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MOLT STRATEGIES AND AGE DIFFERENCES IN MIGRATION TIMING AMONG AUTUMN LANDBIRD MIGRANTS IN SOUTHWESTERN IDAHO

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ABSTRACT.—Intraspecific patterns of autumn migration timing are not well known, particularly in the western United States. Here, we (1) describe autumn migration timing and age ratios of landbird migrants in southwestern Idaho, (2) examine differences in timing among age and sex classes, and (3) demonstrate how prebasic molt strategies affect migration timing differences between age classes. As a group, Neotropical migrants were most common from late July through early September, whereas temperate migrants were most common from mid-September into early October. Proportion of hatch-year birds was 74.5% for all migrants combined and ranged from 33.3% to 100% for individual species. Timing differences between sex classes were detected in only a few species and no general patterns emerged. In 22 of 31 Neotropical and temperate migrants examined, there were significant differences in timing between adults and hatch-year birds. In species in which adults begin fall migration before replacing flight feathers, adults migrated earlier than hatch-year birds. Conversely, in species in which adults molt flight feathers on or near the breeding grounds before departing on fall migration, hatch-year birds migrated earlier than adults in all but one case. Therefore, it appears that molt strategy is a powerful determinant of intraspecific migration timing differences and, to our knowledge, this is the first study to document this pattern among migrant passerines of North America. *Received 21 February 2004, accepted 11 March 2005.*

Key words: age differences, autumn migration timing, molt strategy.

Estrategias de Muda y Diferencias en el Momento de Migración Otoñal en Migrantes Terrestres en el Suroeste de Idaho

RESUMEN.—Los patrones intraespecíficos del momento en que tiene lugar la migración de otoño no son bien conocidos, particularmente en el oeste de los Estados Unidos. En este estudio (1) describimos el momento en que sucede la migración de otoño y los cocientes de edades de migrantes terrestres en el suroeste de Idaho, (2) examinamos las diferencias en el momento en que sucede la migración entre sexos y clases de edad y (3), demostramos cómo las estrategias de muda prebásica afectan las diferencias en el momento de migración entre clases de edad. Como un grupo, los migrantes neotropicales fueron más comunes desde finales de julio hasta comienzos de septiembre, mientras que los migrantes de la zona templada fueron más comunes entre mediados de septiembre y principios de octubre. La proporción de aves nacidas durante el año fue del 74.5% para todos los migrantes combinados y varió entre especies entre el 33.3% y el 100%. Sólo se detectaron diferencias entre sexos en el momento de migración en pocas especies, y no existieron patrones

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generales. En 22 de los 31 migrantes neotropicales y de la zona templada que se examinaron existieron diferencias significativas en el momento de migración entre los adultos y las aves en su primer año de vida. En las especies en que los adultos inician la migración otoñal antes de reemplazar sus plumas de vuelo, los adultos migraron antes que las aves jóvenes.

Por el contrario, en las especies en que los adultos mudan sus plumas de vuelo en sus sitios de cría o cerca de éstos antes de iniciar la migración, las aves en su primer año de vida migraron antes que los adultos en todos menos un caso. Por lo tanto, parece que la estrategia de muda es un determinante importante de las diferencias intraespecíficas en el momento en que tiene lugar la migración, y de acuerdo a lo que conocemos, nuestro estudio es el primero que documenta este patrón en paserinos migrantes de América del Norte.

SPECIES OFTEN DIFFER in the timing of autumn migration. There is a general pattern in which species with longer migrations move south earlier in fall than shorter-distance migrants (Rappole et al. 1979). In late summer and early fall, many migrants depart the breeding grounds long before colder autumn weather substantially depresses food resources. This suggests that other factors, such as competition for winter territories or weather patterns during autumn, may be important in determining fall departure times (Rappole et al. 1979). Another factor that could affect the relative timing of autumn migration is the strategy for flight-feather replacement in after-hatching-year birds (Gauthreaux 1982, Rohwer et al. 2005).

Within some species, differences in timing of autumn migration have been detected between sex classes (e.g. Ketterson and Nolan 1985, Ellegren 1991, Woodrey and Chandler 1997, Swanson et al. 1999). Sex-related differences in timing of fall migration are complex (Otahal 1995, Yong et al. 1998, Swanson et al. 1999). In certain species, individuals of both sexes may defend territories during winter; in those species, selection pressure for arrival time on winter grounds may be equal between sexes (Rappole and Warner 1980, Morris et al. 1994, Otahal 1995). In a study of Ruby-crowned Kinglets (see Table 1 for scientific names of this and other species in the present study) in South Dakota, Swanson et al. (1999) found that males migrated later in fall than females. Patterns of sex-related differences in migration timing among migrants of the western United States are relatively unexplored.

Age-related differences in timing of fall migration vary among species. Theoretically,

adults should be more efficient than hatching-year (immature) birds in gaining fat stores and, therefore, may show faster rates of migration (Ellegren 1991, Yong et al. 1998). Depending on when the different age classes begin autumn migration, that could result in adults passing through a stopover site earlier in the season. Other factors, such as the position of the sampling site in relation to the departure point (breeding grounds, in the case of autumn migration) and the distance to the eventual wintering site, may confound results. Ideally, using data from numerous sites should help to clarify intraspecific patterns of migration timing. In a study of migration timing of five species at three sites in eastern North America, Woodrey and Chandler (1997) documented that adults migrated earlier in Red-eyed Vireo (*Vireo olivaceus*); immatures migrated earlier in Magnolia Warbler (*Dendroica magnolia*); and patterns varied in Swainson's Thrush, American Redstart (*Setophaga ruticilla*), and Common Yellowthroat (*Geothlypis trichas*). In a study of >40 species at a New Jersey stopover site, Murray (1966) found that migration timing broadly overlapped across age groups for most species. Gauthreaux (1982) cited a number of studies in which adults preceded immatures and vice-versa. Clearly, more study is needed to elucidate migration patterns between age classes.

One factor potentially affecting age-related migration timing that has received relatively little attention is the timing of preformative and prebasic molts in relation to fall migration. Most studies of migration timing have been done in eastern North America, where there is little variation in molt patterns. Because of the greater variation in molt patterns among western

migratory landbirds (Rohwer et al. 2005), the West may provide a better arena in which to examine the relationship between molt strategy and migration timing. The preformative and prebasic molts vary in extent and timing across species; however, the preformative molt generally includes replacement of most or all body feathers for hatching-year birds; for most adult birds, the prebasic molt is complete, including all flight feathers (Pyle 1997, Howell et al. 2003). Flight-feather molt is an energetically costly and time-consuming endeavor (Murphy and King 1992), requiring sufficient food resources. Furthermore, actively molting birds cannot fly as efficiently as nonmolting birds, and most passerines do not migrate while in the middle of flight-feather replacement (Kjellen 1994, Pyle 1997, Rohwer et al. 2005). Thus, it is likely that molt strategy affects the relative departure timing of fall migration of age classes, because in most species only adults replace flight feathers after the breeding season (Pyle 1997). For instance, if adults complete the prebasic molt on the breeding grounds (many passerine species undergo molt between breeding duties and autumn migration), their departure time may be delayed in comparison with hatching-year birds of the same species (Gauthreaux 1982) and adults of other species that replace flight feathers after arrival on the wintering grounds. Alternatively, adults in species that delay molt until after beginning migration may be able to depart earlier than hatching-year birds that are still completing their preformative molts. Some evidence supporting this scenario comes from migrants in Alaska, where hatching-year birds migrated earlier than adults in 10 of 18 species; adults molted on the breeding grounds in all 10 of these species (Benson and Winker 2001). Benson and Winker (2001) documented earlier migration of adults than hatching-year individuals for only one species, Alder Flycatcher (*Empidonax alnorum*); in this species adults molted after the autumn migration.

Among migratory species, there are several strategies for timing of the adult flight-feather molt in relation to migration; not all species fit neatly into these categories, but they are useful terms for separating birds by molt and migration strategies (Kjellen 1994). Kjellen (1994) lists six strategies, but only three of these routinely occur among western North American migrants common to woodlands or shrublands

(Pyle 1997): (1) premigration strategy: molting entirely before autumn migration, generally after breeding; (2) molt-migration: beginning migration before molting, interrupting migration to molt at a stopover site, and then continuing migration to the wintering grounds; and (3) postmigration strategy: postponement of prebasic flight-feather molt until arrival on the wintering grounds (Kjellen 1994, Pyle 1997, Rohwer et al. 2005).

Most of the migratory passerines in eastern North America exhibit the premigration molt strategy, replacing body and flight feathers within the breeding range before the onset of autumn migration (Pyle 1997, Rohwer et al. 2005). However, several passerine migrants of eastern North America show the opposite, postmigration strategy, in which adults replace flight feathers after arrival on the winter quarters; these include several species of *Empidonax* flycatchers, Eastern Wood-Pewee (*Contopus virens*), Red-eyed Vireo, and Orchard Oriole (*Icterus spurius*) (Hussell 1980, 1982, 1991; Rohwer and Manning 1990; Pyle 1997; Woodrey and Chandler 1997; Rohwer et al. 2005). Of particular interest is that in three species and subspecies pairs that include eastern and western counterparts—Warbling Vireo, Painted Bunting (*Passerina ciris*), and Bullock's and Baltimore orioles (*Icterus galbula*)—the eastern counterpart completes flight-feather molt on the breeding grounds, whereas the western counterpart postpones flight-feather replacement until after the onset of fall migration (Rohwer and Manning 1990, Thompson 1991, Voelker and Rohwer 1998). In the western United States, more species begin or complete autumn migration before replacing flight feathers (Rohwer et al. 2005). Included among these are species for which the area in which the prebasic molt occurs is not known with certainty and, for the purposes of this paper, are considered postmigration molt strategists: Rufous and Calliope hummingbirds; Dusky, "Western" (includes Pacific-slope and Cordilleran), and Gray flycatchers; and Western Wood-Pewee (Pyle 1997, Rohwer et al. 2005). Additionally, there are several species that are known to use a molt-migration strategy, such as western Warbling Vireo (*V. gilvus swainsonii*; Voelker and Rohwer 1998), Western Tanager (Butler et al. 2002), Lazuli Bunting (Young 1991), Black-headed Grosbeak (Rohwer et al. 2005), and Bullock's Oriole (Rohwer and Manning 1990).

As compared with eastern migrants, a higher proportion of western migrants exhibit a molt strategy in which flight-feather molt is delayed until after the onset of autumn migration (either the postmigration molt or molt-migration strategy; Rohwer et al. 2005). This east–west difference is attributed to arid conditions across much of the West during late summer, and several species apparently move into the monsoon region of the southwestern United States and northern Mexico to molt during late summer and early fall (Butler et al. 2002, Rohwer et al. 2005). Such a difference in molt strategies may have ramifications for the relative migration timing of age classes between eastern and western migrants. However, data on the relative timing of age and sex classes of autumn migrants are lacking, especially for the western United States.

Our study explored age ratios and autumn migration timing of landbirds in Idaho. In particular, the study was designed to determine the age-related molt and migration timing patterns of autumn migrants in Idaho to contribute to a broader understanding of regional migration strategies.

METHODS

STUDY SITE

The study was conducted 12 km east of Boise, in Ada County, Idaho (43°36'N, 116°05'W), on Lucky Peak (elevation 1,845 m), the southernmost peak of the Boise Foothills. Four distinct habitat types occur in a mosaic at Lucky Peak and throughout the Boise Foothills: conifer forest, mountain shrubland, shrub-steppe, and willow-dominated riparian shrub (see Carlisle et al. 2004 for additional study site details).

MIST-NET CAPTURES

We captured birds using standard mist nets (12 × 2.6 m, 32-mm mesh) in two habitats. One netting site was located in mountain shrubland habitat near the summit of Lucky Peak. The second site was in a spring-fed, willow-dominated riparian draw (hereafter “willow riparian”) on the western slope of Lucky Peak. Sites were separated by ~600 m. At the mountain shrubland site, we used 8 nets in 1997 and 10 nets from 1998 to 2003. We used six nets at the willow riparian site, which was sampled

during 1998 and 1999. To maximize capture efficiency, nets were located nonrandomly and opportunistically throughout the habitats in areas that concentrated bird movement (Ralph et al. 1993). Net placement was constant during the study (Carlisle et al. 2004). We operated nets daily for 5 h beginning at sunrise, except in cases of extreme temperatures (>32°C or <0°C), high winds, or continuous precipitation. We checked and cleared nets at intervals of 20–40 min. The mountain shrubland site was operated from 12 August to 21 October 1997; from 5 August to 15 October 1998; from 31 July to 15 October 1999; from 18 July to 16 October 2000; and from 16 July to 15 October 2001, 2002, and 2003. The willow riparian site was operated from 21 August to 14 October 1998 and from 2 August to 29 September 1999. We identified captured birds to species, age, and sex with reference to Pyle (1997), and fitted each with individually numbered U.S. Geological Survey aluminum leg bands. Capture numbers were converted to birds per 1,000 mist-net hours to standardize variations in number of net-hours because of weather. For all analyses, age was assigned as either adult (after-hatching-year), immature (hatching-year), or unknown. We also recorded date, extent of skull ossification, fat scores, flight-feather molt, and flight-feather wear for each bird (Pyle 1997, D. F. DeSante et al. unpubl. data). Flight-feather molt categories were none, symmetric, adventitious, and juvenal (D. F. DeSante et al. unpubl. data). With few exceptions, only adult birds were observed to molt their flight feathers in a symmetrical pattern.

STATISTICAL ANALYSES

We assigned species to one of three discrete categories for comparisons: Neotropical migrants (long-distance migrants), temperate-zone migrants (short-distance migrants), and irruptive migrants. We classified Neotropical migrants according to DeGraaf and Rappole (1995), but applied more stringent criteria such that half or more of the distribution must winter south of the United States (Carlisle et al. 2004). On the basis of MAPS (Monitoring Avian Productivity and Survivorship) data from the same study site, we also assigned each migrant species to one of four breeding status codes (Rimmer and McFarland 2000, D. F. DeSante et al. unpubl. data; Table 1). Regular breeders (B)

TABLE 1. Breeding status, flight-feather (FF) molt strategy, age ratios, and migration timing by age classes for migrants ($n \geq 10$) captured in the Boise Foothills, Idaho. Only species with five or more individuals ($n \geq 5$) for both age groups were analyzed for among-age timing differences; dates displayed between the adult and immature columns are for whole species (ages combined) whose small sample size (n) precluded between-age analysis.

Species	Status ^a	Molt strategy ^b	Adults in FF molt ^c (%)	Hatch-year birds (%)	Adults		Immatures	
					Mean date	(<i>n</i>)	Mean date	(<i>n</i>)
Neotropical migrants								
Calliope Hummingbird (<i>Stellula calliope</i>) ^{d,e}	B	Post	0.0	96.2	24 Jul	(5)	29 Jul	(128)
Rufous Hummingbird (<i>Selasphorus rufus</i>) ^{d,e}	M	Post	0.0	86.2	30 Jul	(8)	5 Aug	(50)
Western Wood-Pewee (<i>Contopus sordidulus</i>)	A	Post	0.0	86.8	13 Aug**	(9)	26 Aug	(58)
Dusky Flycatcher (<i>Empidonax oberholseri</i>) ^{d,e}	B	Post	0.2	63.4	31 Jul**	(429)	15 Aug	(743)
Hammond's Flycatcher (<i>E. hammondi</i>) ^e	S	Pre	50.0	77.7	11 Sep	(114)	3 Sep**	(398)
"Western Flycatcher" (<i>E. difficilis</i>) ^{e,f}	M	Post	0.0	55.1	6 Aug**	(22)	25 Aug	(27)
Gray Flycatcher (<i>E. wrigthii</i>) ^g	M	Post	0.0	91.7		21 Aug (14)		
Willow Flycatcher (<i>E. traillii</i>) ^g	M	Post	0.0	33.3		16 Aug (13)		
Cassin's Vireo (<i>Vireo cassinii</i>)	B	Pre	35.6	72.5	13 Sep	(114)	3 Sep**	(300)
Warbling Vireo (<i>V. gilvus</i>) ^e	B	MM	0.0	55.8	3 Aug**	(241)	25 Aug	(304)
House Wren (<i>Troglodytes aedon</i>) ^g	B	Pre	14.3	89.2	27 Aug	(9)	19 Aug	(231)
Swainson's Thrush (<i>Catharus ustulatus</i>)	S	Pre	—	100.0	—		31 Aug	(81)
Nashville Warbler (<i>Vermivora ruficapilla</i>) ^e	B	Pre	38.2	65.4	31 Aug	(219)	18 Aug**	(415)
Orange-crowned Warbler (<i>V. celata</i>)	B	Pre	8.7	73.2	12 Sep	(320)	6 Sep**	(873)
Yellow Warbler (<i>Dendroica petechia</i>) ^e	B	Pre	19.0	87.2	21 Aug	(79)	7 Aug**	(537)
Townsend's Warbler (<i>D. townsendi</i>)	M	Pre	17.2	92.7	8 Sep	(31)	1 Sep**	(396)
MacGillivray's Warbler (<i>Oporornis tolmiei</i>) ^e	B	Pre	37.2	86.8	24 Aug	(158)	6 Aug**	(1,035)
Wilson's Warbler (<i>Wilsonia pusilla</i>)	M	Pre	5.5	71.4	7 Sep	(110)	29 Aug**	(274)
Western Tanager (<i>Piranga ludoviciana</i>) ^{d,e}	B	MM	5.6	87.5	28 Jul**	(90)	25 Aug	(630)
Black-headed Grosbeak (<i>Phainopepla melanoccephalus</i>) ^{d,e}	B	MM	2.6	84.0	31 Jul**	(38)	12 Aug	(164)
Lazuli Bunting (<i>Passerina amoena</i>) ^{d,e}	B	MM	0.0	85.0	27 Jul**	(21)	9 Aug	(119)
Brewer's Sparrow (<i>Spizella breweri</i>)	B	Pre ^h	79.2	53.9	23 Aug	(53)	20 Aug*	(62)
Chipping Sparrow (<i>S. passerina</i>)	B	Pre ^h	37.8	75.7	31 Aug	(91)	27 Aug**	(283)
Bullock's Oriole (<i>Icterus bullockii</i>)	A	MM	0.0	93.3		30 Jul (30)		
Temperate migrants								
Northern Flicker (<i>Colaptes auratus</i>)	S	Pre	—	100.0			25 Aug (14)	
Red-naped Sapsucker (<i>Sphyrapicus nuchalis</i>)	M	Pre	0.0	50.0			24 Sep (14)	

TABLE 1. Continued.

Species	Status ^a	Molt strategy ^b	Adults in FF molt ^c (%)	Hatch-year birds (%)	Adults		Immatures		
					Mean date	(n)	Mean date	(n)	
Ruby-crowned Kinglet (<i>Regulus calendula</i>) ⁱ	B	Pre	0.4	51.1 ^j	24 Sep	(1,853)	22 Sep*	(1,940)	
Golden-crowned Kinglet (<i>R. satrapa</i>) ⁱ	S	Pre	0.0	94.1	21 Sep	(19)	19 Sep	(303)	
Townsend's Solitaire (<i>Miyadestes townsendi</i>)	M	Pre	31.1	80.6	28 Sep	(56)	20 Sep**	(233)	
Hermit Thrush (<i>Catharus guttatus</i>)	B	Pre	15.8	89.5	24 Sep	(21)	21 Sep	(179)	
American Robin (<i>Turdus migratorius</i>)	B	Pre	36.7	71.5	26 Sep	(37)	17 Sep*	(93)	
Cedar Waxwing (<i>Bombicilla cedrorum</i>)	A	Pre	100.0	95.0		10 Sep	(20)		
Yellow-rumped Warbler (<i>D. coronata</i>)	B	Pre	30.1	86.8	18 Sep	(149)	15 Sep**	(979)	
Spotted Towhee (<i>Pipilo maculatus</i>)	B	Pre	52.9	83.6	6 Sep	(167)	6 Sep	(853)	
Vesper Sparrow (<i>Pooecetes gramineus</i>)	A	Pre	33.3	76.9	31 Aug	(6)	18 Aug	(20)	
Lincoln's Sparrow (<i>Melospiza lincolni</i>) ^g	M	Pre	100.0	92.9		11 Sep	(16)		
Fox Sparrow (<i>Passerella iliaca</i>)	M	Pre	0.0	88.1	20 Sep	(8)	13 Sep	(59)	
Dark-eyed Junco (<i>Junco hyemalis</i>)	B	Pre	9.0	81.4	3 Oct	(590)	2 Oct**	(2,581)	
White-crowned Sparrow (<i>Zonotrichia leucophrys</i>)	M	Pre	1.2	72.7	21 Sep	(601)	20 Sep*	(1,580)	
Golden-crowned Sparrow (<i>Z. atricapilla</i>) ^g	M	Pre	0.00	95.5		21 Sep	(22)		
Irruptive migrants									
Northern Pygmy-owl (<i>Glaucidium gnoma</i>)	M	Pre	50.0	50.0		21 Sep	(13)		
Steller's Jay (<i>Cyanocitta stelleri</i>)	S	Pre	0.0	50.0		3 Oct	(10)		
Black-capped Chickadee (<i>Poecile atricapillus</i>)	A	Pre	40.0	90.6	2 Sep	(15)	27 Aug	(123)	
Mountain Chickadee (<i>P. gambeli</i>)	B	Pre	50.0	94.0	9 Sep	(29)	5 Sep	(471)	
Red-breasted Nuthatch (<i>Sitta canadensis</i>)	B	Pre	28.6	89.3	15 Sep	(50)	11 Sep	(416)	
Brown Creeper (<i>Certhia americana</i>)	B	Pre	0.0	92.7		1 Oct	(41)		
Pine Siskin (<i>Carduelis pinus</i>)	S	Pre	22.2	71.4	9 Aug**	(85)	19 Aug	(212)	
Cassin's Finch (<i>Carpodacus cassinii</i>)	B	Pre	60.0	81.6	5 Oct	(8)	17 Sep*	(36)	
Class M	M	-	4.0	75.6		16 Sep	(3,496)		
Class A	A	-	27.3	88.2		24 Aug	(287)		
Class B	B	-	11.9	73.5		14 Sep	(21,747)		
Class S	S	-	34.3	82.3		8 Sep	(1,309)		

^a Breeding status (see text): B = regular breeder, S = sporadic breeder, M = migrant, A = altitudinal migrant.

^b Adult flight-feather molt strategy; data from Pyle (1997), Rohwer et al. (2005), and present study. MIM = molt-migration.

^c Percentage of adults in active symmetric flight-feather molt.

^d Because these species (especially adults) migrate very early in the sampled season, it is possible that some birds migrated before 16 July and that our timing data are biased late for those species. Additionally, if only (or largely) adult birds were missed by this potential sampling bias, actual differences between adult and immature birds may be greater than our data indicate.

TABLE 1. Continued.

^a For species with significant portions of population migrating before early August, data are 2000–2003 only.

^f Likely both Pacific-slope (*Empidonax difficilis*) and Cordilleran (*E. occidentalis*) flycatchers based on Pyle (1997).

^g Data augmented by capture data from riparian site; see text.

^h Variable molt strategy: most adults replace all their flight feathers on the breeding grounds but some adults retain them to the wintering grounds; also, some hatch-year birds may retain juvenal body plumage through fall migration (Willoughby 1991, Pyle 1997).

ⁱ Dates presented here are based on 15 August–30 September, because birds cannot be aged reliably after 30 September because of early skull ossification; thus, migration timing results are biased early and are shown for purposes of age comparison only.

^j Tentative; possibly biased toward adults because of early skull ossification but used only from 15 August to 30 September for age ratio.

* Age class that migrates significantly earlier ($P < 0.05$).

** Age class that migrates significantly earlier ($P < 0.01$).

were defined as birds within their normal breeding range that bred at the study site in most or all years; sporadic breeders (S) were defined as birds within normal breeding range that bred less regularly at the site; “pure” migrants (M) were birds outside of breeding range that occurred only as migrants at the site; and altitudinal migrants (A) were birds within their normal breeding range that bred at lower elevations and used the site only during migration. For example, a species could be labeled as a Neotropical migrant with a B for breeding status (e.g. Dusky Flycatcher, a common breeder and migrant at the site) or as a temperate-zone migrant with an M for breeding status (e.g. White-crowned Sparrow, a common migrant that does not breed at the site).

Distinguishing migrants from local breeders.—A number of species described here bred at the site or nearby in addition to occurring as passage migrants (all species designated as regular or sporadic breeders). Individuals that were known to be local breeders (banded at the MAPS station at the site, birds in juvenal molt, or adults captured with dependent juveniles or in heavy symmetric molt) were excluded from analyses. Nonetheless, several birds that were likely dispersing from the nearby area were captured during the study, particularly in late July. Although capture totals for local birds were generally very small in comparison with numbers encountered during migration, the possibility exists that, if nonmigrants are included, data on migration timing may be biased toward earlier in the season. Thus, in those species, we needed to separate migrants from breeding or locally dispersing individuals. Therefore, we plotted numbers of new captures against date to examine early-season capture patterns in both age classes. Generally, these plots showed a distinct peak in captures far outnumbering the early-season captures. By cutting out the early tails of these plots, we minimized the influence of nonmigratory individuals on estimates of migration timing. After these plots were examined, a date was chosen before which all captures were considered nonmigrants; we did this for 21 species. Cut-off dates were chosen conservatively; in most cases, the number of excluded early-season birds was negligible when compared to migrant totals. In cases where adult and immature birds exhibited differences in timing, either only one age class was subjected to a date cut-off or separate

date cut-offs were chosen for each age class. In general, a clear pattern of low captures of local individuals early in the season followed by a brief drop in capture totals then an increasing pulse of migrants was evident in these plots. In other cases, a certain age class or species built toward a migration peak early in the season and thus all new captures were included.

Migration timing.—For each species, we examined intraspecific relationships in migration timing. In most cases, data came only from the mountain shrubland banding station, because of more complete coverage of the full migration season and the sampling of a broader range of migrants (J. D. Carlisle unpubl. data). However, for five species in which sample sizes from the mountain shrubland site were limited, captures of migrants from the willow riparian banding station were added to enable analysis (indicated in Table 1). Mean migration dates for each species, and for each age and sex class within a species (when discernible), are presented. We used Kolmogorov-Smirnoff tests to examine differences in migratory timing within species (Zar 1996). To examine annual differences in timing patterns, we also summarized timing differences by year for the 17 species with at least 10 individuals of each age class in each year.

Definition of passage dates (and peaks of passage) was potentially biased in a few ways. First, separation of migrants from local breeders and winterers (see above) was subjective, but we believe that this is the most appropriate means of separation and that nearly all local birds were excluded from analyses. Second, whether to present mean or median dates as measures of central tendency has advantages either way (Zar 1996); we elected to go with mean dates because they are likely closer to the peak for each species–age class. Lastly, because some birds (especially adults of some post- or molt-migration strategists; see footnote in Table 1) may have migrated before 16 July, our data may be slightly biased. However, such a bias would only reduce perceived differences in migration timing between ages and, therefore, does not detract from the main thesis of this study.

For sex class comparisons, we used only species that had ≥ 15 individuals per age–sex class and in which $\geq 70\%$ of individuals within each age class were reliably sexed (Pyle 1997). In cases where cut-off dates between migrants and nonmigrants differed between ages, we

included all data past the earlier of the two cut-off dates to be conservative in testing for differences between age classes; neither the direction nor the significance of the results were changed in comparison with tests on all captures.

Flight-feather molt.—We examined the relationship between timing of the prebasic flight-feather molt and migration timing of age classes for each species. For this analysis, we used flight-feather molt data from the present study (proportion of migrating adults for each species that were exhibiting symmetric flight-feather molt at time of capture), in combination with molt information in Pyle (1997) and Rohwer et al. (2005), to assign species to one of three molting strategies: premigration, molt-migration, or postmigration (Kjellen 1994). Because molt-migration and postmigration strategies should affect differential timing of age classes similarly, these groups were combined for comparisons. Then, using results from the Kolmogorov-Smirnoff tests as described above, we compared between-age migration timing in the context of molt strategies to look for a general pattern across the woodland migrant community in Idaho.

Results were considered statistically significant when $P \leq 0.05$.

RESULTS

FLIGHT-FEATHER MOLT

Half (12 of 24) of the Neotropical migrants in the present study used a postmigration or molt-migration molt strategy, whereas all temperate-zone and irruptive migrants used a premigration molt strategy (Tables 1 and 2). Among species using either the postmigration or molt-migration strategy, proportion of adults engaged in symmetric molt when captured ranged from 0.0% to 5.6% (mean = 0.94%), and only three of those nine species showed any signs of flight-feather replacement (Table 1). On the other hand, 25 of 28 species in the premigration molt category exhibited symmetric molt and proportions of molting individuals ranged from 0.0% to 83.8% (mean = 26.6%). Pure (class M) migrants exhibited the least occurrence of flight-feather molt, whereas altitudinal (A) migrants and sporadic breeders (S) had the highest occurrence (Table 1). In general, most birds captured that were exhibiting symmetric

TABLE 2. Timing of autumn migration sorted by migration and flight-feather molt strategies for migrants captured in the Boise Foothills, Idaho. Dates presented for each age are means across all years of study, with range of means presented parenthetically. Difference is mean number of days between age classes.

Migration strategy	Molt strategy	Adults	Immatures	Difference
Neotropical	Premigration	2 September (29 August – 4 September)	20 August (16–24 August)	13.2 (9.9 to 17.5)
Neotropical	Postmigration ^a	31 July (29 July – 2 August)	18 August (16–21 August)	-17.3 (-19.3 to -14.5)
Temperate	Premigration	23 September (22–26 September)	19 September (18–20 September)	4.0 (2.4 to 8.0)
Irruptive	Premigration	21 August (16–28 August)	29 August (16 August – 5 September)	-7.4 (-19.9 to 0.8)

^a Includes birds using molt-migration strategy.

flight-feather molt were in the later stages of molt.

MIGRATION TIMING

General patterns.—Capture rates for Neotropical migrants were highest from mid-July through early September and declined steadily throughout September (Fig. 1). By contrast, temperate-zone migrants were uncommon during July and August and most common from mid-September through early October (Fig. 1). Capture rates of irruptive migrants were fairly stable throughout the autumn season but slight peaks in July and September can be attributed to irruptions of Pine Siskins and Mountain Chickadees, respectively (Fig. 1). Timing patterns in temperate-zone migrants were driven largely by three generally abundant species: Ruby-crowned Kinglet, Dark-eyed Junco, and White-crowned Sparrow, which together accounted for 9,145 of the 12,413 temperate-zone migrants in the present study (Table 1). Neotropical migrant patterns were driven by a larger number of species, but especially MacGillivray's Warbler, Dusky Flycatcher, and Orange-crowned Warbler (Table 1).

Migration patterns by sex.—We analyzed 13 species for differences in migration timing between sex classes. Results were characterized by extensive overlap between the sexes in timing of autumn passage in all but a few cases. Adult males departed significantly later than adult females in MacGillivray's Warblers (difference between means: six days; $D = 0.302$, $P < 0.05$), whereas adult males preceded females in Wilson's Warblers by five days ($D = 0.289$, $P < 0.05$). Interestingly, among immature Wilson's Warblers, females preceded males by three days ($D = 0.198$, $P < 0.05$). For both kinglet species, analysis was limited by the early skull ossification exhibited by these species (Pyle 1997). Therefore, we compared timing by sex regardless of age to include October captures. In Ruby-crowned Kinglets, males migrated five days later than females ($D = 0.302$, $P < 0.01$). In Golden-crowned Kinglets, males migrated two days later than females but the difference was not significant.

Migration patterns by age.—Most species (22 of 31 temperate-zone and Neotropical migrants analyzed) showed significant differences in migration timing between age classes and

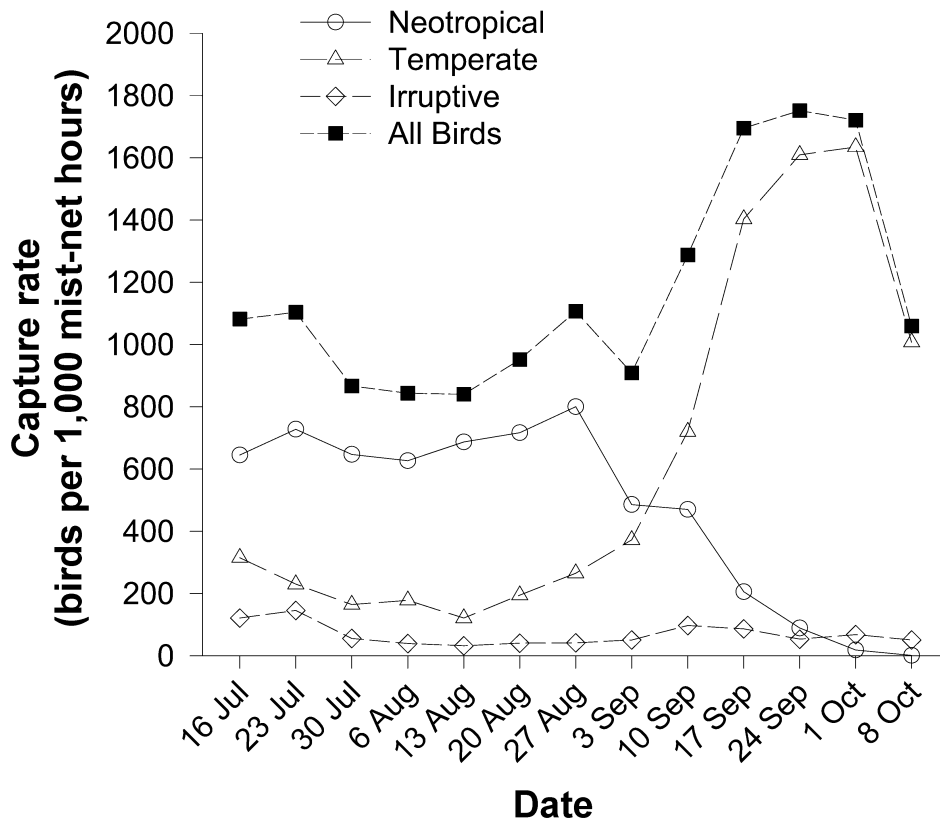


FIG. 1. Capture rates (birds per 1,000 mist-net hours) for Neotropical migrants, temperate migrants, irruptive migrants, and all birds combined at the mountain shrubland netting site at Lucky Peak during autumn of 1997–2003. Data for Neotropical migrants are from 2000–2003 only (years in which entire date span was sampled). Date is first day of week sampled (i.e. 16 Jul represents 16–22 July in non-leap years).

most differences were highly significant (Tables 1, 2, and 3). In the nine species exhibiting a postmigration molt strategy (includes “molt-migration” strategists) for which between-age data were available, adults preceded immature birds by a range of 5–28 days (mean = 14.8 days) (Tables 1, 2, and 3). Additionally, in Gray and Willow flycatchers, species that exhibit a postmigration molt strategy but whose small sample size (*n*) precluded rigorous analysis, adults preceded immatures by 16 and 19 days, respectively.

In 27 species using a premigration molt strategy for which between-age data were available, adults migrated after immature birds in all but one case: Pine Siskin (Table 1). Among premigration molt strategists (excluding Pine Siskins), immatures preceded adults by a range of 0–18

days (mean = 7.0 days). Regardless of molt strategy, Neotropical migrants showed the largest differences in migration timing between ages, whereas temperate-zone migrants and irruptive migrants exhibited smaller differences between age classes (Table 2). Immature Neotropical migrants showed similar migration timing across species and molt strategy groups (Table 2).

DISCUSSION

FLIGHT-FEATHER MOLT

Because most of the birds captured at the site are active migrants, most individuals, even of premigration molting species, should be expected to have completed most of their flight-feather molt before beginning migration (and thus

TABLE 3. Annual variation in age differences in migration timing in species with ≥ 10 individuals of each age class in each year in the Boise Foothills, Idaho. Dates presented for each age are means across all years of study, with range of means presented parenthetically. Difference is mean number of days between age classes.

Species	Migration strategy	Molt strategy	Adults	Immatures	Difference
Dusky Flycatcher	Neotropical	Postmigration ^a	31 Jul (29 Jul – 1 Aug)	15 Aug (13 – 18 Aug)	-16.2 (-18.0 to -14.2)
Hammond's Flycatcher	Neotropical	Premigration	11 Sep (8 – 14 Sep)	3 Sep (22 Aug – 5 Sep)	10.0 (5.3 to 17.0)
Cassin's Vireo	Neotropical	Premigration	13 Sep (11 – 18 Sep)	4 Sep (29 Aug – 11 Sep)	8.9 (5.0 to 14.5)
Warbling Vireo	Neotropical	Molt-migration	3 Aug (30 Jul – 8 Aug)	24 Aug (21 – 26 Aug)	-21.1 (-23.6 to -17.8)
Ruby-crowned Kinglet ^b	Temperate	Premigration	24 Sep (23 – 27 Sep)	22 Sep (21 – 23 Sep)	2.3 (0.8 to 3.5)
Nashville Warbler	Neotropical	Premigration	30 Aug (27 Aug – 2 Sep)	17 Aug (15 – 19 Aug)	12.9 (11.7 to 14.4)
Orange-crowned Warbler	Neotropical	Premigration	12 Sep (7 – 15 Sep)	5 Sep (3 – 8 Sep)	6.4 (4.2 to 9.8)
Yellow-rumped Warbler	Neotropical	Premigration	16 Sep (14 – 18 Sep)	13 Sep (11–15 Sep)	3.0 (0.4 to 6.4)
Yellow Warbler	Neotropical	Premigration	21 Aug (17 – 23 Aug)	7 Aug (31 Jul – 13 Aug)	13.9 (10.1 to 16.7)
MacGillivray's Warbler	Neotropical	Premigration	24 Aug (21 – 28 Aug)	6 Aug (3 – 10 Aug)	17.6 (11.9 to 23.2)
Wilson's Warbler	Neotropical	Premigration	7 Sep (4 – 10 Sep)	30 Aug (26 Aug – 2 Sep)	8.2 (1.8 to 12.6)
Western Tanager	Neotropical	Molt-migration	29 Jul (25 Jul – 1 Aug)	26 Aug (24 – 29 Aug)	-28.1 (-32.2 to -24.3)
Black-headed Grosbeak	Neotropical	Postmigration ^a	31 July (25 Jul – 4 Aug)	14 Aug (14–21 Aug)	-13.7 (-19.5 to -5.8)
Spotted Towhee	Temperate	Premigration	7 Sep (2 – 17 Sep)	5 Sep (30 Aug – 11 Sep)	2.3 (-6.3 to 8.4)
Chipping Sparrow	Neotropical	Premigration	29 Aug (24 Aug – 5 Sep)	26 Aug (21 – 30 Aug)	3.3 (-0.8 to 5.5)
Dark-eyed Junco	Temperate	Premigration	4 Oct (1 – 7 Oct)	30 Sep (25 Sep – 5 Oct)	3.5 (-2.4 to 8.3)
White-crowned Sparrow	Temperate	Premigration	20 Sep (17 – 22 Sep)	20 Sep (13 – 25 Sep)	0.7 (-3.5 to 4.8)

^a Molts after beginning of fall migration, possibly using molt-migration strategy.

^b Dates presented here are based on 15 August–30 September, because birds cannot be aged reliably after 30 September because of early skull ossification in immature birds; thus, migration timing results shown here are biased early and are shown for purposes of comparison only.

before arriving at the study site). Indeed, most of the migrants we captured that were exhibiting symmetric molt had nearly completed growing their new feathers. Nonetheless, postmigration molting species showed a lower percentage of adults molting flight feathers in comparison with premigration strategists. The few postmigration molt strategists that were exhibiting flight-feather molt were likely anomalies, and the possibility exists that they began molt on the breeding grounds because they had terminated breeding activities early and conditions were favorable (Butler et al. 2002).

No temperate-zone or irruptive migrants in this study used a postmigration or molt-migration molt strategy. Therefore, it appears that only long-distance migrants are prone to adopting such a strategy (e.g. Rohwer et al. 2005).

MIGRATION TIMING

Migration patterns by sex.—Overall, we found few differences in autumn migration timing between sex classes. Our data for Ruby-crowned Kinglets match the findings of Swanson et al. (1999) in that males migrate later than females. Adult MacGillivray's Warblers in Idaho follow this pattern as well. Interestingly, timing differences between the sexes were found in Wilson's Warblers, but in opposite directions for each age class. The relative absence of sexual differences in migration timing in fall contrasts with the condition in spring in which male passerines tend to migrate significantly earlier than females to establish breeding territories (e.g. Otahal 1995, Yong et al. 1998). This suggests that competition for wintering territories does not shape intersexual differences in autumn migration timing as strongly as does the drive for males to arrive quickly to breeding territories in spring, at least among most migrants in Idaho.

Migration patterns by age.—Because a subjective method (based on the authors' experience at the site) was used to define migration windows for species with local breeding components (see above), it is possible that differences in migration timing between ages of just a few days could be biased by our definition of migration windows. However, larger differences (which represent most species in the study) are very unlikely to be artifacts.

In almost all cases, molt strategy correctly predicted the direction of the age differential

in autumn migration timing among woodland migrants in Idaho. Adults molting after migration preceded immatures, whereas adults molting before migration passed through our study site later than immatures. Thus, molt strategy appears to be a powerful predictor of between-age timing patterns. The fact that immature Neotropical migrants have similar migration timing regardless of the adult molt strategies (and that adults in the different molt strategy groups differ by ~33 days) strongly suggests that the time required for adult birds to replace flight feathers and the location of this molt strongly influences inter- and intraspecific differences in migration timing.

There were several species for which differences were marginal, nonsignificant (largely because of small sample size), or both; in almost all those cases, the observed differences were in the direction predicted by molt strategy. Only one species, Pine Siskin, showed a between-age timing pattern opposite that predicted by molt strategy. Pine Siskins are irruptive migrants and appear to exhibit an unpredictable migration strategy at our study site. In most years, they are present in small numbers, but they appeared in larger numbers during two years of the study. A large irruption of almost 200 Pine Siskins in July of 2001, composed of a high proportion of adults, drove the unexpected age-related timing pattern. Also, because at least one irruption (2001) involved a breeding component, it is uncertain whether these data truly represent migration timing. Thus, for all species excluding Pine Siskins, molt strategy consistently predicted the age differential in migration timing.

One factor that may complicate migration-timing analyses is the distance that migrants travel from their breeding grounds to a particular stopover site (Woodrey and Chandler 1997, Benson and Winker 2001). At this point, we do not know with certainty the breeding origins of most migrants at stopover sites. Because adults are expected to migrate more efficiently and faster than the inexperienced immatures (Ellegren 1991), the farther the distance of the stopover site from the breeding area, the more potential there is for the sampled difference in timing to vary from the original differences in departure date (Woodrey and Chandler 1997). For instance, adults that complete molt on the breeding grounds probably begin migration

later in autumn than immature birds. However, by the time the migrants reach a stopover site hundreds or even thousands of kilometers from the breeding area, it is possible that adults will have nearly caught up to the immatures, reducing any perceived differences in migration timing. The high percentage of species in which hatching-year birds preceded adults in Alaska is consistent with this scenario (Benson and Winker 2001). In Idaho, this may be the case for certain species that originate far to the north of our site, such as the Gambel's race of White-crowned Sparrows (*Z. l. gambeli*), in which we observed much overlap between ages. In Alaska, hatching-year White-crowned Sparrows preceded adults by 10 days (Benson and Winker 2001). On the other hand, Idaho is far enough north that timing differences were perceptible in most species in the study, and these differences may diminish farther south in the United States. Thus, differences in age class timing between our study area and studies conducted farther south might be explained by differential rates of migration. For instance, Yong et al. (1998) observed no differences in autumn migration timing between age classes of Wilson's Warblers in New Mexico, whereas in Idaho immatures preceded adults by nine days. Also, on the basis of data from specimens collected across the western United States, most of which were from the Southwest, Johnson (1970) concluded that there were no differences in autumn migration timing between adult and immature Hammond's Flycatchers. By contrast, in Idaho we found that immatures preceded adults by eight days. Thus, if adults are able to migrate faster than young birds, the lack of difference found by Johnson (1970) may simply reflect the disproportionate number of samples from an area where adults had already caught up to immatures.

Interestingly, Neotropical migrants exhibited much larger differences in migration timing between ages than birds of the other two migrant strategies. One possible explanation for that difference is that Neotropical migrants depart from the breeding grounds earlier than temperate-zone migrants (Rappole et al. 1979). An early departure for fall migration reduces the amount of time between termination of the breeding effort and onset of migration. This tight scheduling of breeding, molt, and migration in Neotropical migrants may make

the time required for adults to replace flight feathers more of a factor in the age differential in timing of migration. For instance, immature Neotropical migrants of both premigration and postmigration molt strategies migrated at the same time of year, whereas adults of the other molt strategies differed by over a month. Because no temperate-zone migrants in this study used a postmigration molt strategy, it is tempting to point to the presence of a postmigration molt strategy (and, thus, early departure of adults) among some Neotropical migrants as the reason for the larger age differential in Neotropical migrants. However, although the age difference is slightly smaller in premigration molting (than in postmigration molting) Neotropical migrants, the degree of differential migration timing of age classes in this group is still greater than that seen in temperate-zone migrants (using the same molt strategy). Because temperate-zone migrants have evolved later autumn migration strategies than Neotropical migrants (Rappole et al. 1979) and tend to migrate shorter distances, temperate-zone migrants generally have greater separation between cessation of breeding activities and onset of migration. This reduced urgency for vacating the breeding grounds among temperate-zone migrants may allow adults to finish molting and depart relatively soon after immatures have departed.

What accounts for the differences in molt strategies among species? The prevailing opinion is that relative resource availability between breeding, stopover, and wintering sites is responsible for shaping these patterns (Young 1991, Jenni and Winkler 1994, Voelker and Rohwer 1998, Butler et al. 2002). For instance, whereas low- to mid-elevation areas of the western United States generally dry up during late summer (and presumably become less productive of food for migrants), monsoons in late summer in northern Mexico and the southwestern United States provide a flush of productivity at this time of year (e.g. Young 1991, Voelker and Rohwer 1998, Butler et al. 2002, Rohwer et al. 2005). We now know that several western species or populations, including western Warbling Vireo, Lazuli Bunting, Western Tanager, Black-headed Grosbeak, and Bullock's Oriole, undergo a molt migration in which adults depart the breeding grounds and migrate to this monsoon area to molt their flight

feathers before continuing on to the wintering grounds (Rohwer and Manning 1990, Young 1991, Voelker and Rohwer 1998, Butler et al. 2002, Rohwer et al. 2005). The importance of the monsoon region for the stopover and autumn molting of a number of species should not be underestimated and deserves further attention (Leu and Thompson 2002). On the basis of the timing of migration and molt strategies of Idaho migrants, the possibility exists that other western species exhibiting a postmigration molt strategy, such as Dusky, "Western," and Gray flycatchers, Western Wood-Pewee, and certain populations of Chipping Sparrows, undergo a molt-migration as well, but the requisite studies are yet to be completed (see also Rohwer et al. 2005). Also, on the basis of capture timing and feather condition of migrants off the coast of California (Richardson et al. 2003, P. Pyle pers. comm.), a few other potential species to consider include Cassin's Vireo, populations of Hermit (*D. occidentalis*) and Townsend's warblers, Lark Sparrow (*Chondestes grammacus*), and Hooded Oriole (*I. cucullatus*). The situation with Cassin's Vireo and Townsend's Warbler is curious because all adults captured in Idaho had completed prebasic molt and their timing was relatively late, whereas some adults captured off California were in worn plumage and were captured relatively early in the autumn season (P. Pyle pers. comm.), a time frame that fits all other postmigration molt strategists in the study. This may suggest that different populations of these species have different molt strategies.

Continental patterns of age-related migration timing.—Rohwer et al. (2005) have shown that there is a marked difference between eastern and western North America in the proportion of species that molt after onset of autumn migration. If molt strategy can predict age-related autumn migration timing patterns as we suggest here, we would expect a different pattern than that observed here at sites where premigration molt strategists predominate. Thus, it would be interesting to examine intraspecific timing patterns of "eastern" migrants, heavily dominated by species in which adults molt prior to autumn migration, in the context of molt strategy. We predict that similar analyses conducted at sites in the northern and northeastern United States or central and eastern Canada (far enough north so that adults would not have "caught up" to immature birds) would show that immatures

of most or all premigration molt strategists would precede adults during fall migration. Along similar lines, it would be interesting to conduct more among-site comparisons along north-south axes (e.g. Woodrey and Chandler 1997) to determine whether, as suggested here, increasing distance from departure areas to stopover sites limits our ability to detect intra-specific migration timing differences.

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