CONTRASTS IN SCHEDULING OF MOLT AND MIGRATION IN EASTERN AND WESTERN WARBLING-VIREOS

GARY VOELKER[1] AND SIEVERT ROHWER

*Burke Museum and Department of Zoology, Box 353010, University of Washington,
Seattle, Washington 98195, USA*

ABSTRACT.—Using museum specimens, we determined that Eastern (*Vireo gilvus*) and Western (*V. swainsonii*) warbling-vireos have contrasting schedules for their prebasic molt relative to fall migration. Adult *gilvus* replace their primaries rapidly (38 days) and complete prebasic molt after breeding but while still on the breeding grounds. In contrast, adult *swainsonii* that breed north of Mexico begin prebasic body molt on the breeding grounds and appear to continue it during migration. These birds leave the United States and Canada before initiating remigial molt, and our data suggest that many of them stop in northwestern Mexico to begin replacing flight feathers. Adult *swainsonii* take longer to replace their primaries (55 days) than do adult *gilvus*, presumably because most or all of their migration has been accomplished prior to the initiation of molt. Hatching-year *swainsonii* that breed north of Mexico remain in the United States and Canada until their first prebasic molt (body only) is completed, and thus are present long after adults have left. Both species undergo a prealternate molt of body plumage, and occasionally innermost secondaries and the innermost pair of rectrices, on the wintering grounds. Our results, along with previous studies of molt and migration, highlight the importance of the southwestern United States and northwestern Mexico to the nonbreeding biology of several species of passerines that breed in western North America. *Received 21 January 1997, accepted 1 July 1997.*

THE INTEGRATION OF MOLT into the annual cycle of a bird involves interesting life-history tradeoffs that have only begun to be explored. In large birds, time constraints on molting cause the extent of molt in the current year to be traded off against future breeding (Pietiainen et al. 1984, Langston and Rohwer 1996, Shugart and Rohwer 1996); late molting in passerines also may have detrimental effects on future breeding and survival (Nilsson and Svensson 1996). In the north temperate zone, migratory passerines have the option of scheduling the annual postbreeding molt before or after fall migration. Jenni and Winkler (1994) provide an excellent review of these patterns for European passerines. Most European migrants that winter north of the Sahara molt on their breeding grounds prior to fall migration. This strategy may result because food supplies differ little between their summer and winter quarters, and because molting during the cooler postmigratory season would entail greater thermoregulatory costs (Jenni and Winkler

1994). In contrast to short-distance migrants, many European passerines that winter south of the Sahara postpone their prebasic molt until during or after the fall migration, especially if they winter in southern Africa. These species generally encounter a long, productive rainy season when they arrive in their African winter quarters and are able to molt slowly during a time when food may be abundant (Jenni and Winkler 1994). Other species that overwinter in Ghana may molt more rapidly due to a shorter rainy season (Bensch et al. 1991).

Knowledge of the scheduling of molt relative to fall migration in passerines is far less complete in North America than in Europe. However, contrasts emerging between North American and European passerines are yielding insight into the life-history tradeoffs involved in the scheduling of molt and migration. Most migratory passerines that breed in eastern North America molt on the breeding grounds (Pyle et al. 1987). In contrast, adults of several passerine species that breed mainly west of the Rocky Mountains migrate entirely or part of the way to their wintering grounds before commencing prebasic molt (e.g. Western Wood-Pewee [*Contopus sordidulus*], Phillips and Parkes 1955; Gray [*Empidonax wrightii*] and Dusky [*E. oberholseri*]

[1] Present address: Barrick Museum, University of Nevada Las Vegas, 4505 Maryland Parkway, Box 454012, Las Vegas, Nevada 89154, USA. E-mail: voelker@hrc.nevada.edu

flycatchers, Johnson 1963; Lazuli Bunting [*Passerina amoena*], Young 1991; western populations of Painted Bunting [*Passerina ciris*], Thompson 1991). In another western species, the Bullock's Oriole (*Icterus bullockii*), both adults and juveniles undertake fall migration prior to molting (Rohwer and Manning 1990).

Exceptions to these patterns suggest that other selective forces or phylogenetic constraints influence the scheduling of molt. Two western species, Hermit Warbler (*Dendroica occidentalis*) and Townsend's Warbler (*D. townsendi*), molt on their breeding grounds (Jackson et al. 1992). Unlike the western species that migrate prior molting, these warblers breed in montane forests that surely are more productive in late summer than the lowlands west of the Rocky Mountains (Jackson et al. 1992). Curiously, two eastern species, Least Flycatchers (*Empidonax minimus*) and Orchard Orioles (*Icterus spurius*), migrate to their tropical wintering areas prior to undergoing prebasic molt (Dickey and Van Rossem 1938, Hussell 1980, Sealy and Biermann 1983). Do other ecological factors affect the tradeoff optima for these species, or have they recently been derived from western lineages and not yet evolved the eastern pattern of molting on the breeding grounds prior to the fall migration?

In this paper, we describe molts, and document differences in scheduling of molt and migration for Eastern (*Vireo gilvus*) and Western (*V. swainsonii*) warbling-vireos (Sibley and Monroe 1990). We also identify the probable migration route of *gilvus*, and show that *swainsonii* undergoes part of its prebasic molt during migration.

METHODS

Nomenclature and species identification.—We follow Johnson et al. (1988; see also AOU 1983) in recognizing *Vireo gilvus* and *V. leucophrys* (Brown-capped Vireo) as distinct species. Thus, we have excluded any Mexican brown-capped races (e.g., *eleanorae, amauronotus, strenuus*; see Sutton and Burleigh 1940) from consideration. Following Sibley and Monroe (1990; but not AOU 1983), we recognize two species of warbling-vireo, *gilvus* (Eastern Warbling-Vireo), and *swainsonii* (Western Warbling-Vireo). Where these species meet in Alberta, they differ in morphology and vocalizations (J. Barlow *in* Sibley and Monroe 1990) and by about 3% sequence divergence in their mitochondrial DNA (Murray et al. 1994).

We considered as potentially misidentified any specimen collected in Alberta, Saskatchewan, and Manitoba, and any United States specimen collected west to the Rocky Mountains near the region where the ranges of these species abut. Specimens from Texas pose no identification problems because their ranges do not meet (Rappole and Blacklock 1994). Specimens from areas of potential overlap were identified by bill measurements, which suffice for identification north of Mexico (Phillips 1991). Due to variations in bill shape among races of *swainsonii*, and the lack of information on wintering ranges of these races, we did not attempt to separate specimens to species in wintering areas where *gilvus* and *swainsonii* may co-occur.

Specimens.—We examined 1,228 specimens from 26 museums (see Acknowledgments). Because these species rarely winter in the United States (Remsen et al. 1996), our initial request was for specimens collected from 1 July to 31 December, regardless of locality, and specimens collected from 1 January to 30 April from south of the United States. May and June specimens were excluded because Nearctic passerines generally do not molt while breeding. These specimens were sorted into biweekly categories (e.g. 1 to 15 August and 16 to 31 August) and a second round of loans was requested that targeted underrepresented time periods and regions. In the second loans we were seeking specimens of *swainsonii* from the molting region; thus, we requested warbling-vireos collected south of the United States from 1 July to 30 April.

Scoring molt.—We followed Rohwer (1986) for determining if molt was adventitious. In examining specimens for molt we used a 2× magnifying lamp lighted with a 60-watt incandescent bulb, and a small forceps and dissecting probe to lift feathers and quantify molt. For body molt, we estimated the percentage of feathers growing in each of five regions: chin and throat, breast, belly, head, and back (see Rohwer 1986). We used Rohwer's (1986) scale of 0, 10, 30, 50, 70, and 90% of feathers in development. An overall body-molt score was calculated for each specimen by averaging the scores of the five body regions.

For scoring flight-feather molt we followed Rohwer's (1986) practice of estimating the fraction of full length (by 0.1 intervals) attained by each growing feather. Feathers scoring 1.0 were almost fully grown (0.95 or more) or known to have just completed growth because they still had sheathing at their base. We used "N" to designate new feathers in specimens collected when they might have been molting. Warbling-vireos have a total of 20 primaries, 18 secondaries, and 12 rectrices. Because P10 (most distal) is tiny, we did not score it for molt. We scored molt of flight feathers on both sides of each specimen.

We used Pimm's (1976) regression method to estimate duration of molt. We followed the molt terminology of Humphrey and Parkes (1959). Following Langston and Rohwer (1996), we define a molt series as a set of flight feathers that are replaced by a single

set of rules. To identify the feathers of a series and the rules by which they are replaced, each growing (focal) feather is placed in one of three categories based on its stage of replacement and the stage of replacement of adjacent feathers (Yuri and Rohwer 1997). Terminal feathers are those replaced last in a molt series (always less fully grown than adjacent feathers). Nodal feathers are those replaced first in a molt series (always more fully grown than adjacent feathers). Other growing feathers provide directional information, showing whether replacement proceeds proximally to distally (i.e. focal feather less fully grown than the next proximal feather but more fully grown than the next distal feather), or distally to proximally. See Yuri and Rohwer (1997) for a detailed explanation of the rules of feather replacement and the identification of molt series.

Age determination.—We followed Pyle et al. (1987) by referring to birds as either hatching year (HY; birds in their first calendar year) or after hatching year (AHY; birds in at least their second calendar year). Interestingly, only *swainsonii* can be aged by plumage characters after the first prebasic molt (see Results).

Winter and breeding ranges of gilvus.—The breeding range of this species (treated as *V. g. gilvus* in AOU 1957) extends from southwestern Alberta east across southern Canada to Nova Scotia, south to southeastern Montana, northern and eastern North Dakota, eastern South Dakota, eastern Nebraska, Kansas, southeastern Colorado, eastern Texas, southern Louisiana, northern Alabama, southeastern Tennessee, western North Carolina, and Virginia (AOU 1957, Sibley and Monroe 1990). The wintering range of *gilvus* is southern Mexico (Chiapas) south to Nicaragua (Phillips 1991). The breeding and wintering ranges do not overlap.

Winter and breeding ranges of swainsonii.—This species breeds from southeastern Alaska, northern British Columbia, northern and western Alberta, central Wyoming, Colorado (except southeastern), southwestern South Dakota, and western Nebraska south to southern California, southern Nevada, central and southeastern Arizona, southern New Mexico, western Texas, the southern tip of Baja California, and Morelos and Oaxaca in southern Mexico (Sibley 1940, AOU 1957 [including range of all non-*V. g. gilvus* races], Wilbur 1987, Sibley and Monroe 1990). The winter range extends from southern Sonora east to Veracruz and south to El Salvador (Sibley and Monroe 1990, Phillips 1991).

Molt and migration.—To infer where *gilvus* and *swainsonii* molt, and when they molt in relation to the fall migration, we plotted the collecting localities of molting and nonmolting specimens on maps of North America. For *gilvus*, these plots also allowed us to infer the route of fall and spring migration, which currently are unclear.

RESULTS

First prebasic molt and age determination.—We examined 30 *swainsonii* in first prebasic molt that were collected throughout the breeding range from 4 July to 16 August. None was replacing flight feathers. Body molt was intense; all but one specimen (MVZ 37024) was replacing feathers in all five body regions. The head or the head and back were the first body regions to finish this molt. Feathers of the belly and flanks seemed to be the last to be replaced. As suggested by Sutton (1948), undertail coverts were replaced at about the time that the juvenal rectrices were completing their growth.

Soon after fledging, *gilvus* replace their greater secondary coverts, rendering young birds indistinguishable from adults (Sutton 1948). Rectrix shape is unreliable as an aging character. The few known-age *gilvus* (based on skull-ossification data) could not be separated into age classes based on the shape of their rectrices (see Pyle et al.1987).

Unlike *gilvus*, HY *swainsonii* do not replace the buffy-tipped greater secondary coverts during their first prebasic molt, making it possible to distinguish them from AHY *swainsonii* in fresh basic plumage. None of 30 specimens undergoing their first prebasic body molt was replacing greater secondary coverts. An additional 62 *swainsonii* in first basic plumage had incompletely ossified skulls (collected 1 August to 30 September); 55 of these specimens had buffy-tipped coverts. Among these 55 specimens, those with worn coverts were losing their buffy tips, suggesting that the other seven HY birds that lacked these buffy tips had lost them through wear. All adults (i.e. fully ossified skulls) in fresh basic plumage lacked buffy tips on their greater secondary coverts. Because *swainsonii* (unlike *gilvus*) do not replace their greater secondary coverts during the first prebasic molt, HY and AHY birds can be distinguished into early winter, but not later when AHY birds have replaced their primaries and when their secondary coverts become worn.

Definitive prebasic molt.—This molt involves the replacement of all feathers. In both species, the primaries constitute a single molt series. Primary molt begins at P1 and proceeds distally to P9 (Table 1). In four *gilvus* and two *swainsonii*, P1 was the sole nodal primary (Table 1); other specimens of both species indicate

TABLE 1. Patterns of replacement for secondaries, primaries, and rectrices of *Vireo gilvus* and *V. swainsonii*. Numbers refer to focal feathers (right side of wing and tail only).

	Focal feather																							
	S9	S8	S7	S6	S5	S4	S3	S2	S1	P1	P2	P3	P4	P5	P6	P7	P8	P9	R1	R2	R3	R4	R5	R6
gilvus																								
Proximal to distal										5	12	7	8	6	9	12				2	3	4	4	
Distal to proximal					6	7	6	5																
Nodal feathers	1	7							4	11	7	3						10	5	2	1	1	1	2
Terminal feathers				6																			1	5
swainsonii																								
Proximal to distal										4	10	11	6	4	2	4				4	4	3	3	
Distal to proximal					5	3	3	4																
Nodal feathers	1	11							3	10	8	1							8	3	2	2	1	1
Terminal feathers			4															3						5

gilvus
$$Y = 200.809 + 2.066X$$

Julian Date vs. Molt Score (Sum of Both Wings)

swainsonii
$$Y = 207.038 + 3.041X$$

Julian Date vs. Molt Score (Sum of Both Wings)

FIG. 1. Regression of date on primary molt score for adult *V. gilvus* and *V. swainsonii*.

that P1 to P3 may be dropped nearly simultaneously. The regression of collection date on molt score suggested that primary molt lasts about 38 days in *gilvus* and about 55 days in *swainsonii* (Fig. 1).

Typical of most passerines, both species replaced their secondaries in two series: S1 to S6 and S7 to S9. Without exception, the outer series of secondaries was replaced distally to proximally (i.e. S1 to S6); S8 typically was the nodal feather of the inner series of secondaries (Table 1). In *gilvus*, either S9 or S7 was dropped next in this series; in *swainsonii*, S9 always was dropped prior to S7. In both species, S7 to S9 were being replaced when P3 to P5 were the outermost growing primaries; these inner secondaries usually are fully grown prior to the loss of S1. Molt of the outer series of secondaries was completed in both species about when P9 became fully grown.

In both species, the rectrices seem to be divided into two molt series, R1 to R5, and R6. In *gilvus*, R6 was a terminal feather in five specimens but nodal in two; in *swainsonii*, R6 was terminal in five specimens and nodal in one (Table 1). For R6 to be nodal it had to have been dropped before R5, meaning that R6 constitutes a separate molt series (Yuri and Rohwer 1997). In both species, molt proceeds from R1 to R5 in the inner series; however, in many specimens, these rectrices are lost in such rapid succession that several may appear to be nodal (Table 1).

As with the first prebasic molt, the definitive prebasic body molt is intense in *gilvus* and appears to begin soon after the start of primary
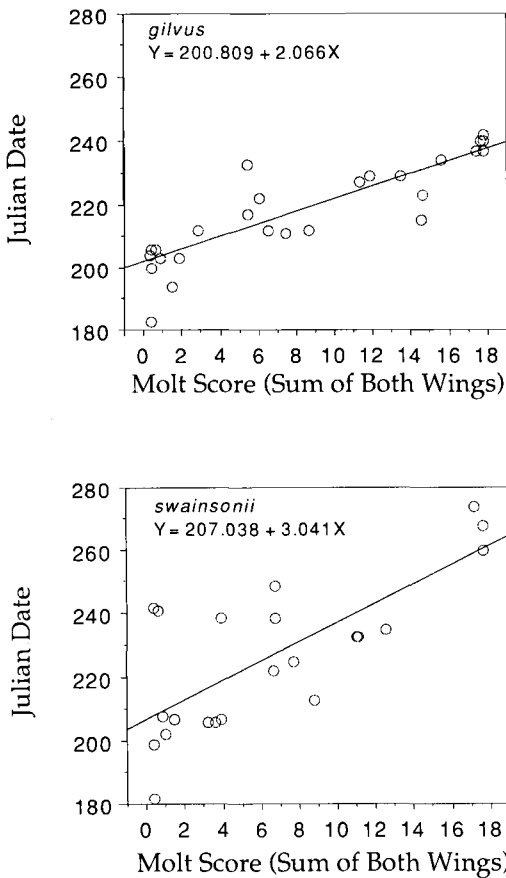
TABLE 2. Prealternate molt in *gilvus* and *swamsonii* (combined data).

Date	n	% in molt	Avg. body-molt score	% replacing secondaries	% replacing rectrices
1 to 15 February	19	32	9	17	0
16 to 28 February	20	2	6	0	0
1 to 15 March	21	43	11	56	0
16 to 31 March	23	74	14	29	17
1 to 15 April	25	68	9	35	0
16 to 30 April	20	50	9	10	20

replacement. Of the 26 specimens in primary molt, only four had not started molting in all five body regions. Although limited, our data suggest that the intensity of body molt increases as the primary series nears completion and then drops off sharply during the replacement of P9. Body molt in *swainsonii* follows the pattern for *gilvus* but continues beyond the replacement of the flight feathers. Specimens collected after the completion of their flight feather molt in October (2 of 6), November (4 of 17), and December (11 of 25) showed low-intensity body molt (total body molt score <10%) and little worn body plumage. Only 3 of 39 (8%) early January specimens were molting body feathers, suggesting that the definitive prebasic body molt usually is completed by the end of December.

Prealternate molt.—Both species have been reported to have a prealternate molt that is limited to the head and breast (Dearborn 1907, Dickey and Van Rossem 1938). Our data confirm a prealternate molt, although it appears to be more extensive on the body (several specimens molting in all body regions), and occasionally includes S7 to S9, and rarely R1 (Table 2). Although we did not attempt to separate wintering specimens to species (see Methods), *swainsonii* clearly undergoes this molt because 56 of the 63 specimens in prealternate molt were from exclusively *swainsonii* wintering areas. Seven specimens in prealternate molt were collected in sympatric wintering areas, representing 63% of the specimens examined from this area during the prealternate molt period. Because several of these birds were identified by their collectors as *gilvus* (possibly on the basis of song), and because earlier workers have reported prealternate molts in both species (Dearborn 1907, Dickey and Van Rossem 1938), we suspect that *gilvus* also has a prealternate molt.

Molt in relation to migration.—Sutton (1948) noted that the first prebasic molt of *gilvus* occurs on the breeding grounds. Adults also undergo the prebasic molt on the breeding grounds and appear to complete this molt prior to initiating fall migration (Fig. 2). The migratory route of *gilvus* is not well documented, but a plot of all localities of specimens collected north of the wintering range suggests that they migrate along the Gulf Coast (Fig. 2).

We found no adult specimen of *swainsonii* replacing flight feathers north of Mexico (Fig. 3). Given that the breeding range of *swainsonii* extends well south into Mexico, it is not surprising that molting specimens occurred throughout Mexico. However, it seems likely that migrants from the north initiate their flight feather molt in Sonora and Chihuahua in northwestern Mexico. Six molting specimens and four specimens in fresh plumage were from this area. Because *swainsonii* does not winter here, and because its breeding range in northwestern Mexico is confined to the Sierra Madre Occidental along the Sonoran/Chihuahuan border (Howell and Webb 1995), some of these specimens were probably migrants from farther north. With just two exceptions, every specimen collected from 16 August to 31 December south of Sonora and Chihuahua (n = 56) was either molting primaries, or had all new primaries (Figs. 3 and 4). The absence of late summer and fall specimens with worn primaries from throughout the winter range of *swainsonii* suggests that most adults from the United States and Canada stop in northwestern Mexico to molt their primaries (and much of their body plumage) before completing their fall migration (Fig. 4).

Even though adult *swainsonii* feature an early departure from the breeding grounds, many begin their prebasic body molt before they arrive in Mexico. Figure 5 shows the state of body feathers from 1 July to 30 September for adults collected in the United States and Canada. Of
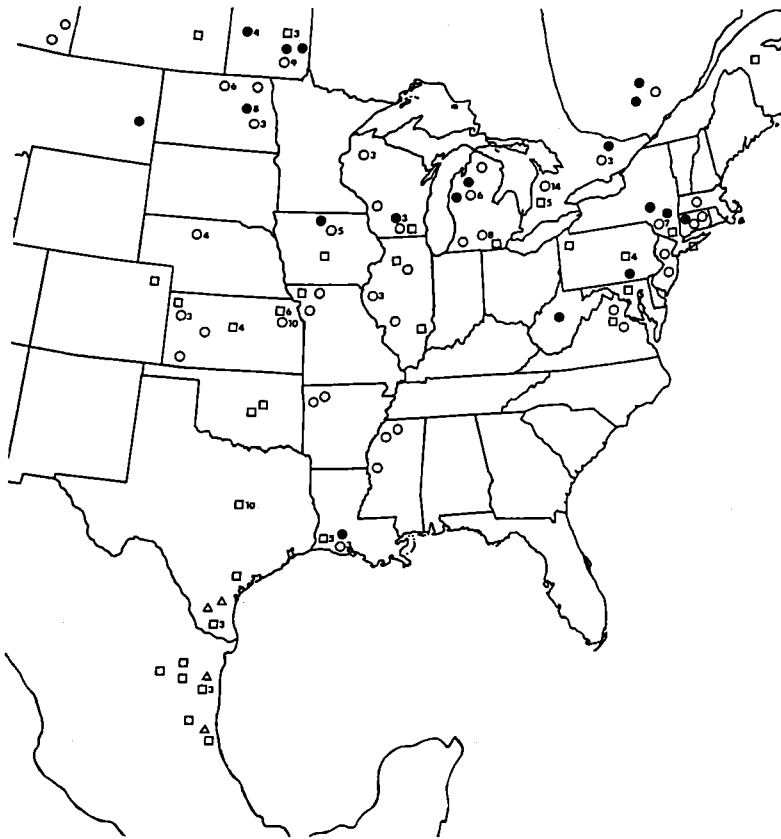
FIG. 2. Geographic distribution of nonmolting (open symbols) and molting (filled symbols) *V. gilvus* specimens collected north of the winter range. Circles, specimens collected from 1 July to 15 August; squares, specimens collected from 1 September to 30 October; triangles, specimens collected in April.

363 specimens, 58% were in body molt (defined here only as molting in more than one body region), and none had all new body feathers.

HY *swainsonii* undergo prebasic body molt on the breeding grounds, and thus occur in the United States and Canada well after adults have left. From 16 August to 30 September, we found 25 adults versus 203 HY birds that had been collected north of Mexico; many of these HY specimens were taken in southern Canada and the northern United States.

DISCUSSION

Molt patterns and duration of molt.—Both *gilvus* and *swainsonii* replace their remiges according to the rules followed by most passerines. Several specimens indicate that the rectrices are broken into two molt series (R1 to R5 and R6); this pattern has been documented in a number

of other species (Jenni and Winkler 1994, Yuri and Rohwer 1997), and closer attention to documenting the rules of replacement may demonstrate that division of the rectrices into two molt series is widespread among passerines (Yuri and Rohwer 1997).

Although quantitative molt data from other vireos are scanty, some comparisons are possible. Adult *gilvus* are similar to most other north-temperate vireos in undergoing their prebasic molt on the breeding grounds (Pyle et al. 1987). Thus far, *swainsonii* is the only vireo known to replace its body feathers during migratory flights (Fig. 5) and to undergo a molt migration. Neither *gilvus* nor *swainsonii* exhibits the odd first prebasic partial replacement of primaries exhibited by White-eyed Vireos (*V. griseus*; George 1973, Lloyd-Evans 1983). Finally, like *swainsonii*, HY Hutton's Vireos (*V. huttoni*) appear to retain their buffy secondary co-

FIG. 3.   Geographic distribution of all adult *V. swainsonii* specimens replacing flight feathers. Circles, specimens collected from 1 July to 15 August; squares, specimens collected from 16 August to 30 September; triangles, represent collected from 1 October to 31 December.

verts (Pyle et al. 1987, Davis 1995) rather than replace them during the first prebasic molt.

Not surprisingly, *swainsonii* takes longer to replace its primaries than does *gilvus* (Fig. 1).

Because *swainsonii* migrates southward before molting its flight feathers, presumably it is under less time pressure to molt rapidly, whereas *gilvus* must replace all of its primaries prior to
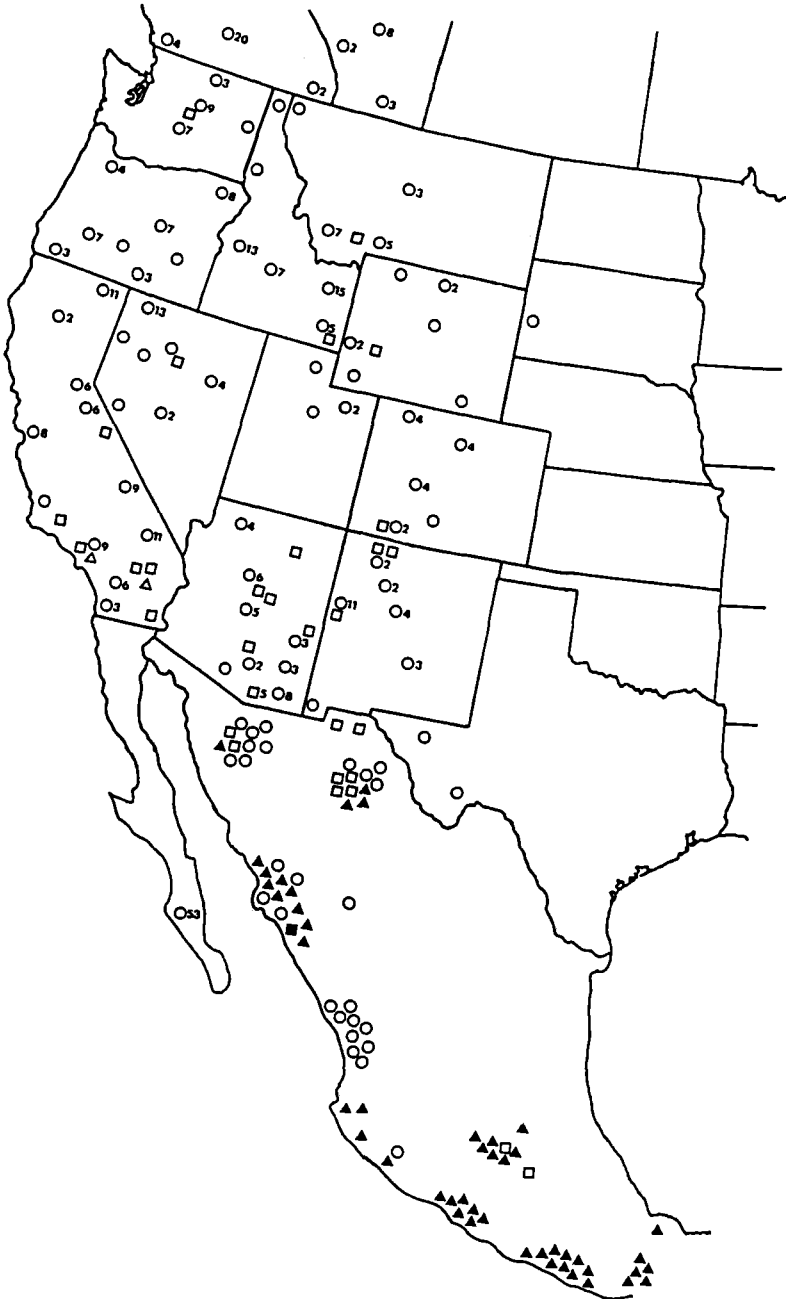
FIG. 4.   Geographic distribution of all adult *V. swainsonii* not undergoing flight-feather molt. Open symbols are specimens collected prior to molt (i.e. with worn feathers); filled symbols are specimens that had completed flight-feather molt. Circles, specimens collected from 1 July to 15 August; squares, specimens collected from 16 August to 30 September; triangles, specimens collected from 1 October to 31 December.
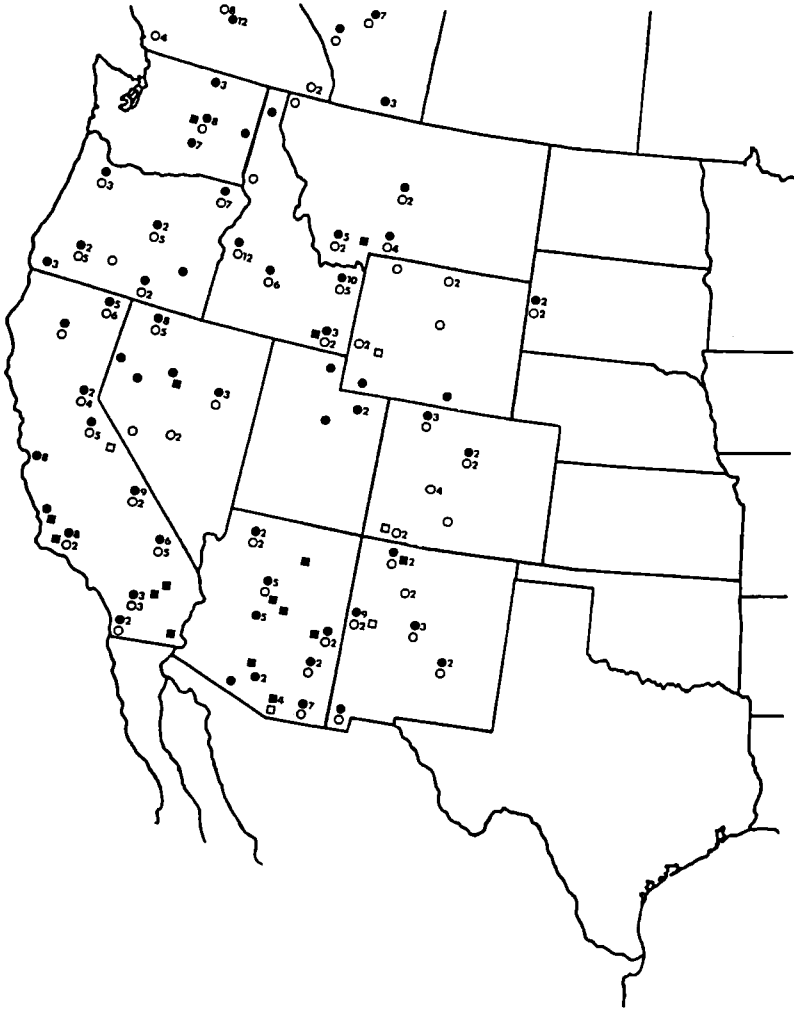
FIG. 5. Status of body molt for all adult *V. swainsonii* from the United States and Canada. Open symbols are nonmolting specimens in worn plumage; filled symbols are specimens replacing body feathers in at least two feather regions. Circles, specimens collected from 1 July to 15 August; squares, specimens collected from 16 August to 30 September.

migration to avoid migrating with gaps in its wings.

Hybridization and the scheduling of molts.—European data show that differences in molt and migration schedules are under genetic control (Berthold and Querner 1982). Presumably, this is also true for the differences in scheduling of molt and migration (and in the presence or absence of prealternate molts) between closely related birds breeding in eastern and western North America. If so, such differences would constitute a strong source of selection against hybrids (Kroodsma 1974, Rohwer and Man-

ning 1990). Hybrids between species that molt before the fall migration and species that molt after the fall migration might end up molting twice in a single fall or, perhaps, not at all. A female oriole that was a probable Bullock's × Baltimore (*I. galbula*) hybrid illustrates these costs (Rohwer and Manning 1990). This female was collected on her wintering range yet was completing what must have been the second prebasic molt in the same fall because she was growing P8 in both wings in a field of new primaries. Presumably, she had already molted on the breeding grounds, as do Baltimore Orioles,

and was undergoing a complete molt (her second) of her primaries on the winter range, as do Bullock's Orioles. Such molt problems could greatly reduce hybrid fitness. Furthermore, where they breed to the east of the Rocky Mountains, Bullock's Orioles persist in migrating prior to the prebasic molt, suggesting that differences in molt and migration between Baltimore and Bullock's orioles are genetic and, thus, potential sources of selection against hybrids (Rohwer and Johnson 1992).

Interestingly, most of the east–west species pairs that rarely hybridize or that have narrow hybrid zones (presumably because of selection against hybrids) also feature differences in the timing of postbreeding molt relative to fall migration; e.g. Lazuli and Indigo (*Passerina cyanea*) buntings, Black-headed (*Pheucticus melanocephalus*) and Rose-breasted (*P. ludovicianus*) grosbeaks (Cannell et al. 1983, S. Rohwer pers. obs.), and Bullock's and Baltimore orioles. In contrast, the hybrid zone between the Red-shafted and the Yellow-shafted forms of the Northern Flicker (*Colaptes auratus*) is much wider (Moore and Price 1993), and both forms molt on their breeding grounds (Test 1945).

Migratory routes for gilvus.—Despite replacing flight feathers on the breeding grounds, it seems clear from specimen localities in our sample (Fig. 2) that *gilvus* has a significant land-based migration around the Gulf of Mexico, a route suggested by Remsen et al. (in press). *Gilvus* is considered an uncommon spring and rare fall migrant through Texas (Rappole and Blacklock 1994), but 14 *gilvus* specimens from our sample were collected in Texas (10 killed at TV towers near Dallas). These specimens do not preclude alternative routes, but data suggest that alternatives are rare. A short trans-Gulf crossing, such as from Alabama, Mississippi, or Louisiana to Tamaulipas or Veracruz in Mexico, is unlikely. *Gilvus* is a rare spring migrant and a casual fall migrant in southwestern Louisiana (Remsen et al. 1996, in press), is rare in Mississippi (Toups and Jackson 1987) and Alabama (Imhof 1976), and is virtually absent from the coast of Veracruz (based on long-term mist netting; K. Winker pers. comm.). Additionally, *gilvus* has been recorded only once among tens of thousands of birds killed during migration in Florida (Stoddard and Norris 1967, Crawford 1978, Taylor and Kershner 1986).

Additional data from the Caribbean region support a land-based migration route for *gilvus*. It has not been recorded from Haiti and the Dominican Republic (Wetmore and Swales 1931), or from Puerto Rico (Raffaele 1989), and has only been recorded once each in Cuba and Jamaica (Bond 1971). Finally, *gilvus* is not known from the Yucatan Peninsula (Paynter 1955) or the Campeche Bank (Paynter 1953, Howell 1989), and the Isthmus of Tehuantepec is not a major landfall for autumn trans-Gulf migrant passerines (Winker 1995a). In summary, the specimen data that we accumulated, in conjunction with the paucity of records from elsewhere in the southeastern United States and the Caribbean, suggest that *gilvus* has a land-based migration during both spring and fall.

Timing of molt and migration in swainsonii.—Stewart et al. (1974) noted that AHY *swainsonii* pass through California before HY birds. Our results show unequivocally that adult *swainsonii* from throughout the United States and Canada migrate well in advance of HY birds. Although adults appear to be undergoing prebasic body molt during this migration (Fig. 5), HY birds clearly remain on the breeding grounds to finish this molt. We suggest that this difference is due to the fact that HY birds cannot migrate efficiently with juvenal body feathers. Juvenal body feathers are more loosely textured than feathers of subsequent plumages (Jenni and Winkler 1994). This loose texture makes them more susceptible to abrasion and probably creates more aerodynamic drag. Thus, the poor quality of their plumage may force HY *swainsonii* to complete their prebasic body molt prior to fall migration, rather than first migrating to the more productive Southwest as do adults.

It seems clear that AHY *swainsonii* replace body feathers during their fall migratory flights; if they had completed body molt prior to migrating, then at least some birds from the United States should have had all new body feathers. That none did suggests that most (if not all) birds pass into Mexico before completing body molt (Fig. 5). Other passerines molt during migratory flights. Several swallow species replace body feathers while migrating (Jenni and Winkler 1994, Yuri and Rohwer 1997), as do Least Flycatchers (Ely 1970), Blue Tits (*Parus caeruleus*; Svensson and Merilä 1996),

and Rose-breasted Grosbeaks (Cannell et al. 1983). Still other temperate-breeding passerines begin the prebasic molt of flight and body feathers while still on breeding grounds and then arrest the molt prior to fall migration (Jenni and Winkler 1994).

Adult *swainsonii* apparently migrate to northwestern Mexico prior to replacing their flight feathers. This molt migration allows them to avoid late-summer droughts typical of western North America (Baldwin 1973) and to exploit the flush of food associated with late-summer monsoons in southwestern North America (Nielson 1986) for most of their prebasic molt (Rohwer and Manning 1990). This food flush is especially evident in the Sonoran and Chihuahuan deserts (Szarek 1979). Migrating to the southwestern United States and northwestern Mexico to molt has been documented in four passerines from western North America (*Icterus bullockii,* Rohwer and Manning 1990; *Passerina ciris,* Thompson 1991; *Passerina amoena,* Young 1991; *Vireo swainsonii,* this study). These species represent three independent lineages that have relatives in eastern North America that molt before migration. As more studies contrast the molt and migration schedules of eastern and western relatives, further support for the evolutionary lability of fall molt and migration schedules is likely to emerge.

Contrasts in the scheduling of molt in migratory passerines.—Why are various passerines of western North America migrating to the southwestern United States and northwestern Mexico before undergoing molt? A general explanation is that these species are moving to regions where food is more abundant than on the breeding grounds. A similar interruption of fall migration has been documented for European passerines that pause to molt in the Sahel zone immediately south of the Sahara Desert. Here, too, a late-summer rainy season triggers a food flush (Morel 1973, Bensch et al. 1991). A few species replace some or all of their primaries south of Europe and north of their wintering areas in southern Africa (Hedenström et al. 1993, Lindström et al. 1993, Jenni and Winkler 1994). Presumably, these species molt in the Sahel zone. These molt migrations invite comparisons between the productivity of habitats on the breeding grounds in late summer versus habitats where these birds undergo their post-breeding molt.

If certain passerines from western North America and many trans-Saharan migrants from Europe move to places of abundant food to molt, why do other species molt on their breeding grounds? Several possibilities exist. First, in Europe and North America, most short-distance migrants that winter in temperate latitudes molt on their breeding grounds. They do so probably because food resources are similar in both areas and because molting where they have local knowledge of foraging conditions is an advantage over learning to find food in a new area. Second, it is frequently argued that migrants should be in fresh plumage for sustained flights over barriers such as water or deserts. However, the many European passerines that cross the Mediterranean Sea and the Sahara in worn breeding plumage demonstrate that the costs of migrating in worn breeding plumage may be mitigated by molting in areas rich in food. For many North American migrants, an alternative to the "fresh plumage" argument is that the winter range is many times smaller than the breeding range; thus, competition for food may be so severe on the winter range that molting would be difficult even if rainy seasons produced abundant food (Rohwer 1971, Terborgh 1989). The molt-migration strategy of *gilvus* would seem to support the importance of competition on the wintering grounds, because *gilvus* migrate in fresh basic plumage but do not seem to cross the Gulf of Mexico (Fig. 2).

Conservation implications.—Studies of molt highlight the potential significance of the southwestern United States and northwestern Mexico to the conservation of migrant passerines that breed in relatively arid habitats in western North America. The identification of migration routes and stopover sites may be critical to conserving Neotropical migrants (Winker 1995b), many of which appear to have declining populations (Terborgh 1989). Molt studies can make a significant contribution to the conservation of western migrants by identifying regions where migrants concentrate for the fall molt. Such data are begging to be extracted from museum specimens, although a shortage of specimens taken during late summer and early fall from the southwestern United States and northwestern Mexico has been

problematic (Rohwer 1986, Rohwer and Manning 1990, Young 1991). Additional collecting would greatly facilitate such studies.

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