AGE RATIOS OF COASTAL AND INLAND FALL MIGRANT PASSERINES IN CENTRAL CALIFORNIA

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INTRODUCTION

Changes in the age ratio of migrants in relation to time and route have been reported from different parts of North America (Robbins et al.,1959; Drury and Keith, 1962; King et al., 1965; Murray, 1966; Hussel et al., 1967; Leberman and Clench, 1968, 1969; Clench, 1969; Ely, 1970; Johnson, 1970, 1973). Ralph (1971), using data for three passerine species from an island and an adjacent coastal station in central California, discussed hypotheses relating to the high proportion of immatures. His data might be more meaningful if compared with age ratios at inland stations. This paper reports age ratios for common passerine autumnal migrants from an insular, a coastal, and an inland station. Some supplemental data are presented from three other inland stations. Together these six stations comprise an east-west transect of central California (Fig. 1).

METHODS

Age ratio data are presented from Farallon Island 40 kilometers west of San Francisco to Mono Lake near the California-Nevada state line 330 km to the east. All stations are 37-39° N latitude. Brief summaries of conditions peculiar to each station follow.

The Farallon Island Station of Point Reyes Bird Observatory (PRBO) is a 45-hectare rocky island, the largest and only habitable island of the Farallon Island National Wildlife Refuge. The island is a focal point for migratory land birds flying over the Pacific Ocean especially at dawn. Its three introduced trees tend further to concentrate land birds arriving on the island. Mist nets in the vicinity of these trees were supplemented by a 20-meter Heligoland trap constructed over a prostrate Monterey pine (*Pinus radiata*) and a 2.4 × 2.4 × 1.2 meter-high house trap beneath the two Monterey cypresses (*Cupressus macrocarpa*) which stand in the lee of a two-story living quarters. Occasionally mist nets were operated near the lighthouse and on the grassy marine terrace. Data taken between 16 August and 15 November 1968-1972 are presented here.

The Bolinas Station of PRBO is on the adjacent mainland just within the southern edge of Point Reyes National Seashore. It is located on a marine terrace 60 m above sea level and within 30 m of the cliff overlooking the beach. In favorable weather the Farallon Islands, 30 km to the southwest, are clearly visible from the Bolinas Station. Single- to triple-height mist nets were operated in the oak woodland and coastal scrub that characterize the immediate area. Some granivorous species were also taken in 4-cell Glenhaven "Potter" traps. Data taken between 16 August and 15 November 1968-1972 are presented here.

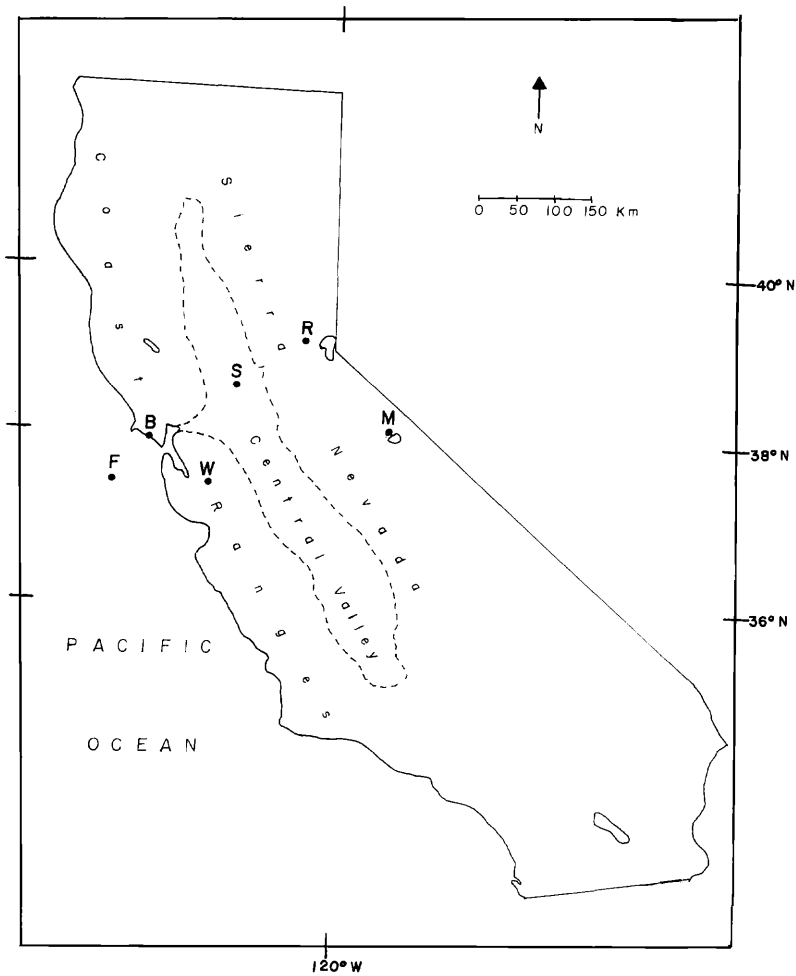

FIGURE 1. Capture stations in central California: Farallon Island (F), Bolinas (B), Wool Ranch (W), Sacramento (S), Robinson Flat (R), Mono Lake (M).

The Wool Ranch Station operated by the Avian Biology Laboratory (ABL) of California State University at San Jose is 55 km from the outer coast. It is situated 615 m above sea level in a hanging valley just east of the 800 m crest to Mission Ridge on the western edge of the inner Coast Range. Mission Ridge overlooks South San Francisco Bay, the San Jose-San Francisco metropolitan area, and westward across to the Santa Cruz Mountains of the outer Coast Range. Nets and a few "Potter" traps were located in a willow-filled draw and in a surrounding 20-hectare prune and walnut orchard. High ground around the Wool Ranch Station is open grassland. Slopes dropping off to the east are covered with oak woodland or grassland depending upon exposure. The orchard and willows

(*Salix* sp.) function as a focal point for migrants grounded on the grassy ridge. Frequently Mission Ridge at dawn stands out like an island above the fog which flows in from the Pacific and obscures land and water areas below 500 m. Data taken from 9 August to 15 November 1970 and 10 August to 30 November 1971 are presented here.

The Sacramento Station at near sea level in the great interior valley of California is 140 km from the coast. Nets were located in riparian vegetation consisting of willows and large cottonwoods (*Populus Fremontii*). This station was operated from 18 August to 7 September 1970.

The Robinson Flat Station near Duncan Peak Lookout at 2,040 m above sea level on the west slope of the Sierra Nevada is about 250 km from the Pacific coast. Nets were located in a small meadow where the major vegetation is mountain alder (*Alnus tenuifolia*) and willow. The surrounding forest consists of predominantly red fir (*Abies magnifica*) and lodgepole pine (*Pinus Murrayana*). This station was operated from 28 August to 26 September 1970.

The Mono Lake Station at 1,950 m above sea level at the eastern base of the Sierra Nevada is about 300 km from the Pacific coast. Nets were located on the northwest shore of this large saline lake in an area of mixed vegetation consisting of willow, cottonwood (*Populus trichocarpa*), and introduced Lombardy poplar (*Populus* sp). This station was operated from 27 August to 27 September 1970.

Birds were aged using species-relevant criteria maintained in files at PRBO and ABL. The stage of progressive skull ossification (Stewart, 1972a) was the most useful single indicator of age in most passerines. We omitted data from less than five percent of the birds captured whose age we did not determine.

All birds were marked with bands issued by the Bird Banding Laboratory. Only data from initial captures were used except at the Bolinas and Wool Ranch stations, where returns of Hermit Thrushes (*Catharus guttata*), Oregon Juncos (*Juncos oreganus*), Chipping Sparrows (*Spizella passerina*), Golden-crowned Sparrows (*Zonoatrichia atricapilla*), Fox Sparrows (*Passerella iliaca*), White-crowned Sparrows (*Z. leucophrys*), and Lincoln's Sparrows (*Melospiza lincolnii*) were counted as adult birds.

"Testing equality of two percentages" (Sokal and Rohlf, 1969) was used as a test of significance ($P = .05$) between stations.

RESULTS

In Tables 1-3 numbers of immatures are compared to numbers of adults in 18 species of commonly captured fall migrants at three stations. Data for five fall seasons at Bolinas (Table 2) show relatively little annual variation in age ratios. Because the annual effort at Bolinas was reasonably constant, changes in gross numbers probably reflect actual annual fluctuations in numbers passing through the Bolinas area.

The greater variation in numbers captured in the same five fall seasons on Farallon Island (Table 1) is due in part to variation in

TABLE 1. Immature/adult numbers of some fall migrants on Farallon Island.

Species	1968	1969	1970	1971	1972	Total	Percent immatures
Western Flycatcher	26/0	7/0	17/0	31/0	35/1	116/1	99.1
Hermit Thrush	20/2	13/3	38/20	6/2	8/6	85/33	72.0[a b]
Swainson's Thrush	7/1	5/4	2/3	21/6	3/5	38/19	66.7[a]
Warbling Vireo	30/1	1/0	3/0	16/0	17/2	67/3	95.7
Orange-crowned Warbler	12/0	3/0	7/2	5/5	1/0	28/7	80.0
Yellow Warbler	42.4	38/0	24/0	45/6	31/0	180/10	94.7[a]
Townsend's Warbler	28/0	13/1	20/0	5/1	17/1	83/3	96.5
MacGillivray's Warbler	12/0	7/0	12/0	3/1	9/0	43/1	97.7
Wilson's Warbler	38/2	19/1	19/1	9/1	17/0	102/5	95.3[b]
Western Tanager	30/2	6/2	5/0	9/0	13/1	63/5	92.7[b]
Black-headed Grosbeak	1/0	1/0	1/0	5/0	2/1	10/1	91.0
Oregon Junco	7/0	46/11	111/14	2/0	37/5	203/30	87.1[b]
Chipping Sparrow	38/0	34/0	20/0	13/0	42/0	147/0	100.0[b]
White-cr. Spar. (*gambelii*)	69/12	51/22	42/13	24/10	170/23	356/80	81.7
White-cr. Spar. (*pugetensis*)	81/12	59/40	87/31	14/12	45/10	286/105	73.1[b]
Golden-crowned Sparrow	253/25	121/61	214/56	14/7	155/107	757/256	74.7[a b]
Fox Sparrow	7/1	27/3	23/5	8/1	12/2	77/12	86.5[b]
Lincoln's Sparrow	11/2	13/1	12/0	19/2	28/2	83/7	92.2[b]

[a]significant difference from Bolinas

[b]significant difference from Wool Ranch

TABLE 2. Immature/adult numbers of some fall migrants at a coastal station (Bolinas)

Species	1968	1969	1970	1971	1972	Total	Percent immatures
Western Flycatcher	121/1	300/1	283/3	175/0	480/0	1359/4	99.7[a]
Hermit Thrush	88/12	178/26	199/28	133/15	78/5	676/86	88.7
Swainson's Thrush	53/5	73/6	84/2	76/5	73/9	359/27	93.0[a]
Warbling Vireo	24/2	73/0	89/3	139/7	53/0	378/12	96.9
Orange-crowned Warbler	25/5	17/2	12/4	19/6	16/1	89/18	83.2
Yellow Warbler	11/4	46/3	29/6	31/9	26/8	143/30	84.1[a]
Townsend's Warbler	6/2	38/0	14/2	12/0	14/0	84/4	95.4
MacGillivray's Warbler	1/1	5/1	2/1	4/0	4/0	16/3	84.2[a]
Wilson's Warbler	18/1	55/4	43/5	42/2	51/4	209/16	92.9[a]
Western Tanager	66/6	15/3	41/0	13/0	14/0	149/9	94.3[a]
Black-headed Grosbeak	5/1	6/1	5/1	13/0	2/2	31/5	86.0
Oregon Junco	53/9	72/15	49/9	54/9	28/10	256/52	85.1[a]
Chipping Sparrow		3/0		4/0		7/0	100.0[a]
White-cr. Spar. (*gambelii*)	17/1	21/7	12/1	17/1	17/0	84/10	89.4[a]
White-cr. Spar. (*pugetensis*)	81/16	155/46	136/32	82/48	31/6	485/148	76.6[a]
Golden-crowned Sparrow	56/11	117/37	61/19	90/2	27/15	351/84	80.7[a]
Fox Sparrow	23/5	73/16	47/14	15/8	21/2	179/45	80.0
Lincoln's Sparrow	1/1	27/2	2/1	6/4	7/1	43/9	82.7

[a]difference significant from Wool Ranch

TABLE 3. Immature/adult numbers of some fall migrants at an inland station (Wool Ranch)

Species	1970	1971	Total	Percent immatures
Western Flycatcher	154/15	392/15	546/30	94.8
Hermit Thrush	226/319	263/128	489/447	52.2
Swainson's Thrush	26/20	44/30	70/50	58.3
Warbling Vireo	24/2	38/2	62/4	93.9
Orange-crowned Warbler	12/7	28/7	40/14	74.1
Yellow Warbler	17/10	16/10	33/20	53.5
Townsend's Warbler		3/0	3/0	100.0
MacGillivray's Warbler		7/3	7/3	70.0
Wilson's Warbler	13/17	15/7	28/24	53.8
Western Tanager	9/6	25/11	34/17	66.6
Black-headed Grosbeak	6/1	41/5	47/6	88.7
Oregon Junco	110/127	705/210	815/337	70.7
Chipping Sparrow	53/33	260/71	313/104	75.1
White-cr. Spar. (*gambelii*)	83/38	134/23	217/61	78.0
White-cr. Spar. (*pugetensis*)	48/40	28/12	76/52	59.3
Golden-crowned Sparrow	579/358	249/203	828/561	59.6
Fox Sparrow	105/41	51/13	156/54	74.2
Lincoln's Sparrow	5/5	12/1	17/6	73.9

capture effort among the years. Important also, however, is the island's apparently greater sensitivity to chance precipitation of wind-drifted waves of migrants. Observable differences in immature/adult numbers between those arriving in waves and those arriving in smaller numbers between waves is discussed below.

Differences in gross numbers and some differences in immature adult ratios between years at the Wool Ranch may be in part attributed to longer coverage in 1971. Gross numbers of the subject species captured on the Wool Ranch (5,574) make that 2-year sample numerically comparable with the 5-year samples from Bolinas (5,460) and Farallon Island (3,300).

Due to the small sample sizes of warblers at inland stations we have combined data for five species of common western parulids (Fig. 2). A significant difference is found in percentages of immatures between the coastal stations (Farallon Island and Bolinas) and each inland station, but there are no significant differences among the four inland stations. Together the two coastal stations had 91 percent immature in contrast to 59 percent immature for the four inland stations.

In the following species the percentage of immatures is significantly higher at Bolinas than at the Wool Ranch: Hermit Thrush, Swainson's Thrush (*Catharus ustulata*), Western Tanager (*Piranga ludoviciana*), Oregon Junco, Chipping Sparrow, both subspecies of the White-crowned Sparrow (*Zonotrichia leucophrys gambelii* and *Z. l. pugetensis*), and the Golden-crowned Sparrow. Although there is a lower percentage of immatures at the Wool Ranch for the Fox Sparrow and Lincoln's Sparrow, the difference is not significant when compared with Bolinas, but is significant when compared with Farallon Island.

In no species (except the Yellow Warbler) is there a significantly *higher* percentage of immatures on Farallon Island than Bolinas. However, in three species (Hermit Thrush, Swainson's Thrush, Golden-crowned Sparrow) the percentage of immatures on Farallon Island is significantly *lower* than Bolinas. This lower percentage of immatures on Farallon Island is because of a wave-day effect. (Definition of a wave-day was the arrival of over 1,000 migrants on the island.) Generally on other days there were less than 100 migrants present. On wave-days a significantly higher proportion of adults occurred as compared with all-other-days in the Hermit Thrush, Puget-Sound White-crowned Sparrow, and Golden-crowned Sparrow (Fig. 3). Although this wave-day effect occurs in the Puget-Sound White-crowned Sparrow, it apparently does not occur in the Gambel's White-crowned Sparrow.

In three species, the Western Flycatcher (*Empidonax difficilis*), Warbling Vireo (*Vireo gilvus*), Black-headed Grosbeak (*Pheucticus melanocephalus*), there is no significant difference in percentage of immatures between Farallon Island, Bolinas, and the Wool Ranch. Although the sample is small, the percentage of immatures at three inland stations (lumped together) from Sacramento to Mono Lake is also high for the Western Flycatcher (91-7%; n = 11) and Warbling Vireo (91.7%; n = 22).

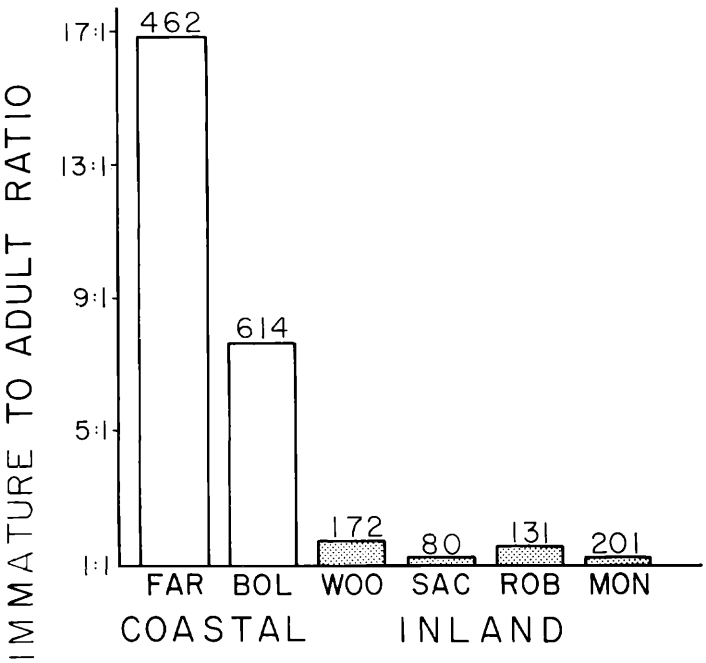

FIGURE 2. Combined age ratios of common western parulids (Orange-crowned Warbler *Vermivora celata*, Yellow Warbler *Dendroica petechia*, Townsend's Warbler *Dendroica townsendi*, MacGillivray's Warbler *Oporornis tolmiei*, Wilson's Warbler *Wilsonia pusilla*) at coastal and inland stations in central California. Open bars for coastal stations, stippled bars for inland stations. Numbers above bars are sample sizes.

DISCUSSION

Among the hypothesized postulates of Drury and Keith (1962) was the statement that the high ratios of immatures to adults on the Atlantic coast were due largely to genetically induced navigational errors. Ralph (1971) subscribed to this hypothesis for fall migrants on the central California coast and predicted that samples taken farther from the mainland would have a higher percentage of immatures for any given species. Generally our data agree with this hypothesis, but it is only supported statistically in the Yellow Warbler. The lower percentage of immatures on Farallon Island in the Hermit Thrush, Puget-Sound White-crowned Sparrow, and Golden-crowned Sparrow is due to the wave-day effect. Wave-days occur on Farallon Island because of a combination of factors associated with weather fronts (Ainley, Stewart, and Mewaldt, in prep.). Migrating species wintering along the coast include adults returning to coastal habitats where they spent the previous winter. For example, Vargas (1971) found that 30 percent of wintering Golden-crowned Sparrows at Bolinas returned the following year. Some adults returning to the immediate coast could drift or be blown off

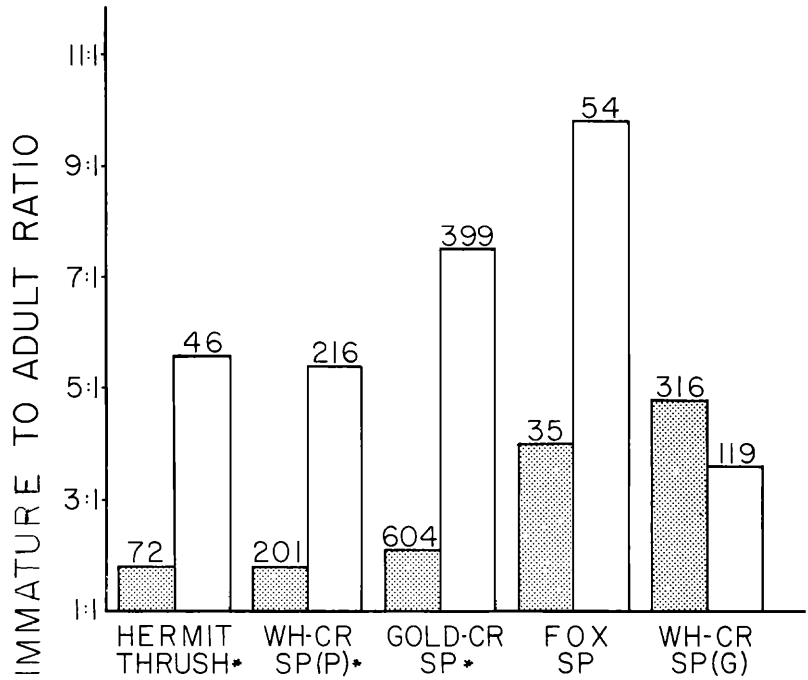

FIGURE 3. Ratios of immatures to adults of several species on wave-days compared with all-other-days on Farallon Island 1968-72. Stippled bars are wave-days, open bars are all-other-days. Numbers above bars are sample sizes. * differences significant ($P = .05$).

course to Farallon Island when weather fronts occur. The absence of large numbers of adult Gambel's White-crowned Sparrows on wave-days (Fig. 3) may be because its main wintering ground is well inland and not on the immediate coast (Grinnell and Miller, 1944).

Assuming there is no bias in favor of catching immature birds and that adults migrate at the same speed and use similar habitats as immatures, the high percentage of immatures at inland stations in the Western Flycatcher, Warbling Vireo, and Black-headed Grosbeak suggest either aging techniques are erroneous, adults use other routes than sampled by our stations, or that most adults migrate earlier than mid-August. Are the aging techniques erroneous? Skull ossification is a reliable technique for aging the Warbling Vireo (Stewart, 1972) and Black-headed Grosbeak (PRBO, unpubl. data). In the Western Flycatcher some adults return in the spring with an incompletely ossified skull (Johnson, 1973; PRBO, unpubl. data) but the larger "windows" in the immatures during August and September distinguish them from adults that have smaller unossified areas or have completely ossified skulls (PRBO, unpubl. data). Immature Western Flycatchers have new, buffy wing coverts in contrast to the worn coverts of adults (Johnson, 1974). Both ossification and condition of wing coverts were used to age the Western Flycatcher.

Could the location of our stations have been such that we missed the migration routes of certain species? Comparison of numbers of early fall migrants at Bolinas show that the Western Flycatcher and Warbling Vireo are the two most abundantly captured species. The Western Flycatcher is by far the most abundant early fall migrant at Wool Ranch as well. In contrast the relative abundance of these two species in the central valley of California is much lower. Compared to other common species, the Western Flycatcher and Warbling Vireo had a low relative abundance during a 10-week-end census of Caswell State Park during the fall of 1966 (Marie Mans, unpubl. data). The same is true at banding stations in the central valley during the height of migration (Cogswell, 1962; Stewart, 1972b). Although information concerning migration in the Sierra Nevada foothills is scarce, all existing evidence suggests that most individuals of the Western Flycatcher and Warbling Vireo migrate along the coast during the fall migration. Relatively little is known about possible routes of the Black-headed Grosbeak.

That adults of the Western Flycatcher, Warbling Vireo, and Black-headed Grosbeak migrate before immatures is suggested by the following evidence: the higher percentage of adult Western Flycatchers at Wool Ranch in early August gradually declining into September (Fig. 4) suggests that the peak of adult migration in this

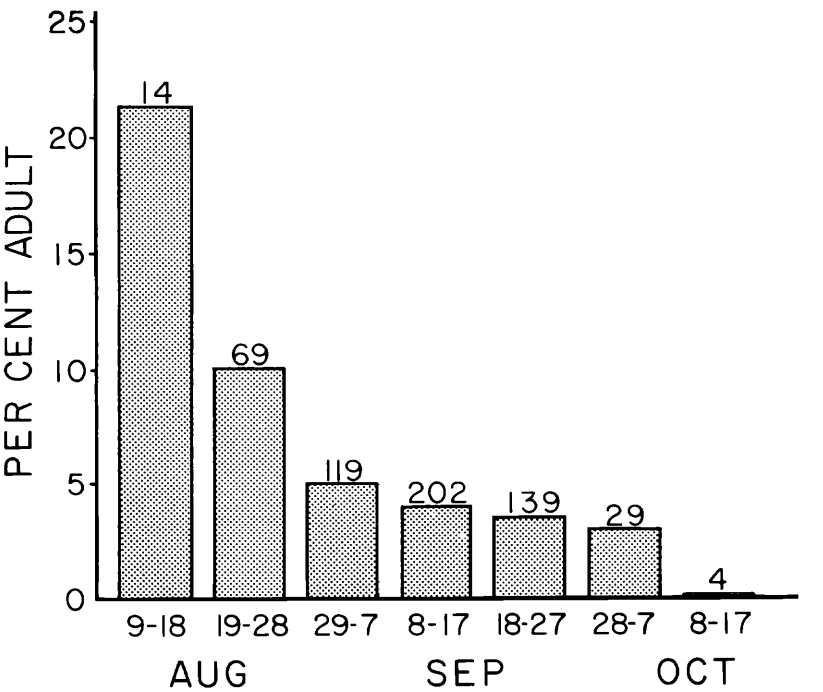

FIGURE 4. Percentage of adult Western Flycatchers at the Wool Ranch in fall 1970-71. Numbers above bars are sample sizes.

species is earlier than mid-August. Similarly four of the six adult Black-headed Grosbeaks were captured before 22 August at the Wool Ranch. The timing and location of the postnuptial molt in these species is important to consider. If remex molt did not take place in the United States in adult Western Flycatchers, Warbling Vireos, and Black-headed Grosbeaks, it would add support to the hypothesis that they migrate earlier than immatures. Molt of remiges has never been detected in these three species at Bolinas where continuous netting occurred throughout the year. Individual Wilson's Warblers, Orange-crowned Warblers, and Swainson's Thrushes (species that also breed locally and winter in western Mexico) have been captured with remex molt during the summer and fall (PRBO), unpubl. data). Michener and Michener (1951) captured over 400 adult Black-headed Grosbeaks during a 25-year period in Pasadena, California, but only one was undergoing postnuptial molt. This individual was caught on 30 September with an injured but mended wing. Stewart (in prep.) has found no remex molt in skins of the Warbling Vireo (western races) and Black-headed Grosbeak taken in the United States.

Thus we interpret the high percentage of immatures in the Western Flycatcher, Warbling Vireo, and Black-headed Grosbeak at inland stations as evidence that in these species peak migration of adults occurs prior to the postnuptial molt and earlier than peak migration of immatures. Our data support Johnson's (1973) contention that this hypothesis is correct for the Western Flycathcher.

SUMMARY

Age ratios are presented for common fall migrant passerines at an insular, a coastal, and inland stations on an east-west transect of California. In general the percentages of immatures are highest at the insular and coastal stations and much lower at inland stations. In five common parulids the 91 percent immature at coastal stations contrasts to the 59 percent immature at inland stations. Exceptions to this general pattern are found for some species in which lower percentages of immatures were reported from the insular station than on the coast. Apparently this is because on wave-days immatures occur in substantially lower percentage than on other days in these species. The high percentage of immatures at coastal and inland stations in the Western Flycatcher, Warbling Vireo, and Black-headed Grosbeak is discussed. Our evidence suggests that in fall adults of these three species migrate prior to the postnuptial molt and before peak migration of immatures.

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