate the onset and rate of molt for adult vireos captured at two sites at Fort Hood, Texas (western site = unfilled circles, dashed line, eastern site = filled circles, solid line), and for Black-capped Vireo specimens collected in Texas (indicated by "×", gray line). Steeper slope indicates slower molt and higher line position indicates later molt.
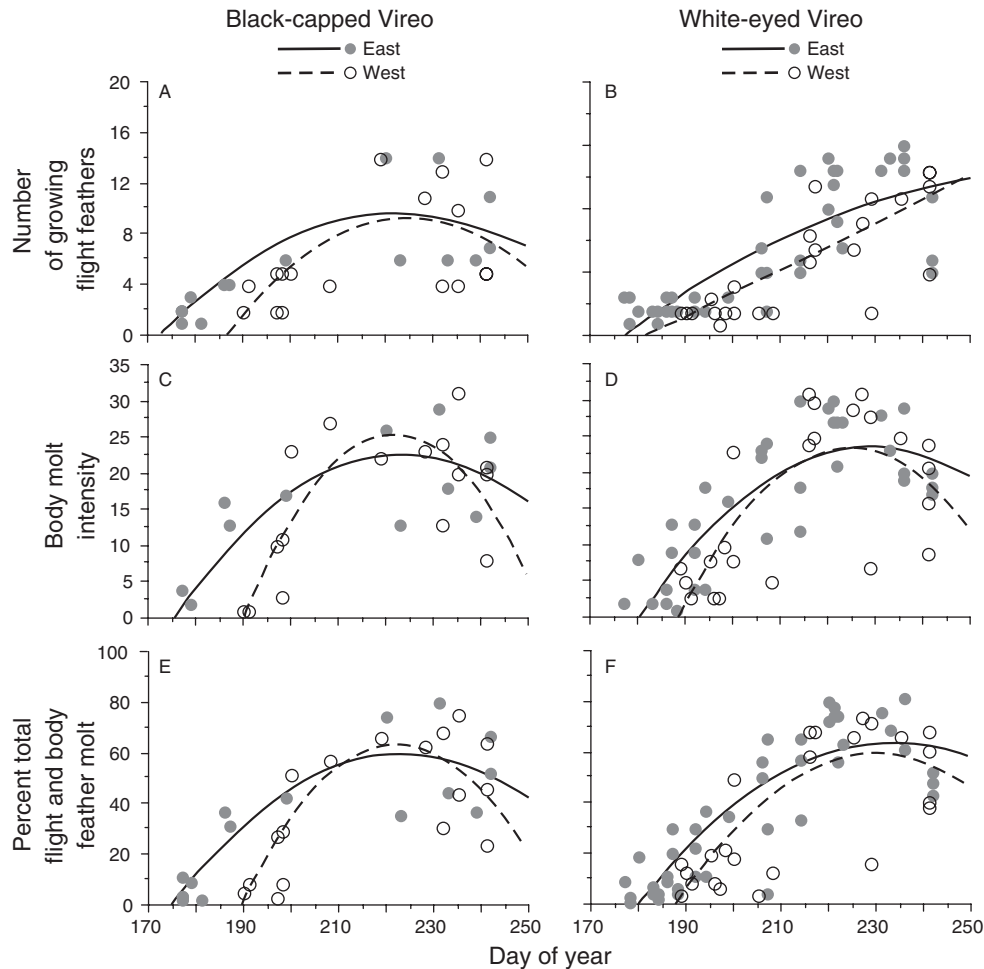
FIGURE 4. Changes in (A, B) flight feather and (C, D) body feather molt intensity over time in vireos captured at two sites at Fort Hood, Texas. Percent overall molt intensity (E, F) is the sum of the number of growing flight feathers per side and body molt intensity divided by their highest possible combined value (maximum possible number of growing flight feathers = 22, maximum possible body molt score = 32). Peak molt intensity was similar between eastern and western study sites within each species, but molt intensity increased slightly later and more rapidly in the western site (quadratic lines shown for visual aid).

White-eyed Vireos were sampled in 2008 (a dry year), but nine of 13 adults captured between 21 June and 1 July were molting, a significantly higher proportion ($\chi^2_1 = 7.9$, $P = 0.005$) than over a later time frame in 2007 (to 10 July), making this a conservative test.

Body condition. Body condition during the onset of molt did not differ significantly between or among years in either species (Black-capped Vireos: body mass: 2006 [dry year] = 9.1 ± 0.4 g, $n = 11$, dates 20 June–4 July; 2007 [wet year] = 9.4 ± 0.6 g, $n = 11$, dates 21 June–8 July; ANCOVA, interaction term = year*tarsus length: $F_{1,18} = 0.3$, $P = 0.61$; Fig. 6; White-eyed Vireos: 2006 = 11.9 ± 0.6 g, $n = 22$, dates 21 June–6 July; 2007 = 11.4 ± 0.7 g, $n = 27$, dates 21 June–8 July; 2008 [dry year] = 11.7 ± 0.5 g, $n = 14$, dates 20 June–1 July; $F_{2,57} = 0.3$, $P = 0.77$; Fig. 6; dry years pooled: $F_{1,59} = 0.2$, $P = 0.67$).

DISCUSSION

MOLT SEQUENCE AND INTENSITY

In contrast to the common sequence of flight feather replacement described here and in other passerines (Jenni and Winkler 1994), the relative timing of replacement among molt series seems to vary. Black-capped and White-eyed Vireos drop S1 when P5 is very early in growth, and S6 finishes growing about the same time as P10, similar to other vireos (Voelker and Rohwer 1998, Voelker 2000). In contrast, in Western Tanagers (*Piranga ludoviciana*) secondary molt starts only after P5 is fully grown, adding 11 days (~25%) to the molting period (Butler et al. 2002), and some European Greenfinches (*Carduelis chloris*) drop S1 after molt has progressed to P7, adding up to 19 days (~20%) to the molting period (Newton and Rothery 2005). This variation surely
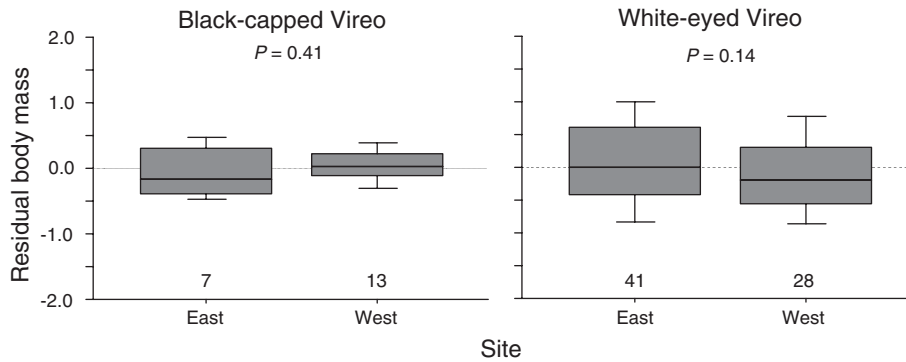
FIGURE 5.   Residuals of body mass regressed on tarsus length of molting adult vireos were not significantly different between eastern and western sites at Fort Hood, Texas, in 2006. Sample sizes shown at bottom. From top to bottom, horizontal lines in each box plot indicate: the upper quartile + 1.5 × interquartile range, the upper quartile, the median, the lower quartile, and the lower quartile – 1.5 × interquartile range.

reflects adaptation to aerodynamic and temporal demands, but descriptions of molt are needed for more species before comparative tests can be made.

Tail molt in both species started with the loss of the inner three or four rectrices, followed closely by sequential molt of the outer rectrices. The paucity of Black-capped Vireos captured when the tail would have been growing and very short (primary molt 20%–70% complete) was not due to adults not hearing our playback. They were frequently seen moving through vegetation toward the playback, but stopping short of pursuing it into the net. White-eyed Vireos also responded shyly, but their greater abundance permitted greater capture success. Intense tail molt also occurs in warbling-vireos (Voelker and Rohwer 1998). Too few data currently exist for a comparative test of tail molt patterns, but across species, intense tail molt should be associated with a tail-independent foraging mode during molt such as gleaning or ground foraging (Rohwer and Butler 1977). We know of no study showing

tail molt extending as far as secondary molt beyond primary molt in a passerine, suggesting that secondary molt is delayed to extend the time between molting primaries and molting secondaries (Jenni and Winkler 1994).

POPULATION-SCALE EFFECTS OF NEST
SUCCESS ON MOLT

Birds started molting later in the clumped habitat in west Fort Hood, where Black-capped Vireos have high nest failure rates due to predators and cowbirds (Noa et al. 2007), than in east Fort Hood. This corresponds with our expectation of later molt in the high nest failure site because of the high likelihood that Black-capped and White-eyed Vireos renest after nest failure (Grzybowski 1995, Hopp et al. 1995), thus extending breeding activities. This agrees with studies of other passerines showing that late-breeding individuals are also late molters (Siikamäki et al. 1994, Nilsson and Svensson 1996, Hemborg 1999), and that onset of molt is linked to the cessation of breeding activities (Rivera et al. 1998). Late molt can be costly, however, because it can result in more rapid feather production (Dawson 2004) and lower feather quality (Dawson et al. 2000) in some species, which can reduce winter survival and subsequent reproductive success (Nilsson and Svensson 1996). Therefore, nest predators and brood parasites may reduce adult fitness not only directly by killing offspring, but also indirectly through a molt-mediated reduction in survival, which may take effect months after the predation or parasitism occurs.

We cannot exclude the possibilities that differences between study sites other than nest failure rate caused the molt differences that we found, or that late-molting adults compensated in some way so that they produced high-quality feathers. Noa et al. (2007) found that Black-capped Vireos were less abundant, and that second-year males were more common, in donut habitat than in shrubland at Fort Hood, suggesting a difference in habitat quality or preference. However, any explanation for site differences in molt must be consistent with the

TABLE 5.   Distribution of vireos sampled in five-day intervals near the onset of molt in wet (La Niña) and dry (El Niño) years, and the percentage of those individuals that were molting. Estimated start of molt in 2006 was 25 June for Black-capped Vireos and 1 July for White-eyed Vireos. Dashes indicate no data.

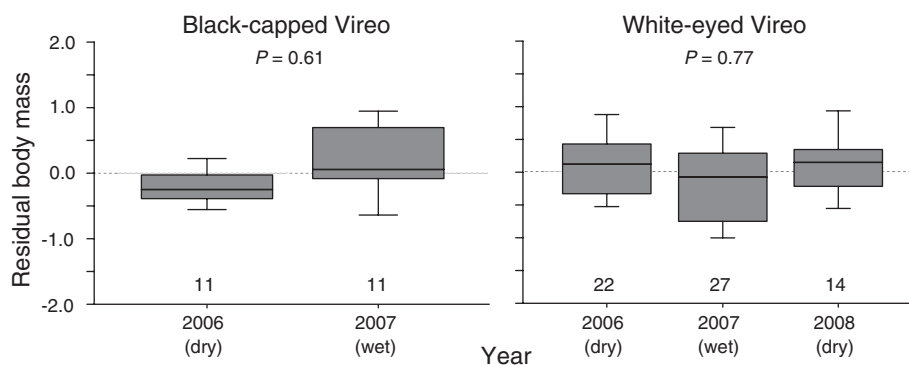| Species Year | Samples per five-day period | | | | | |
	21–25 June	26–30 June	1–5 July	6–10 July	n	Percent molting
Black-capped Vireo						
2006 (dry)	6	8	3	—	17	82
2007 (wet)	3	3	1	—	7	29
White-eyed Vireo						
2006 (dry)	7	7	10	8	32	56
2007 (wet)	6	6	3	14	29	21
2008 (dry)	2	7	5	—	14	64

FIGURE 6.   Residuals of body mass regressed on tarsus length of adult vireos during late spring, near the onset of molt, did not vary significantly with yearly differences in precipitation at Fort Hood, Texas. Sample sizes shown at bottom. From top to bottom, horizontal lines in each box plot indicate: the upper quartile $+ 1.5 \times$ interquartile range, the upper quartile, the median, the lower quartile, and the lower quartile $- 1.5 \times$ interquartile range.

observation that adult vireos were in similar body condition in sites where molting started early or late. In other species with small-scale geographic differences in molt rate, faster molt was associated with higher body mass during molt (Heise and Rimmer 2000, Borras et al. 2004). Furthermore, in a parallel study, we found no differences between birds in east and west sites in baseline or stress-induced concentrations of the glucocorticoid corticosterone (LKB, TJH, and LMR, unpubl. data), which have been correlated with habitat quality (Marra and Holberton 1998) and long-term stress (Wingfield and Romero 2001) in birds. Kostecke and Cimprich (2008) found higher Black-capped Vireo survival in west than east Fort Hood, although they focused on high-quality shrubby (not donut) habitat in the west.

EL NIÑO EFFECTS ON MOLT

Molting birds were more common over the same time period in late June and early July in 2006, a dry El Niño year, than in 2007, a wet La Niña year. This pattern reversed in White-eyed Vireos in 2008 as La Niña conditions subsided, suggesting an oscillation in molt onset correlated with the El Niño–Southern Oscillation (ENSO). We conclude that heavy spring precipitation delayed molt in these dry-country breeders, as would be predicted if wet conditions caused adults to extend reproductive activities. Food availability during the breeding season is well-known to limit reproduction in insectivorous birds (Martin 1987), especially in relation to the number of nesting attempts made by adults (Rodenhouse and Holmes 1992, Zanette et al. 2006). The proclivity of Black-capped and White-eyed Vireos to raise multiple broods and renest (Grzybowski 1995, Hopp et al. 1995) makes them likely to exhibit strong variation in the duration of breeding activities in response to variation in food availability. Therefore, molt was likely delayed in 2007 because the dramatically greater primary productivity in the La Niña year provided more abundant leaf-eating insect prey for breeding adults, which supported renesting.

The effects of global climate change and ENSO on birds have been the subject of many studies around the planet. For passerines, ENSO has been shown to affect abundance (Grant and Grant 1987, Jaksic and Lazo 1999), reproductive schedules (Baptista 1984, Wilson and Arcese 2003, Hau et al. 2004), reproductive success (Sillett et al. 2000, Christman 2002, Wilson and Arcese 2003), and winter survival (Sillett et al. 2000). To our knowledge, this study is the first to show an effect of ENSO on molt. Together, sensitivity of the timing of molt to weather conditions in the preceding months, time constraints on molt (especially at high latitude; Bonier et al. 2007), and costs of low-quality feather production due to late, rapid molt (Dawson et al. 2004), suggest a complex and underappreciated molt-mediated threat to bird populations.

IMPLICATIONS FOR THE EVOLUTION
OF MOLT SCHEDULING

Complete breeding-ground molt in these vireos was somewhat surprising, because other insectivores breeding in Texas molt after migrating to wetter areas to the south or west (Thompson 1991, Butler et al. 2006). Texas typically experiences a sharp decline in rainfall at the onset of molt, presumably making most vireo habitat very dry. Moving directly to the wintering grounds or to the Mexican monsoon region would require a relatively short migration (Voelker 2004), and would take adults to an area of greater rainfall and productivity.

As originally noted by Voelker (2000), vireos provide a good example of the evolutionary lability of molt scheduling in North American passerines. Three different molt schedules have been described in detail among six vireo species that migrate to breed in North America: complete or partial molt on the breeding grounds, and stopover molt in the Mexican monsoon region (summarized by Rohwer et al. 2005). Furthermore, primary molt durations vary by nearly 100% between the fastest and slowest molters: 38 days in Eastern Warbling-Vireos (sexes combined; Voelker and Rohwer 1998), but 70 days in male Gray Vireos (Voelker 2000).

Time may eventually be revealed as the dominant selective factor in the evolution of molt strategies among vireos, as suggested previously (Mulvihill and Rimmer 1997, Voelker and Rohwer 1998, Voelker 2000). Black-capped Vireos seemed to stop molting at our two study sites at about the same time in 2006, despite starting two weeks apart, and our long-term estimate using specimens showed a very similar ending date, suggesting a strong advantage to ending molt by a particular time, even if it means molting rapidly. This apparent limit on molt is striking, because these populations are so much farther south than other species that have been studied. The importance of time on the scheduling of molt could be tested by comparing White-eyed Vireos in Texas to: (1) White-eyed Vireos in Florida, which breed at the same latitude and so should molt at the same rate, and (2) White-eyed Vireos at the northern limit of their breeding range, which should molt faster than vireos in Texas and Florida. The similarity of our specimen- and field-based estimates of molt onset and duration in Black-capped Vireos validates the assumption that results obtained from these different study methods are comparable.

CONSERVATION IMPLICATIONS

We found a correlation between the frequency of nest failure and the onset and rate of molt in Black-capped Vireos, suggesting a possible role for cowbird or predator management in efforts to conserve Black-capped Vireo populations. The 50-day molt estimate for west-site Black-capped Vireos was only four days shorter than the long-term estimate based on museum specimens, but 2006 marked the end of an 18-year cowbird removal program that reduced cowbird parasitism from 90% to about 5% of Black-capped Vireo nests at Fort Hood (Hayden et al. 2000, Kostecke et al. 2006). Therefore, the delayed molt in west-site Black-capped Vireos in 2006 may reflect only a fraction of the potential effect of cowbird parasitism: if cowbirds were not controlled and parasitism rates were much higher, the onset of molt might be delayed even more.

Efforts to conserve birds should consider the potential impact of human disturbance when and where molt occurs. Stress during molt can decrease feather growth rates (Romero et al. 2005) and reduce feather quality (King and Murphy 1984). The secretive behavior of Black-capped Vireos in the middle of molt suggests a cost of responding to disturbance when the tail is mostly missing and overall molt intensity is high. Juvenile Black-capped Vireos and adults and juveniles of the endangered Golden-cheeked Warbler (*Dendroica chrysoparia*) also molt in Texas before migrating (LKB, TJH, and LMR, unpubl. data), offering an opportunity to consider molt in the management of two endangered birds simultaneously. Another opportunity exists in the Mexican monsoon region, where several western migrants converge to molt in July and August. Our ability to address conservation concerns at this time of year relies upon further detailed descriptions of molt, and greater understanding of how climatological variation and human disturbance affect birds before and during molt.

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