J. Field Ornithol., 65(2):169–185

AUTUMN POPULATIONS OF LANDBIRDS ALONG CENTRAL COASTAL CALIFORNIA 1976–1986

DANIEL M. TAYLOR[1], DAVID F. DESANTE[2], GEOFFREY R. GEUPEL, AND KEITH HOUGHTON[3]

Point Reyes Bird Observatory
4990 Shoreline Highway
Stinson Beach, California 94970 USA

Abstract.—The autumn migration of 110 species or distinct races of birds was monitored from 1976 to 1986 by a standardized mist-netting program on the coast of central California. A peak in migration numbers occurred between mid-August and late October in a given year. Young birds were captured 9.1 times more frequently than adults. The number of birds banded annually in the autumn was not correlated with the number banded in the summer. There was no correlation between the number of young and adult birds banded in a given year. The 44 most common bird taxa had high annual variation in numbers and young : adult ratios, sometimes by a factor >10. The young : adult ratios were higher for species of woodland habitat, breeders along the coast and interior mountains of California, and much higher for neotropical migrants and permanent residents with a winter influx of individuals. Adults of species breeding in California mountains varied greatly in annual capture rates. The high annual variation emphazies that long-term studies are necessary to understand the importance of an area to individual or groups of species during migration periods. A higher diversity of species and greater number of individuals were captured during autumn than summer, and habitat along migratory routes may be as essential as breeding and wintering habitat.

POBLACIONES OTOÑALES DE AVES TERRESTRES A LO LARGO DE LA CALIFORNIA COSTANERA CENTRAL ENTRE EL 1976 Y EL 1986

Sinopsis.—Se estudió migración otoñal de unas 110 especies o razas distintas de aves en la costa central de California desde el 1976 hastal el 1986 usando un programa normalizado de atrapamiento en redes. Un aumento en el número de migratorios ocurrió entre mediados de agosto y finales de octubre en un particular año. Aves jóvenes fueron capturadas 9.1 veces más frecuentemente que aves adultas. El número de aves anilladas anualmente durante el otoño no se correlacionó con el número anillado en el verano. No existe correlación entre el número de juveniles y el número de adultos anillados en un año en particular. Los 44 taxones más comunes de aves tuvieron una alta variación en números y en razón anual de jóvenes : adultos, a veces por un factor de más de 10. Las razones de jóvenes : adultos fueron mayores para especies de habitat bosquecino, los que se reproducen a través de las montañas costaneras y del interior de California, y mucho mayor para migrantes neotropicales y residentes permanentes con un influjo de individuos en invierno. Los adultos de las especies que anidan en las montañas de California mostraron grandes variaciones en las razones de captura anual. La alta variación anual enfatiza que estudios a largo plazo son necesarios para entender la importancia de un área para una especie o para grupos de especies durante los períodos migratorios. Se capturó una mayor diversidad de especies y mayores números de individuos durante el otoño que durante el verano. Se concluye que habitats a lo largo de rutas migratorias pueden ser tan esenciales para la supervivencia como habitats de anidamiento y de invernar.

[1] *Current address: 244 N. 12th, Pocatello, Idaho 83201 USA.*
[2] *Current address: The Institute for Bird Populations, P.O. Box 554, Inverness, California 94937 USA.*
[3] *Current address: 115 Green Lane, Bradwell, Norfolk, NR318DE England.*

Banding data have provided considerable insight into aspects of avian biology, including composition and abundance of migrant species (Mewalt and Kaiser 1988), population trends (DeSante and Geupel 1987, Faaborg and Arendt 1992, Hagan et al. 1992, Hussell et al. 1992), age class dynamics (Ralph 1971, 1981), habitat use (Karr 1981, Winker et al. 1992) and weather effects (Faaborg et al. 1984, Hagan et al. 1992, Hussell 1981). Since 1976 personnel of the Point Reyes Bird Observatory have monitored the passage of small landbirds in central coastal California at the Palomarin Field Station (hereafter Palomarin) using a standardized mist-netting program. Using Palomarin data from the autumns of 1976–1986, the objectives of this study were to: (1) describe the composition and abundance of birds mist-netted and banded at Palomarin in autumn, including an analysis of select groups defined according to breeding habitat, breeding range, and migratory behavior; (2) determine the timing of passage through Palomarin during autumn for total birds, adult birds and young birds; (3) and examine the annual variability of the total birds, adult birds, young birds, common individual species and the three groups classified above.

STUDY AREA AND METHODS

The Palomarin Field Station lies 12 km north of the Golden Gate Bridge of San Francisco on a marine terrace immediately adjacent to the Pacific Ocean, just inside the southern end of the Point Reyes National Seashore in Marin County, California (37°56′N and 122°45′W). See DeSante and Geupel (1987) for a complete description of the study area.

An array of 20 12-m nylon mist-nets was established at 14 permanent stations. Fourteen of the 20 nets were located at eight sites in mixed evergreen forest, and the remaining six were at sites in coastal scrub habitat. The 20 mist-nets were run daily from 18 Aug. to 25 Nov. for 6 h per day, beginning 15 min after local sunrise. The nets were always opened and closed in the same order. Thus, 120 net h were accumulated in each morning of netting. This standardized regime was faithfully adhered to from 1979 through 1986. Prior to 1979, the standardization of start and end time was not quite so rigorous, but the total net hours were virtually identical to later years.

All birds captured were brought back to the field station for processing, banding, weighing and measuring. Age was determined by the degree of skull pneumatization and other morphological, mensural, and plumage characteristics as appropriate for the various species (Pyle et al. 1987). Birds in their first calendar year are referred to as young birds. Birds in their second or later year are called adult birds. We were unable to age with absolute confidence 24% of the birds encountered and we called these unknown age (hereafter UN) birds. As yet unsanctioned aging techniques, especially for the abundant kinglet species (Fairfield and Shinkoff 1978), suggest that nearly all UN birds were young birds. The two kinglet species were not used in age ratio analysis, and the remaining UN birds

(about 6% of the total) were ignored in comparisons between young and adult birds.

Data were collected from all bird species or distinct races for which at least one individual was banded during the 100-d period from 18 Aug. to 25 Nov. 1976–1986. These bird taxa were grouped (Table 1) according to habitat preference (three groups), breeding range (five groups), and migratory behavior (six groups). These classifications were based upon the seasonal occurrence, habitat preferences, nest locations and foraging behaviors of individual birds in the vicinity of Palomarin. Additional information for breeding ranges, migratory behavior, habitat preferences, nest location and foraging behavior were obtained from Bent (1942, 1948, 1949, 1953, 1968), Grinnell and Miller (1944), Harrison (1979), and Scott (1983).

The data were analyzed for means, range, standard error of the means and confidence intervals for the means, and by Spearman Rank Correlations (Zar 1984). Total birds refers to the number of new individuals banded per 100 net h. As a result of the severe decline in productivity of locally breeding birds at Palomarin in 1986 (DeSante and Geupel 1987), we separated this year from the previous decade for some of our analyses.

RESULTS

Composition and abundance of mist-netted birds.—A total of 17,108 birds were captured and banded during the 11 autumns 1976–1986 at Palomarin. For the 10-yr period 1976–1985 the mean for total birds banded per 100 net h (hereafter 100 nh) was 16.06. The 10-yr mean for young birds was 11.065/100 nh, about 69% of the total. The 10-yr mean for UN birds was 3.79/100 nh, about 24% of the total. The 10-yr mean for adult birds was 1.21/100 nh, about 8% of the total.

There were a total of 110 distinct bird species and races captured at Palomarin 1976–1986 (Table 1). Ruby-crowned Kinglets (scientific names in Table 1) were the most abundantly banded with 2731 individuals, followed by Western Flycatchers with 2045, whereas 47 taxa had 10 total captures or fewer. There were 41 species and three additional distinct races averaging at least three banded individuals per autumn that we examined statistically (Table 2) and refer to in this paper as "common species." The individual common species peak years of abundance occurred significantly more often in years of overall high migration ($r_s = 0.757$, $P < 0.05$), but their low years were not correlated with years of overall low migration ($r_s = 0.483$, $P > 0.10$). Nearly every year, however, had at least two common species reach their peak or low, and the maximum year for individual peaks in 1977 included only 21% of these common species (Fig. 1).

About 65% of birds were coastal breeders, 20% were mountain breeders, 9% were northern coastal breeders, 6% were northern breeders and <1% interior breeders or vagrants (Table 3). Interior breeders and vagrants were represented by a fair number of species, but only a few individuals per species.

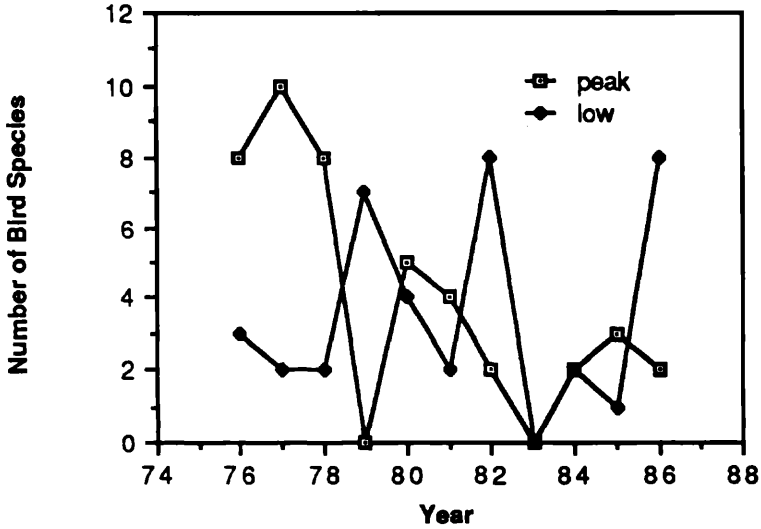


FIGURE 1. Peak and low years of common species (>30 total captures) at Palomarin Field Station.

About 38% of birds were long-distance migrants wintering at Palomarin, 32% were long-distance migrants to the tropics, 10% were permanent residents, 10% were residents with a winter influx, 6% were short-distance migrants found primarily in the summer, and 4% were short-distance migrants found primarily in the winter (Table 3). Neotropical migrant species were caught in relatively lower numbers compared with other groups, whereas the few species of long-distance migrants wintering at Palomarin, such as Ruby-crowned Kinglets and Hermit Thrushes, often had high numbers of individuals (Table 2).

About 78% of birds bred in woodland habitat, 21% in shrubland habitat, and less than 1% in grassland habitat. This distribution may reflect the locations of our nets; 70% were placed in woodlands and 30% in shrublands.

The ratio of known young to adult birds was 9.1:1. The young : adult ratio varied dramatically between common species (Table 2), but the 10-yr means were always >1.0 for every species. For the common taxa with a low percentage of UN birds, the lowest young : adult ratio of 1.53:1 was shown by the House Finch, followed by "Audubon's" Warbler (young : adult = 1.71:1); the highest was shown by the Western Flycatcher (young : adult = 60.88:1) followed by Hermit Thrust (young : adult = 44.72:1).

We found no consistent patterns within or between phylogenetic groups with young : adult ratios (Table 2). Migratory groups, however, did reveal some distinct patterns (Table 3). Long-distance and short-distance migrants wintering at Palomarin, permanent residents, and short-distance

TABLE 1. Number of birds banded at Palomarin Field Station 18 Aug.–25 Nov. 1976–1986 and their groupings.

Species	Groupings			Total
	Habitat preference	Breeding geography	Migratory behavior	*n*
Sharp-shinned Hawk (*Accipiter striatus*)	W	M	W	87
Cooper's Hawk (*A. cooperii*)	W	C	D	2
Red-tailed Hawk (*Buteo jamaicensis*)	G	C	I	1
American Kestrel (*Falco sparverius*)	G	C	I	1
California Quail (*Callipepla californica*)	S	C	P	36
Mourning Dove (*Zenaida macroura*)	G	C	S	3
Black-chinned Hummingbird (*Archilochus alexandri*)	W	I	N	1
Anna's Hummingbird (*Calypte anna*)	S	C	I	146
Calliope Hummingbird (*Stellula calliope*)	W	M	N	1
Rufous Hummingbird (*Selasphorus rufus*)	W	D	N	61
Allen's Hummingbird (*S. sasin*)	S	C	N	5
Belted Kingfisher (*Ceryle alcyon*)	W	C	I	1
Red-breasted Sapsucker (*Sphyrapicus ruber*)	W	M	W	64
Downy Woodpecker (*Picoides pubescens*)	W	C	P	17
Hairy Woodpecker (*P. villosus*)	W	C	P	16
Northern Flicker (*Colaptes auratus*)	W	C	W	1
"Red-shafted" Flicker (*C. a. cafer*)	W	D	C	19
Olive-sided Flycatcher (*Contopus borealis*)	W	C	N	3
Western Wood-pewee (*C. sordidulus*)	W	C	N	69
Willow Flycatcher (*Empidonax traillii*)	S	M	N	30
Least Flycatcher (*E. minimus*)	W	V	N	1
Western Flycatcher (*E. difficilis* and *occidentalis*)	W	C	N	2045
Empidonax (*Empidonax* sp.)	W	C	N	1
Black Phoebe (*Sayornis nigricans*)	G	C	I	11
Say's Phoebe (*S. saya*)	G	I	W	1
Ash-throated Flycatcher (*Myiarchus cinerascens*)	W	I	N	1
Barn Swallow (*Hirundo rustica*)	S	C	L	13
Steller's Jay (*Cyanocitta stelleri*)	W	C	P	30
Scrub Jay (*Aphelocoma coerulescens*)	S	C	P	13
Chestnut-backed Chickadee (*Parus rufescens*)	W	C	P	401
Plain Titmouse (*P. inornatus*)	W	I	P	1
Bushtit (*Psaltriparus minimus*)	S	C	P	188
Red-breasted Nuthatch (*Sitta canadensis*)	W	M	D	93
Pygmy Nuthatch (*S. pygmaea*)	W	C	P	4
Brown Creeper (*Certhia americana*)	W	C	I	107
Rock Wren (*Salpinctes obsoletus*)	G	I	I	2
Bewick's Wren (*Thryomanes bewickii*)	S	C	P	118
House Wren (*Troglodytes aedon*)	W	T	N	4
Winter Wren (*T. troglodytes*)	W	C	I	117
Marsh Wren (*Cistothorus palustris*)	G	C	I	2
Golden-crowned Kinglet (*Regulus satrapa*)	W	C	I	1150
Ruby-crowned Kinglet (*R. calendula*)	W	M	W	2731
Blue-gray Gnatcatcher (*Polioptila caerulea*)	S	I	N	16
Western Bluebird (*Sialia mexicana*)	G	C	P	6
Swainson's Thrush (*Catharus ustulatus*)	W	C	N	473
Hermit Thrush (*C. guttatus*)	W	C	W	1459
American Robin (*Turdus migratorius*)	G	C	D	4

TABLE 1. Continued.

Species	Groupings: Habitat preference	Groupings: Breeding geography	Groupings: Migratory behavior	Total *n*
Varied Thrush (*Ixoreus naevius*)	W	D	W	139
Wrentit (*Chamaea fasciata*)	S	C	P	185
Northern Mockingbird (*Mimus polyglottos*)	S	I	I	2
Brown Thrasher (*Toxostoma rufum*)	S	V	N	1
Loggerhead Shrike (*Lanius ludovicianus*)	G	I	D	2
European Starling (*Sturnus vulgaris*)	G	C	D	1
Solitary Vireo (*Vireo solitarius*)	W	M	N	24
Hutton's Vireo (*V. huttoni*)	W	C	P	124
Warbling Vireo (*V. gilvus*)	W	C	N	1130
Red-eyed Vireo (*V. olivaceus*)	W	V	N	1
Tennessee Warbler (*Vermivora peregrina*)	W	V	N	3
Orange-crowned Warbler (*V. celata*)	W	C	N	155
Nashville Warbler (*V. ruficapilla*)	W	M	N	8
Yellow Warbler (*Dendroica petechia*)	W	C	N	276
Chestnut-sided Warbler (*D. pensylvanica*)	W	V	N	2
Magnolia Warbler (*D. magnolia*)	W	V	N	2
Black-throated Blue Warbler (*D. caerulescens*)	W	V	N	1
Yellow-rumped Warbler (*D. coronata*)	W	M	W	13
"Myrtle" Warbler (*D. c. coronata*)	W	N	W	56
"Audubon's" Warbler (*D. c. auduboni*)	W	M	D	47
Black-throated Gray Warbler (*D. nigrescens*)	W	M	N	62
Townsend's Warbler (*D. townsendi*)	W	D	N	363
Hermit Warbler (*D. occidentalis*)	W	M	N	36
Townsend's X Hermit Warbler (*D. townsendi* X *occidentalis*)	W	D	N	1
Palm Warbler (*D. palmarum*)	S	V	N	5
Blackpoll Warbler (*D. striata*)	W	V	N	10
American Redstart (*Setophaga ruticilla*)	W	V	N	8
Northern Waterthrush (*Seiurus noveboracensis*)	W	V	N	1
Connecticut Warbler (*Oporornis agilis*)	W	V	N	1
MacGillivray's Warbler (*O. tolmiei*)	W	M	N	26
Common Yellowthroat (*Geothlypis trichas*)	G	C	S	3
Wilson's Warbler (*Wilsonia pusilla*)	W	C	N	442
Yellow-breasted Chat (*Icteria virens*)	S	I	N	1
Scarlet Tanager (*Piranga olivacea*)	W	V	N	1
Western Tanager (*P. ludoviciana*)	W	M	N	156
Rose-breasted Grosbeak (*Pheucticus ludovicianus*)	W	V	N	2
Black-headed Grosbeak (*P. melanocephalus*)	W	C	N	44
Lazuli Bunting (*Passerina amoena*)	S	I	N	11
Rufous-sided Towhee (*Pipilo erythrophthalmus*)	S	C	I	156
California Towhee (*P. crissalis*)	S	C	P	26
Rufous-crowned Sparrow (*Aimophila ruficeps*)	S	I	P	12
Chipping Sparrow (*Spizella passerina*)	W	M	G	10
Lark Sparrow (*Chondestes grammacus*)	G	I	S	1
Sage Sparrow (*Amphispiza belli*)	S	I	P	1
Grasshopper Sparrow (*Ammodramus savannarum*)	G	C	N	2
Fox Sparrow (*Passerella iliaca*)	S	D	W	580
Song Sparrow (*Melospiza melodia*)	S	C	P	234

TABLE 1. Continued.

Species	Groupings			Total
	Habitat preference	Breeding geography	Migratory behavior	*n*
Lincoln's Sparrow (*M. lincolnii*)	S	M	W	85
White-throated Sparrow (*Zonotrichia albicollis*)	S	V	W	8
Golden-crowned Sparrow (*Z. atricapilla*)	S	N	W	909
White-crowned Sparrow (*Z. leucophrys*)	S	C	P	37
"Gambel's" White-crowned Sparrow	S	N	W	112
"Puget-sound" White-crowned Sparrow	S	D	W	336
"Nuttall's" White-crowned Sparrow	S	C	P	143
Dark-eyed Junco (*Junco hyemalis*)	W	C	D	628
Brewer's Blackbird (*Euphagus cyanocephalus*)	G	C	I	1
Orchard Oriole (*Icterus spurius*)	W	V	N	1
Northern Oriole (*I. galbula*)	W	I	N	7
Purple Finch (*Carpodacus purpureus*)	W	C	S	546
House Finch (*C. mexicanus*)	G	S	C	51
Pine Siskin (*Carduelis pinus*)	W	C	D	144
Lesser Goldfinch (*C. psaltria*)	S	I	D	19
American Goldfinch (*C. tristis*)	S	C	S	116

[a] G = grassland, or the edges of grassland; S = scrub; W = woodland.

[b] I = interior (central valleys of California); M = interior mountains of California; C = California coast west of the central valleys; D = North American coast north of California; N = inland and north of California; V = vagrants (east of the continental divide).

[c] P = permanent residents; I = permanent residents with fall influx of individuals wintering at Palomarin; N = neotropical migrants; W = long-distance migrants that breed north of California and winter at Palomarin; S = short-distance migrants that live in California, but are at Palomarin primarily in summer; D = short-distance migrants that live in California but are at Palomarin primarily in the winter.

migrants summering at Palomarin all had very similar young : adult ratios. The two groups with much higher young : adult ratios were long-distance migrants to the neotropics and permanent residents with an autumn influx. Adults of the former group avoided the coast in migration, whereas in the latter group the autumn influx of wintering birds was almost all young birds.

The young : adult ratios of California coastal and interior mountain breeders were higher than the other categories (Table 3), and these groups included most of the long-distance migrants to the tropics and residents with an autumn influx. The northern coastal breeders and northern interior breeders had low ratios, and many adults of the species in these groups winter at Palomarin. The rare interior breeders also had a low young : adult ratio.

Woodland birds had a young : adult ratio that was nearly three times higher than shrubland birds.

Timing of migration.—The peak mean number of total birds was mid-October (Fig. 2A) with 21.65/100 nh, but the eight 10-d periods from

TABLE 2. Species of birds banded an average of three or more times annually at Palomarin Field Station 18 Aug.–25 Nov. 1976–1985.

Species		Total[a]	HY[b]	AHY[c]	HY/AHY[d]
Sharp-shinned Hawk	Mean[e]	0.08	0.03	0	—
	SE[f]	0.02	0.01	—	—
	CV[g]	71	105	—	—
Anna's Hummingbird	Mean	0.13	0.07	0.03	2.89
	SE	0.03	0.02	0.01	0.99
	CV	69	102	85	—
Rufous Hummingbird	Mean	0.06	0.05	0.01	10.20
	SE	0.03	0.03	—	—
	CV	175	186	190	—
Red-breasted Sapsucker	Mean	0.06	0.02	0.01	—
	SE	0.02	0.01	0.01	—
	CV	80	93	396	—
Western Wood-Pewee	Mean	0.07	0.06	+[h]	6.75
	SE	0.01	0.01	+	1.55
	CV	57	59	—	—
Willow Flycatcher	Mean	0.03	0.03	+	30.00
	SE	0.01	0.01	+	—
	CV	92	95	—	—
Western Flycatcher	Mean	1.82	1.80	0.02	60.88
	SE	0.33	0.33	0.01	25.54
	CV	56	57	140	—
Chestnut-backed Chickadee	Mean	0.44	0.28	0.04	7.63
	SE	0.19	0.12	0.04	2.18
	CV	136	130	103	—
Bushtit	Mean	0.19	0.07	0.01	5.95
	SE	0.04	0.01	+	2.08
	CV	70	56	97	—
Red-breasted Nuthatch	Mean	0.10	0.06	0.01	8.97
	SE	0.05	0.04	0.01	6.67
	CV	170	190	157	—
Brown Creeper	Mean	0.10	0.07	0.01	5.62
	SE	0.02	0.01	0.01	—
	CV	49	43	170	—
Bewick's Wren	Mean	0.12	0.08	0.02	4.05
	SE	0.02	0.01	+	—
	CV	48	51	79	—
Winter Wren	Mean	0.12	0.10	0.01	16.25
	SE	0.02	0.02	+	6.25
	CV	69	73	0	—
Golden-crowned Kinglet	Mean	1.12	0.38	+	—
	SE	0.36	0.10	+	—
	CV	102	83	—	—
Ruby-crowned Kinglet	Mean	2.46	0.24	0.15	—
	SE	0.31	0.05	0.07	—
	CV	40	69	158	—
Swainson's Thrush	Mean	0.46	0.41	0.03	23.78
	SE	0.01	0.07	0.01	6.84
	CV	53	52	87	—

TABLE 2. Continued.

Species		Total[a]	HY[b]	AHY[c]	HY/AHY[d]
Hermit Thrush	Mean	1.38	1.24	0.06	44.72
	SE	0.25	0.22	0.02	23.37
	CV	58	55	76	—
Varied Thrush	Mean	0.13	0.03	0.02	—
	SE	0.04	0.01	0.01	—
	CV	96	105	151	—
Wrentit	Mean	0.17	0.12	0.01	8.78
	SE	0.02	0.01	+	1.82
	CV	30	26	90	—
Hutton's Vireo	Mean	0.11	0.08	0.01	14.06
	SE	0.02	0.01	+	—
	CV	42	49	—	—
Warbling Vireo	Mean	1.05	1.02	0.03	37.30
	SE	0.37	0.35	0.02	—
	CV	110	108	176	—
Orange-crowned Warbler	Mean	0.15	0.12	0.02	6.32
	SE	0.02	0.02	+	1.49
	CV	40	44	74	—
Yellow Warbler	Mean	0.26	0.20	0.05	4.91
	SE	0.03	0.03	0.01	0.95
	CV	40	45	89	—
Black-throated Gray Warbler	Mean	0.06	0.06	+	27.00
	SE	0.02	0.02	+	—
	CV	100	102	—	—
"Myrtle" Warbler	Mean	0.05	0.03	0.01	2.75
	SE	0.01	0.01	+	0.75
	CV	68	87	—	—
"Audubon's" Warbler	Mean	0.03	0.02	0.01	3.33
	SE	0.01	0.01	+	—
	CV	125	111	211	—
Townsend's Warbler	Mean	0.28	0.23	0.02	10.27
	SE	0.03	0.03	0.01	2.15
	CV	38	43	116	—
Hermit Warbler	Mean	0.03	0.03	+	13.50
	SE	0.01	0.01	+	—
	CV	95	94	—	—
Wilson's Warbler	Mean	0.43	0.40	0.02	17.96
	SE	0.04	0.04	+	4.25
	CV	28	30	79	—
Western Tanager	Mean	0.15	0.14	0.01	11.32
	SE	0.04	0.04	+	3.90
	CV	82	83	141	—
Black-headed Grosbeak	Mean	0.04	0.04	0	—
	SE	0.01	0.01	0	—
	CV	56	56	0	—
Rufous-sided Towhee	Mean	0.14	0.11	0.03	5.63
	SE	0.02	0.02	0.01	1.36
	CV	39	44	97	—

TABLE 2. Continued.

Species		Total[a]	HY[b]	AHY[c]	HY/AHY[d]
Fox Sparrow	Mean	0.54	0.44	0.08	5.46
	SE	0.06	0.06	0.01	0.38
	CV	37	40	48	—
Song Sparrow	Mean	0.23	0.20	0.02	7.12
	SE	0.05	0.05	0.01	1.22
	CV	69	76	90	—
Lincoln's Sparrow	Mean	0.08	0.07	0.01	11.17
	SE	0.01	0.01	+	—
	CV	58	66	—	—
Golden-crowned Sparrow	Mean	0.84	0.68	0.13	6.00
	SE	0.15	0.12	0.02	0.82
	CV	55	57	57	—
"Gambel's" White-crowned Sparrow	Mean	0.10	0.10	0.01	10.56
	SE	0.02	0.02	+	—
	CV	75	67	141	—
"Puget-sound" White-crowned Sparrow	Mean	0.36	0.28	0.07	5.08
	SE	0.06	0.05	0.02	0.90
	CV	53	53	76	—
"Nuttall's" White-crowned Sparrow	Mean	0.16	0.15	+	30.60
	SE	0.05	0.05	+	—
	CV	104	107	—	—
Dark-eyed Junco	Mean	0.58	0.44	0.07	9.05
	SE	0.14	0.12	0.02	1.75
	CV	78	83	81	—
Purple Finch	Mean	0.54	0.41	0.06	9.74
	SE	0.04	0.06	0.01	3.73
	CV	21	43	44	—
House Finch	Mean	0.05	0.03	0.02	1.53
	SE	0.03	0.02	0.01	—
	CV	220	255	205	—
Pine Siskin	Mean	0.14	0.10	0.02	4.59
	SE	0.04	0.03	0.01	0.84
	CV	105	94	136	—
American Goldfinch	Mean	0.12	0.09	0.02	4.50
	SE	0.03	0.02	0.01	1.34
	CV	73	81	82	

[a] Total birds banded per 100 net-h, including birds of unknown age.
[b] Total hatching year birds banded per 100 net-h.
[c] Total after-hatching year birds banded per 100 net-h.
[d] Ratio of hatching year to after-hatching year birds.
[e] Mean for 10 yr, 1976–1985.
[f] SE = standard error of the mean for 10 yr, 1976–1985.
[g] CV = coefficient of variation among years 1976–1985.
[h] + = less than 0.005 birds per 100 net-h.

TABLE 3. Groups of birds banded at Palomarin Field Station from 18 August to 25 November, 1976–1985. Group definitions are at the bottom of Table 1. Information presented are as in Table 2.

Group		Total	HY	AHY	HY/AHY
Habitat					
Grassland	Mean	0.09	0.06	0.02	2.84
	SE	0.03	0.02	0.01	0.87
	CV	114	132	—	—
Shrubland	Mean	3.41	2.66	0.48	5.70
	SE	0.33	0.30	0.04	0.51
	CV	31	35	29	—
Woodland	Mean	12.55	8.34	0.71	15.03
	SE	1.33	0.91	0.13	—
	CV	34	35	59	—
Migratory behavior					
Long-distance migrant wintering at Palomarin	Mean	6.10	3.21	0.55	7.17
	SE	0.51	0.31	0.09	1.12
	CV	26	30	50	—
Neotropical migrant	Mean	5.10	4.78	0.21	26.32
	SE	0.58	0.55	0.03	3.73
	CV	36	36	43	—
Permanent resident	Mean	1.66	1.16	0.17	7.36
	SE	0.31	0.24	0.03	1.26
	CV	59	64	49	—
Resident with winter influx	Mean	1.63	0.74	0.08	18.74
	SE	0.36	0.10	0.02	8.78
	CV	70	43	60	—
Short-distance migrant (mostly in summer)	Mean	0.67	0.51	0.10	7.27
	SE	0.08	0.07	0.02	1.68
	CV	37	45	50	—
Short-distance migrant (mostly in winter)	Mean	0.88	0.68	0.11	7.12
	SE	0.20	0.16	0.02	1.44
	CV	72	72	69	—
Breeding geography					
Interior	Mean	0.07	0.06	0.01	4.76
	SE	0.01	0.01	+	1.71
	CV	61	64	211	—
Mountain	Mean	3.15	0.81	0.20	15.57
	SE	0.34	0.10	0.07	6.57
	CV	34	39	117	—
Coastal	Mean	10.42	8.31	0.66	13.97
	SE	1.08	0.86	0.07	2.07
	CV	33	33	33	—
Northern Interior	Mean	1.00	0.81	0.15	6.25
	SE	0.15	0.12	0.02	0.88
	CV	46	47	53	—
Northern Coastal	Mean	1.37	1.03	0.20	5.54
	SE	0.12	0.10	0.02	0.45
	CV	27	29	38	—
Vagrant	Mean	0.04	0.04	+	—
	SE	0.01	0.01	—	—
	CV	57	58	158	—

mid-August to early November all had means over 15/100 nh. The ranges of the first nine 10-d periods varied by a factor of 2.4–4.5, and showed that in a given year a major peak in migration could have occurred any time from mid-August to early November (Fig. 2A). The peaks of young birds/100 nh (Fig. 2B) were somewhat earlier than adult birds/100 nh (Fig. 2C), which included proportionately more winter resident individuals.

Annual variability of total birds, age classes, species, and groups.—The year with the highest rate of capture was 1977 with 25.18/100 nh, about 2.52 times as much as the minimum of 10.00/100 nh in 1979. Young birds/100 nh had a proportional difference between the peak and lowest years similar to total birds, with 2.65 times as many birds between the maximum of 17.08/100 nh in 1977 and the minimum of 6.45 in 1986. Adult birds/100 nh showed a slightly greater proportional difference between the peak and lowest years than either total birds or young birds, with 3.07 times as many birds between the maximum of 2.06/100 nh in 1981 and the minimum of 0.67/100 nh in 1985. Adult birds also had a slightly higher variability (CV = 39%) than young birds (CV = 27%). There was no correlation between the number of young birds and adult birds in a given year ($r_s = -0.16$, $P > 0.50$ for 1976–1985, $r_s = -0.05$, $P > 0.50$ for 1976–1986). The year 1976 was the second highest for young birds banded, but the second lowest for adult birds. There was no correlation between the number of birds banded during the summer (data from DeSante and Geupel 1987), and the number captured the following autumn for either young birds ($r_s = -0.05$, $P > 0.50$) or adult birds ($r_s = 0.434$, $P > 0.20$).

Of the common species (Table 2), most (32 of 44) had a peak year of birds/100 nh at least double their 10-yr mean, and a few (six of 44) peaked at over four times their 10-yr mean. Differences between annual maximums and minimums of birds/100 nh were at least double for all of the common species, and usually much greater. Seven of these 44 species had maximum-minimum differences greater than a factor of 10, with the extreme of 36.78 times as many Chestnut-backed Chickadees/100 nh in 1977 versus 1976. Fourteen of the 44 common species had at least 1 yr with no captures, and whereas many of these species averaged only a few captures per autumn, four of them averaged at least 10 captures.

Annual variation of the young : adult ratio for the common species (Table 2) was usually quite large. Of the 44 common species, 26 had an adequate sample size to compare young : adult ratio, and 23 had a CV over 50% and eight a CV over 100%. Several (11 of 26) of the common species had peak years in their young : adult ratios that were double their 10-yr means, and Hermit Thrush and Purple Finch had peak years that were over four times their 10-yr means. Differences between the maximum and minimum years for young : adult ratios were at least double for nearly all comparable common species (24 of 26), more than five times for the majority (16 of 26), and more than 10 times for some (eight of 26). The most extreme was the Hermit Thrush, whose maximum young : adult ratio was 49.8 times higher than the minimum. Thus the ratio of

young to adult birds varied greatly between species and between years for a given species, a pattern similar to that for numbers of birds/100 nh.

For groups of birds based on migratory behavior there was a general trend of increasing annual variation with decreasing abundance (Table 3) as would be expected statistically. There was lower variability for both long-distance migrants wintering at Palomarin and short-distance migrants summering at Palomarin, however, which indicated these groups migrated consistently along the coast. In contrast, short-distance migrants wintering at Palomarin, and permanent residents with a winter influx, had high variability. Several species in these groups (e.g., Winter Wren and Red-breasted Nuthatch) were eruptive migrants.

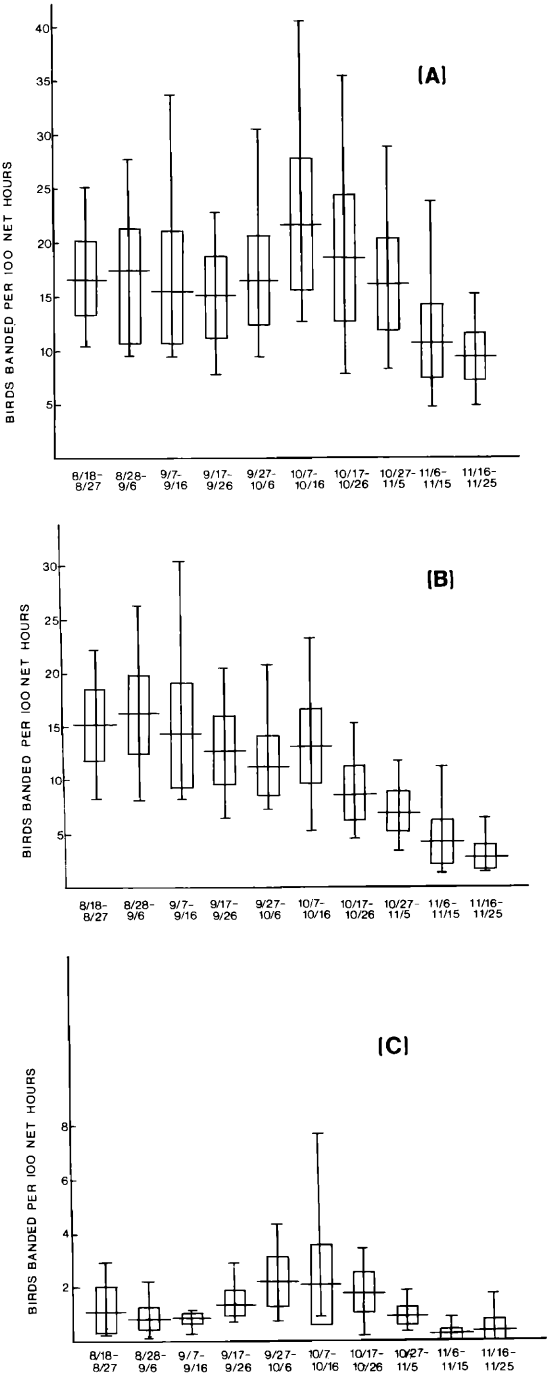
For groups of birds based on breeding geography, the two large groups of coastal and montane breeders had similar annual variation for total, adult and young birds, except that the annual variation of adult montane breeders was very high (Table 3). Thus young and adult coastal breeders and young montane breeders were relatively consistent migrants along the coast, whereas adult montane breeders were erratic. The northern coastal breeders had the lowest variability of any group, and species in this group were both consistent migrants along the coast and also often winter at Palomarin.

The amount of annual variation was similar for birds of woodland and shrubland habitats, except that adult shrubland birds were much less variable than adult woodland birds (Table 3). A much higher proportion of shrubland birds were resident species, whereas woodland birds included most of the erratic montane breeders.

DISCUSSION

The high annual variation in the number of autumn migrants captured at Palomarin was similar to that found in other autumn banding studies in Sweden (Svensson 1978) and along the Baltic Sea (Busse 1973). Annual abundance of autumn migrants on the Farallon Islands was also found to be significantly variable over a 10-yr period (DeSante 1983). Thus, high annual variation in numbers of migrating birds is typical for several areas. High annual variation was especially true for individual species, some of which varied between years by a factor of 10 or more in this study. The complications of abundance, variation, ratio of young to adults, and timing of migration (not quantified for individual species in this study) all indicate that each individual species' passage through Palomarin is different. Infrequent sampling within a season or over just a few years could completely miss species, or drastically underestimate the area's importance to them as a stopover site.

Most of the species captured at Palomarin in autumn were also recorded on the Farallon Islands (DeSante and Ainley 1980, Pyle and Henderson 1991), and at Wool Ranch near the south end of San Francisco Bay (Mewalt and Kaiser 1988). All three sites captured large numbers of migrants that winter in central coastal California or the neotropics. Both


(A)
BIRDS BANDED PER 100 NET HOURS
40
35
30
25
20
15
10
5
8/18-8/27
8/28-9/6
9/7-9/16
9/17-9/26
9/27-10/6
10/7-10/16
10/17-10/26
10/27-11/5
11/6-11/15
11/16-11/25
(B)
BIRDS BANDED PER 100 NET HOURS
30
25
20
15
10
5
8/18-8/27
8/28-9/6
9/7-9/16
9/17-9/26
9/27-10/6
10/7-10/16
10/17-10/26
10/27-11/5
11/6-11/15
11/16-11/25
(C)
BIRDS BANDED PER 100 NET HOURS
8
6
4
2
8/18-8/27
8/28-9/6
9/7-9/16
9/17-9/26
9/27-10/6
10/7-10/16
10/17-10/26
10/27-11/5
11/6-11/15
11/16-11/25

Palomarin and Wool Ranch had a large component of resident species lacking on the Farallon Islands, but the Farallons had many more vagrants.

Ralph (1981) found a relatively high proportion of adults in Red-breasted Nuthatches on the U.S. east coast, in contrast to the pattern of this eruptive species at Palomarin. Perhaps during an eruption year adult Red-breasted Nuthatches move around only locally, or at least will not cross large regions of unsuitable habitat (e.g., the central valley of California).

The much larger numbers of young birds than adult birds found at Palomarin is consistent with the findings of earlier coastal studies (DeSante 1983, DeSante and Ainley 1980, Ralph 1971, Stewart et al. 1974). The lack of correlation between numbers of young and adult birds in a given year at Palomarin is in direct contrast with summer data at Palomarin, which had a strong correlation between these two age groups (DeSante and Geupel 1987). This difference is due to the inherent differences in the populations sampled during these two periods. Autumn banding samples a much more mobile local population than summer banding, and also distant migrants whose numbers can be affected by numerous factors such as food supply (Hutto 1985), daily local weather (Hjorst and Lindholm, 1978, Hussell 1981, Svensson 1978), and long-term weather patterns acting over regional areas (DeSante 1983, Hagan et al. 1992). As adult and young birds from many of these populations do not follow the same migratory routes, as documented by this and earlier studies (Ralph 1971, Stewart et al. 1974), there is no reason for these two age groups to be correlated.

The number of taxa (110) captured at Palomarin in the autumn was more than double the number (51) caught in summer (DeSante and Geupel 1987). The number of individuals in autumn was also higher compared to summer captures (Point Reyes Bird Observatory, unpub. data). High numbers of individuals and species during migration were also found in Minnesota (Winker et al. 1992). Thus, an area is often used by many more bird species and individuals during migration than in the breeding season. Breeding and wintering habitat loss have often been considered probable reasons for landbird population declines (Holmes and Sherry 1988, Tate and Tate 1982), but habitat loss along migration routes is also important (Stevens et al. 1977, Moore and Simmons 1992). Migrating landbird densities vary between habitats (Hutto 1985, Stevens et al. 1977), and are often high in habitats which have been greatly reduced or deteriorated such as desert riparian areas (Stevens et al. 1977,

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FIGURE 2. The number of birds banded per 100 net-h during each of the 10-d periods 18 Aug.–25 Nov. 1976–1985. (2A) = total birds; (2B) = young birds; (2C) = adult birds. Shown for each 10-d period are the mean (long horizontal line), the 95% confident interval of this 10-yr mean (closed rectangle), and the range of the 10 yr.

Terrill and Ohmart 1984). It is critical that we identify and protect important migration habitat.

ACKNOWLEDGMENTS

We would particularly like to thank the more than 100 biologists and volunteers who have helped run the banding operations at Palomarin Field Station. Especially critical efforts were made by L. R. Mewaldt, D. Green, B. Sorrie, P. W. C. Paton, P. Pyle, R. MacDonald, G. Wallace and the Point Reyes National Seashore. The staff at Point Reyes Bird Observatory shared their expertise and helped throughout the project. Financial support was provided by the generosity of the members and board of Point Reyes Bird Observatory and the Chevron Corporation. R. Hutto, W. J. Arendt, N. Nur and an anonymous reviewer provided helpful criticism of the manuscript. This is Point Reyes Bird Observatory contribution #535.

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Received 8 Feb. 1993; accepted 26 May 1993.