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LANDBIRD PRODUCTIVITY IN CENTRAL COASTAL CALIFORNIA: THE RELATIONSHIP TO ANNUAL RAINFALL, AND A REPRODUCTIVE FAILURE IN 1986[1]

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Abstract. The avian productivity of 51 locally breeding species in coastal grassland, coastal scrub, and mixed evergreen forest habitats was estimated from 11 years of standardized mist-netting data collected between 10 May and 17 August at Point Reyes Bird Observatory's Palomarin Field Station. A relationship between the number of young birds banded per 100 net hr and the amount of annual (winter) rainfall during the previous season was apparent for the 10 years 1976 to 1985: productivity was low (19 to 32% below the 10-year mean) in years of extremely low rainfall, increased to a maximum (21 to 39% above the 10-year mean) in years of average or slightly above average rainfall, and decreased substantially (20% below the 10-year mean) in years of very heavy rainfall. The number of young birds banded per 100 net hr in 1986, however, was 62.3% below the previous 10-year mean and fell well outside the above relationship. This high level of reproductive failure occurred in most of the 51 locally breeding species and was independent of migratory behavior, habitat choice, and nest location. It was not independent of foraging behavior, however, as swallows and woodpeckers, species that feed their young on insects produced in decomposer- or detritus-based food chains rather than in primary production-based food chains, showed no significant reduction in productivity. Timing of the decrease in young birds suggests that the onset of reproductive failure occurred in mid-May, well after the nesting season began. Such a large-scale reproductive failure of virtually an entire landbird community has not been reported before and no obvious weather factors appear to explain it. Preliminary data indicate that the reproductive failure was not confined to the vicinity of Palomarin or to central coastal California but rather extended over much of northern California even to the west slope of the Sierra Nevada. It is interesting, but perhaps only coincidental, that several circumstances of this phenomenon, including its timing, appear to coincide remarkably well with the passage of a radioactive "cloud" from the Chernobyl nuclear power plant accident and associated rainfall.

Key words: Landbirds; productivity; reproductive failure; annual rainfall; community dynamics; California; mist-netting.

INTRODUCTION

Because the standard procedure for determining avian productivity, the monitoring of individual nests, is extremely time consuming and labor intensive for landbirds with widely dispersed and well hidden nests, little information exists concerning the long-term productivity of an entire landbird community. In fact, most of the existing data concerning the annual variations in landbird reproductive success have arisen from intensive single-species studies (e.g., Nice 1937, Perrins and Moss 1975, Nolan 1978, Pinkowski 1979, Petrinovitch and Patterson 1983, Tiainen 1983). The determination of reproductive success on a community-wide basis, however, must be a necessary and important component of the effort to understand what controls the dynamics and stability of avian communities, a question that continues to be the subject of ecological debate (Wiens 1983, 1984a; Noon et al. 1985; Dunning 1986). Information regarding annual variations in the reproductive success of various species or guilds of species within the community can provide additional insight toward understanding the dynamics of avian communities. Furthermore, long-term data on the extent and causes of natural fluctuations in the productivity of avian communities are necessary for a proper evaluation of the effects of human-caused environmental disturbances upon these communities. Wiens (1984b) provided convincing arguments for the importance of long-term studies of avian populations and communities.

Weather factors, including temperature, rainfall and snowpack, have been implicated as proximate causes of variations in avian productivity

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in a number of studies (Bryant 1975; Smith and Andersen 1982; Murphy 1983a,b; Tiainen 1983). Coastal central California typically experiences a Mediterranean climate characterized by mild wet winters and warm dry summers. Along the immediate coast, where the Point Reyes Bird Observatory's (PRBO's) Palomarin Field Station is located, the summer drought is ameliorated slightly by the occurrence of persistent fog. Nevertheless, nearly 83% of the annual precipitation falls as rain during the 5 months November to March while only 5% falls during the 5 months May to September. One might expect, therefore, that the amount of annual (essentially, winter) rainfall could affect subsequent reproductive success by affecting the quantity and quality of vegetative growth, which could, in turn, affect the food resources available for raising young as well as the amount of cover available for hiding nests.

For the past 11 years, PRBO personnel have monitored the productivity of 51 locally breeding bird species in coastal grassland, coastal scrub, and mixed evergreen forest habitats at the Palomarin Field Station by means of a standardized mist-netting program. Here, we present some of the results of this study. In particular, we describe the relationship between avian productivity during a given summer and the amount of rainfall during the previous winter, and document an unprecedented reproductive failure that occurred in 1986.

STUDY AREA AND METHODS

An array of 20 12-m nylon mist nets was established at 14 permanent locations at the Palomarin Field Station of the PRBO, just inside the southern end of the Point Reyes National Seashore in Marin County, California (37°56′N and 122°45′W). Fourteen of the 20 nets were located at eight sites along the western edge of the Arroyo Hondo in mixed evergreen forest habitat comprised primarily of coast live oak (*Quercus agrifolia*), California-bay (*Umbellularia californica*), Douglas-fir (*Pseudotsuga Menziesii*), blueblossom (*Ceanothus thyrsiflorus*), and California buckeye (*Aesculus californicus*). The bottom of the arroyo contained a narrow riparian growth of red alder (*Alnus oregona*). Six of these eight forest sites contained double nets stacked one over the other, while the other two forest sites contained single nets. The remaining six single nets were located at six sites in disturbed successional stage coastal scrub habitat adjacent to the arroyo. This habitat was comprised primarily of coyote bush (*Baccharis pilularis*), California sage (*Artemisia californica*), bush monkey flower (*Mimulus aurantiacus*), poison oak (*Rhus diversiloba*), California blackberry (*Rubus vitifolius*), and California coffeeberry (*Rhamnus californica*) interspersed with patches of introduced annual grasses (*Avena, Holcus, Phalaris*), thistles (*Cirseum*), and wild radish (*Raphanus sativa*). Thirty-mm mesh nets were used in the eight protected (from the wind) forest locations whereas 36-mm mesh nets were used in the six more exposed coastal scrub sites.

Disturbed successional stage coastal scrub habitat extended south and southwest for some 450 m from the general location of the nets to the bluffs immediately overlooking the Pacific Ocean. Both disturbed and undisturbed coastal scrub, interspersed with a number of small creeks and drainages, extended west and northwest from the study area for more than 20 km. A second-growth Douglas-fir forest bordered the study area on the north and extended for some 6 km up and over a forested ridge. The mixed evergreen forest of the Arroyo Hondo bordered the study area on the east and was variously 200 to 500 m wide. Moderately grazed coastal grassland and coastal scrub habitat extended for some 5 km to the southeast from the arroyo. Most of the coastal scrub habitat in the area, both to the northwest and to the southeast of the study area as well as that in the study area itself, was located on an old, relatively level marine terrace at about 60 m elevation.

Nets were run daily (weather permitting; i.e., not raining or excessively windy) from 10 May to 17 August during each of the 11 years 1976 to 1986. May 10 corresponds to the earliest date that a HY bird (excluding hummingbirds) was ever captured during the entire 11 years. Hummingbirds were excluded from this analysis because of the unavailability of hummingbird bands during several years of the study. August 17 is 100 days (ten 10-day periods) after 10 May and corresponds to the time after which substantial numbers of migrant birds begin to inundate the study area. There is no doubt that a few migrant individuals of several long-distance migrant species occurred each year prior to 17 August, particularly during the 20 days 29 July to 17 August. These data, however, are included in this analysis because substantial numbers of locally

TABLE 1. Birds banded at the Palomarin Field Station 10 May to 17 August. Comparison of 1986 with the previous 10 years.

Species	Behavioral class				Hatching-year birds						After-hatching-year birds					
					1976–1985						1976–1985					
	M[1]	H[2]	N[3]	F[4]	Mean[5]	SE[6]	1986[5]	% 1986[7]/Mean	No. of SE[8]	CI[9] (%)	Mean[5]	SE[6]	1986[5]	% 1986[7]/Mean	No. of SE[8]	CI[9] (%)
Band-tailed Pigeon	S	W	T	V	0.01	0.01	0.00	0.0	*[10]	*[10]	0.00	0.00	0.00	—	—	—
Mourning Dove	S	G	T	V	0.02	0.02	0.00	0.0	*	*	0.07	0.03	0.00	0.0	*[10]	*[10]
Downy Woodpecker	R	W	C	B	0.57	0.08	0.44	77.2	−1.63	80	0.13	0.05	0.00	0.0	*	*
Hairy Woodpecker	R	W	C	B	0.20	0.06	0.35	175.0	+2.50	95	0.12	0.04	0.00	0.0	*	*
Northern Flicker	S	W	C	B	0.22	0.06	0.53	240.9	+5.17	99.9	0.12	0.03	0.26	216.7	*	*
Olive-sided Flycatcher	L	W	T	S	0.29	0.06	0.09	31.0	−3.33	99	0.60	0.07	0.79	131.7	+2.71	95
Western Wood-Peewee	L	W	T	S	0.12	0.03	0.00	0.0	*	*	0.31	0.11	0.09	29.0	−2.00	90
Western Flycatcher	L	W	B	S	9.03	1.08	3.42	37.9	−5.19	99.9	1.81	0.21	1.40	77.3	−1.95	90
Ash-throated Flycatcher	L	W	C	S	0.02	0.01	0.00	0.0	*	*	0.23	0.06	0.00	0.0	−3.83	99
Tree Swallow	L	G	C	H	0.05	0.03	0.00	0.0	*	*	0.29	0.10	0.44	151.7	+1.50	80
Violet-green Swallow	L	W	C	H	0.10	0.04	0.00	0.0	*	*	0.40	0.11	0.44	110.0	+0.36	20
Northern Rough-winged Swallow	L	G	C	H	0.06	0.03	0.00	0.0	*	*	0.10	0.04	0.00	0.0	*	*
Cliff Swallow	L	S	B	H	0.07	0.03	0.18	257.1	*	*	0.55	0.09	0.00	0.0	−6.11	99.9
Barn Swallow	L	S	B	H	0.84	0.22	0.88	104.8	+0.18	10	0.32	0.08	0.61	190.6	+3.63	99
Steller's Jay	R	W	T	G	0.26	0.05	0.44	169.2	+3.60	99	0.18	0.08	0.35	194.4	*	*
Scrub Jay	R	S	S	G	0.09	0.03	0.00	0.0	*	*	0.09	0.02	0.00	0.0	*	*
Chestnut-backed Chickadee	R	W	C	F	4.76	0.46	1.49	31.3	−7.11	99.99	0.27	0.06	0.61	225.9	+5.67	99.9
Plain Titmouse	R	W	C	F	0.04	0.04	0.00	0.0	*	*	0.00	0.00	0.00	—	—	—
Bushtit	R	S	S	F	4.93	0.86	2.63	53.3	−2.67	95	0.70	0.18	0.53	75.7	−0.94	60
Red-breasted Nuthatch	S	W	C	B	0.11	0.06	0.09	81.8	*	*	0.01	0.01	0.00	0.0	*	*
Brown Creeper	R	W	B	B	2.11	0.25	0.70	33.2	−5.64	99.9	0.09	0.03	0.09	100.0	*	*
Bewick's Wren	R	S	C	F	6.67	0.57	1.76	26.4	−8.61	99.99	0.37	0.09	0.09	24.3	−3.11	98
Winter Wren	R	W	G	G	0.41	0.11	0.00	0.0	−3.73	99	0.06	0.03	0.09	150.0	*	*
Golden-crowned Kinglet	R	W	T	F	0.84	0.31	0.09	10.7	−2.42	95	0.07	0.02	0.00	0.0	*	*
Western Bluebird	R	G	C	G	0.04	0.02	0.00	0.0	*	*	0.16	0.06	0.00	0.0	*	*
Swainson's Thrush	L	W	S	G	2.44	0.34	0.53	21.7	−5.62	99.9	4.77	0.43	5.88	123.3	+2.58	95
Hermit Thrush	L	W	S	G	0.19	0.09	0.09	47.4	*	*	0.04	0.02	0.00	0.0	*	*
American Robin	S	G	T	G	0.20	0.09	0.00	0.0	−2.27	95	0.49	0.09	0.53	108.2	+0.44	30
Wrentit	R	S	S	F	6.81	0.40	3.34	49.0	−8.67	99.99	0.89	0.13	2.46	276.4	+12.08	99.99
European Starling	S	G	C	G	0.06	0.05	0.00	0.0	*	*	0.06	0.03	0.00	0.0	*	*
Hutton's Vireo	R	W	T	F	1.95	0.31	1.05	53.8	−2.90	98	0.15	0.04	0.09	60.0	*	*
Warbling Vireo	L	W	T	F	2.29	0.54	0.00	0.0	−4.24	99	1.83	0.25	1.58	86.3	−1.00	60

TABLE 1. Continued.

Species	Behavioral class				Hatching-year birds						After-hatching-year birds					
					1976–1985						1976–1985					
	M[1]	H[2]	N[3]	F[4]	Mean[5]	SE[6]	1986[5]	% 1986[7]/Mean	No. of SE[8]	CI[9] (%)	Mean[5]	SE[6]	1986[5]	% 1986[7]/Mean	No. of SE[8]	CI[9] (%)
Orange-crowned Warbler	L	W	G	F	4.36	0.45	1.23	28.2	−6.96	99.99	2.44	0.29	0.70	28.7	−6.00	99.9
MacGillivray's Warbler	L	W	G	F	0.28	0.08	0.00	0.0	−3.50	99	0.15	0.04	0.09	60.0	*	*
Wilson's Warbler	L	W	G	F	13.80	1.42	3.86	28.0	−7.00	99.99	2.42	0.17	2.19	90.5	−1.35	70
Black-headed Grosbeak	L	W	T	F	0.58	0.11	0.00	0.0	−5.27	99.9	0.74	0.13	0.70	94.6	−0.31	20
Rufous-sided Towhee	R	S	G	G	1.09	0.14	0.79	72.5	−2.14	90	0.51	0.07	1.05	205.9	+7.71	99.99
Brown Towhee	R	S	S	G	0.26	0.09	0.00	0.0	−2.89	98	0.10	0.02	0.18	180.0	+4.00	99
Rufous-crowned Sparrow	R	S	G	G	0.10	0.03	0.00	0.0	*	*	0.03	0.02	0.00	0.0	*	*
Black-chinned Sparrow	L	S	S	G	0.00	0.00	0.00	—	—	—	0.01	0.01	0.00	0.0	*	*
Savannah Sparrow	S	G	G	G	0.05	0.02	0.00	0.0	*	*	0.01	0.01	0.00	0.0	*	*
Grasshopper Sparrow	L	G	G	G	0.02	0.01	0.09	450.0	*	*	0.02	0.02	0.00	0.0	*	*
Song Sparrow	R	S	S	G	9.88	1.31	3.16	32.0	−5.13	99.9	0.81	0.11	0.79	97.5	−0.18	10
White-crowned Sparrow	R	S	S	G	3.90	0.51	3.51	90.0	−0.76	50	0.40	0.07	0.53	132.5	+1.86	90
Dark-eyed Junco	S	W	G	G	2.57	0.62	0.61	23.7	−3.16	98	0.16	0.04	0.35	218.7	*	*
Red-winged Blackbird	S	G	S	G	0.00	0.00	0.00	—	—	—	0.02	0.01	0.00	0.0	*	*
Brown-headed Cowbird	L	G	S	G	0.00	0.00	0.00	—	—	—	0.09	0.03	0.00	0.0	*	*
Purple Finch	S	W	T	V	2.66	0.64	0.79	29.7	−2.92	98	5.69	1.08	4.74	83.3	−0.88	60
House Finch	S	G	T	V	0.54	0.21	0.09	16.7	−2.14	90	0.76	0.18	0.44	57.9	−1.78	80
Pine Siskin	S	W	T	V	6.37	1.18	1.58	24.8	−4.06	99	4.49	0.78	3.34	74.4	−1.47	80
American Goldfinch	S	S	S	V	1.01	0.23	1.40	138.6	+1.70	80	1.43	0.19	1.14	79.7	−1.53	80
Total					93.26	6.13	35.20	37.7	−9.47	99.99	35.50	2.22	32.57	91.7	−1.32	70

[1] Migratory behavior: L = long-distance migrants, species in which individuals that breed in the neighborhood of the Palomarin Field Station winter primarily in the tropics, and never winter in numbers north of southern California; S = short-distance migrants, in which individuals that breed in the neighborhood of the Palomarin Field Station winter in substantial numbers at the latitude of Palomarin but not in the neighborhood of Palomarin; R = residents, in which individuals that breed in the neighborhood of Palomarin are permanent residents at Palomarin.

[2] Habitat preference: G = grassland species that prefer open, grazed, or mowed grassland habitat or the edges of grassland habitat for foraging when in the neighborhood of the Palomarin Field Station; S = scrubland species that prefer undisturbed or disturbed coastal scrub habitat for foraging when in the neighborhood of Palomarin; W = woodland species that prefer woodland habitat for foraging when in the neighborhood of Palomarin.

[3] Nest location: G = ground nesters; S = shrub nesters; T = tree nesters; C = cavity nesters; B = building or structure nesters. These classifications were made on the basis of observations of individuals nesting in the neighborhood of Palomarin. The four building or structure nesters place their open-cup or closed nests on a human-made structure, against a bank or a tree trunk, or behind the loose bark of a tree trunk.

[4] Foraging behavior during the breeding season: H = hawking; S = sallying; F = foliage gleaning; B = bark gleaning, including both probing and pecking; G = ground gleaning; V = vegetation regurgitating. This last group includes both pigeons and doves and the cardueline finches (Purple and House finches, Pine Siskin, and American Goldfinch), all of which forage, to some extent, during the breeding season on vegetable matter and regurgitate that food to their young.

[5] Birds banded per 1,000 net hr.

[6] Standard error of the mean.

[7] The percentage that the 1986 value was of the previous 10-year mean.

[8] The number of standard errors that the 1986 value was removed from the previous 10-year mean. Calculated as (1986 value − mean value for 1976 to 1985)/SE of the mean for 1976 to 1985.

[9] The largest confidence interval of the 1976 to 1985 mean that the 1986 value was outside of.

[10] Rare species, averaging less than two individuals per year. Sample size too small to allow a meaningful comparison of 1986 with the previous 10 years.

fledged individuals of various resident and short-distance migrant species were still being captured in the nets during these 20 days, especially in years in which the breeding season was prolonged.

The nets were run for 6 hr per day beginning 15 min after local sunrise. The nets were always opened in a standardized order and were always closed in the same order. Thus, 120 net hr were accumulated in each full day of netting. This standardized program was faithfully adhered to from 1979 through 1986. Prior to 1979, the standardization was not quite so rigorous, but the total net hours and timing were quite similar to later years.

All birds captured were brought back to the on-site Field Station (10 to 300 m from the various nets) 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. Juvenile and immature birds in their first calendar year are referred to as hatching-year (HY) birds. Adult birds in their second or later calendar years are called after-hatching-year (AHY) birds. We were unable to age 0.26% of the birds encountered during the 11 years because of difficulty in determining the degree of skull pneumatization. These individuals were excluded from this analysis.

We used the number of HY birds (primarily dispersing juveniles but also, to a lesser extent, dispersing immatures) banded per 100 net hr of operation, and/or the ratio of HY/AHY birds banded during the same period as our measures of avian productivity. It should be noted that this method cannot be used directly to compare productivity between various species or species groups, either in terms of the number of young birds banded per 100 net hr or in terms of the young/adult ratio. This is because capture rates obtained from mist-netting procedures may be biased because of species-specific or age-specific differences in microhabitat preference, foraging height and behavior, flocking behavior, home range size, dispersal distance, and dispersal rate (Karr 1981, DeSante 1983). This method, however, can be used very effectively to compare the productivity of a given species or species group from year to year, and to compare various species and groups of species in terms of their annual variability in productivity. This is because juvenal and immature dispersal, for the most part, is assumed to be independent of local weather conditions.

This paper deals with data collected on 51 locally breeding species of birds (known to have bred at least once within 2 km of the netting operation) of which at least one individual was banded between 10 May and 17 August during the 11-year period 1976 to 1986 (Table 1; scientific names in Appendix). The 51 species were classified according to migratory behavior (three groups), habitat preference (three groups), nest location (five groups), and foraging behavior (six groups). These classifications were based upon the seasonalities of occurrence, habitat preferences, nest locations, and foraging behaviors of individual birds observed in the neighborhood of the Palomarin Field Station and thus are specific to that location. Additional information useful for migratory behavior and habitat preference classifications was obtained from Grinnell and Miller (1944), and for nest location classifications from Harrison (1979).

The comparisons of 1986 with the previous 10 years were based upon summary statistics (mean, standard error of the mean, confidence intervals for the mean, and range) for the years 1976 to 1985. Statistical significance was assumed if the 1986 value fell outside the 95% confidence interval for the mean for 1976 to 1985. The smoothed curve describing the relationship between annual productivity and annual rainfall, along with the 95% confidence interval of the smooth, was obtained by the B-spline adaptive regression technique (DeBoor 1978, Craven and Wahba 1979, O'Sullivan 1985, Silverman 1985).

RESULTS

The annual variability in the number of birds banded per 100 net hr (between 10 May and 17 August) over the 10-year period 1976 to 1985 was similar for HY (CV = 20.8%) and AHY (CV = 19.8%) birds (Fig. 1). Furthermore, for these same 10 years, the number of HY birds in any given year was positively correlated with the number of AHY birds in that same year (r = 0.849). In 1986, however, the number of HY birds banded per 100 net hr dropped dramatically while the number of AHY birds banded per 100 net hr was consistent with the previous 10 years. In fact, the number of HY birds banded per 100 net hr in 1986 was only 37.7% of the mean of the previous 10 years (Fig. 2a). Not only did the 1986 value fall well outside the 99% con-

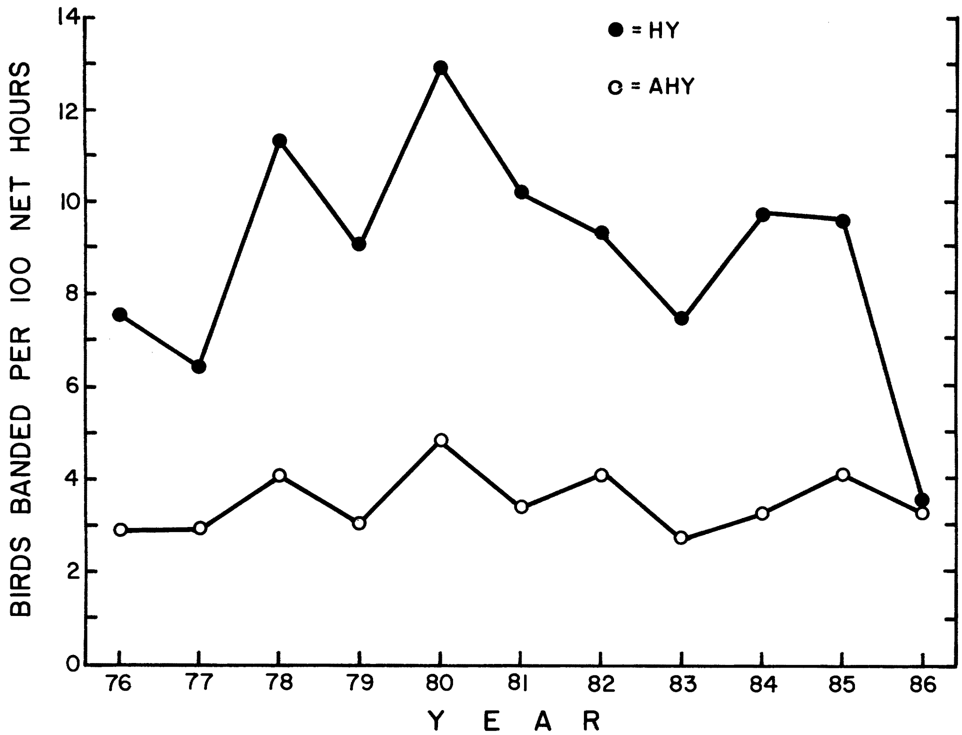


FIGURE 1. Number of birds of all species combined banded per 100 net hr during the period 10 May to 17 August for each of 11 years.

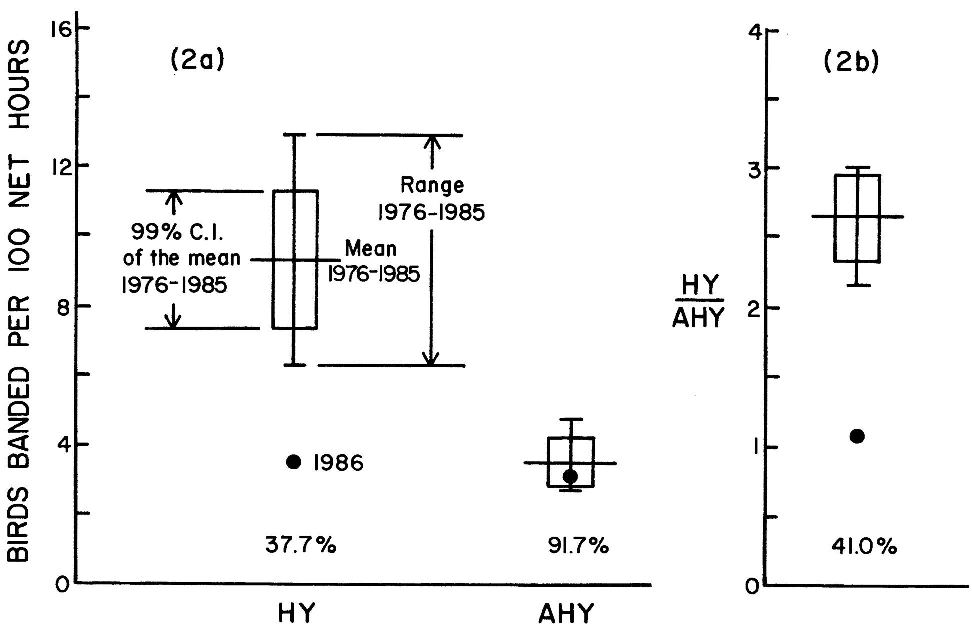


FIGURE 2. Comparison of 1986 with the previous 10 years with respect to banding data during the 100-day period 10 May to 17 August. (2a) Birds banded per 100 net hr. (2b) HY/AHY ratio. Shown in each case are the mean value for the 10 years 1976 to 1985 (long horizontal line), the 99% confidence interval of this 10-year mean (closed rectangle), the range of these 10 years (vertical line terminated by short horizontal lines), the 1986 value (filled circle), and the percentage that the 1986 value was of the previous 10-year mean.

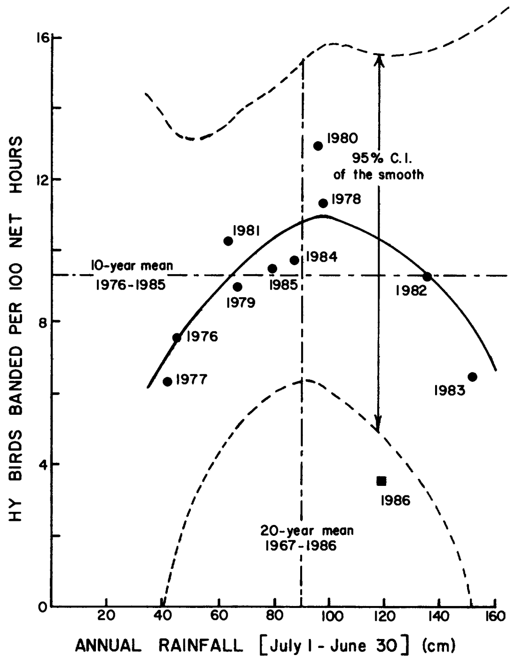


FIGURE 3. Number of HY birds banded per 100 net hr (during the period 10 May to 17 August) as a function of annual rainfall measured from 1 July to 30 June for the 11 years 1976 to 1986. Also shown are the smoothed curve for the 10 years 1976 to 1985 and the 95% confidence interval for the smooth as obtained by the B-spline adaptive regression technique.

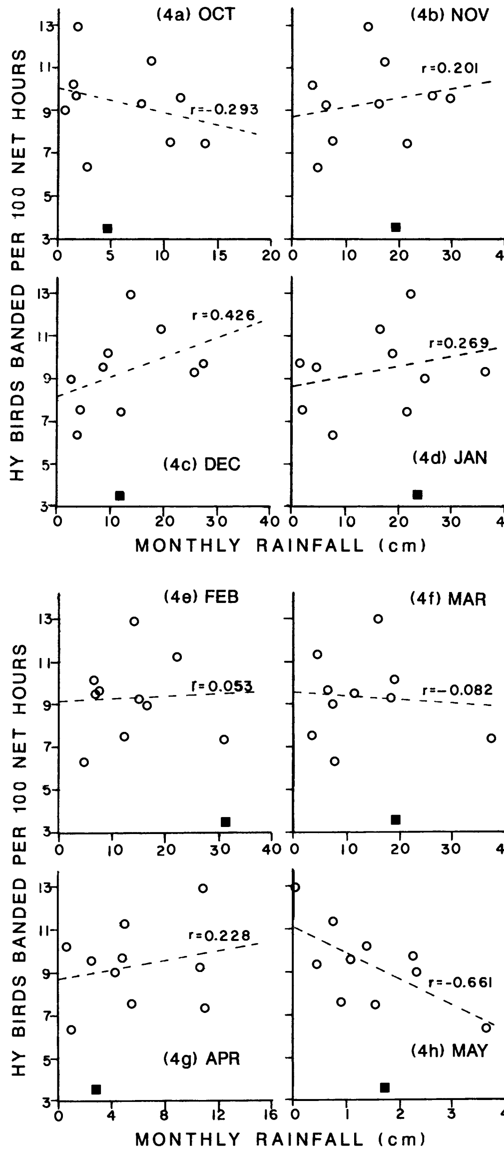


FIGURE 4. Number of HY birds banded per 100 net hr (during the period 10 May to 17 August) as a function of monthly rainfall totals for the 10 years 1976 to 1985 (O) and for 1986 (■). Also shown are the linear regression lines and correlation coefficients for the 10 years 1976 to 1985. (4a) October. (4b) November. (4c) December. (4d) January. (4e) February. (4f) March. (4g) April. (4h) May.

fidence interval of the previous 10-year mean (in fact, well outside the 99.99% confidence interval, being 9.47 standard errors from the mean), it also fell well outside the entire range of values for the previous 10 years. In contrast, the number of AHY birds banded per 100 net hr in 1986 was 91.7% of the previous 10-year mean and fell well within the 99% confidence interval of the previous 10-year mean (and within the 80% confidence interval as well, being only 1.32 standard errors from the mean). Thus, a highly significant decrease in the number of young birds occurred in 1986 without a concomitant decrease in the number of adults.

The annual variability in the HY/AHY ratio over the 10-year period 1976 to 1985 (CV = 11.4%) was considerably less than that for either the number of HY or AHY birds. This was because, during this period, the number of HY birds in any given year was directly related to the number of AHY birds in that same year. As a result, the 99% confidence interval of the 10-year mean for the HY/AHY ratio, as well as the 10-year range of the HY/AHY ratio, was quite narrow (Fig. 2b). The 1986 value of the HY/AHY ratio, however, was only 41.0% of the previous 10-year mean and fell far outside both the 99% confidence interval of the mean (in fact, far outside the 99.99% confidence interval, being 16.37 stan-

TABLE 2. Springtime temperatures (°C) during the period 20 April to 31 May for the past 5 years.

	1982	1983	1984	1985	1986
Minimum (range)	1–11	4–10	3–12	2–12	1–12
Minimum (mean)	5.6	7.2	7.6	6.4	6.2
Maximum (range)	11–26	15–28	16–26	15–25	13–27
Maximum (mean)	18.0	18.8	20.0	19.3	20.0

dard errors from the mean) and the range of the previous 10 years, a highly significant decrease.

THE RELATIONSHIP BETWEEN AVIAN PRODUCTIVITY AND WINTER RAINFALL

The relationship between annual productivity (the number of HY birds of all 51 locally breeding species banded per 100 net hr between 10 May and 17 August) and annual rainfall (measured from 1 July of the previous year to 30 June of the year in question) was consistent for the 10 years 1976 to 1985 (Fig. 3). Productivity appeared to be at a maximum (21 to 39% above the 10-year mean) at average or slightly above average rainfall levels and showed pronounced drops (19 to 32% below the 10-year mean) at both extremely low and extremely high levels of winter rainfall. The number of HY birds banded per 100 net hr in 1986, however, was 62.3% below the 10-year mean, and was well outside the 95% confidence limit of the smoothed curve for the previous 10 years. Certainly, variations in the total annual rainfall were not a cause for the drastically lowered productivity in 1986.

It may be suggested that the amount of rain that falls in a given, perhaps critical, month could influence reproductive success as strongly as the total annual rainfall. This, however, was not the case. Annual productivity (the number of HY birds banded per 100 net hr) over the 10-year period 1976 to 1985 showed no obvious relationship to monthly rainfall totals for any of the 8 months October to May (rainfall during the remaining 4 months was nearly negligible), with the possible exception of May when a weak negative correlation between productivity and rainfall occurred (Figs. 4a–h). While this latter case suggests that late spring storms might adversely affect reproductive success, the weak correlation could well be spurious, being driven primarily by the single extreme 1977 data point. It should not be surprising that no obvious relationships emerged between productivity and individual monthly rainfall totals because the monthly rainfall totals themselves were only weakly correlated with total annual rainfall. In fact, Spearman's rank correlation coefficients between monthly rainfall totals and total annual rainfall over the 10-year period 1976 to 1985 ranged from −0.491 to +0.770 for the 8 individual months October to May and averaged only +0.450. Indeed, as is obvious from Figure 4, monthly winter rainfall totals at Palomarin showed very high variabilities. The coefficients of variation over the 10 years 1976 to 1985 ranged from 60.6% to 82.2% for the 8 individual months October to May and averaged 71.3%. In contrast, the coefficient of variation for total annual rainfall over the same 10 years was 41.6%, quite high but considerably less than the average monthly variabilities. Such a situation is probably characteristic of Mediterranean climates.

It is also evident from these data that the 1985–1986 rainfall, while 38.0% above the previous 10-year mean, was extreme during only one month, February, when a record 31.55 cm occurred (Figs. 4a–h). It is unlikely, however, that this high total February rainfall could alone have been responsible for the 1986 reproductive failure because a similarly high total February rainfall (31.19 cm) occurred in 1983 and was followed by extremely heavy March and April total rainfalls as well (a record 37.59 cm in March and a record 11.05 cm in April). Yet, reproductive success in 1983 was reduced only 20.4% from the 10-year mean while reproductive success in 1986 was reduced 62.3% from the 10-year mean. Thus, the various total monthly rainfalls in 1985–1986 provide no obvious explanation for the 1986 reproductive failure.

Springtime temperatures did not provide an obvious explanation for the 1986 reproductive failure at Palomarin either (Table 2). Slightly clearer than usual weather during the period 20 April to 31 May produced nightly minimum temperatures that averaged 7.5% below the previous 4-year mean and daily maximum temperatures that averaged 5.1% above the previous

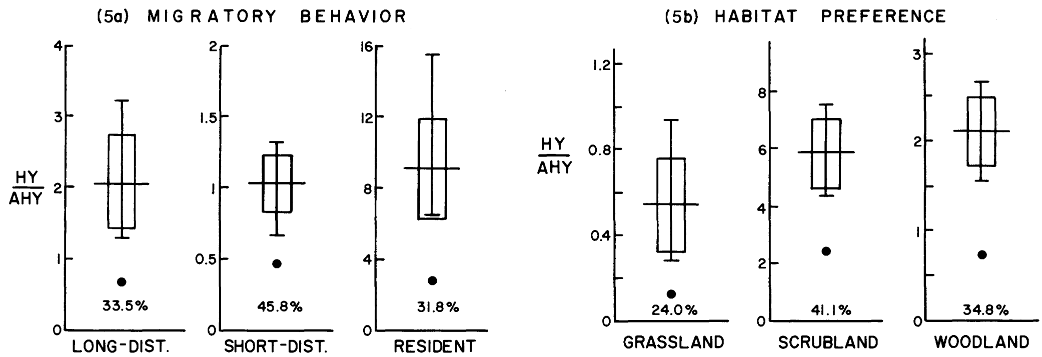


FIGURE 5. Comparison of 1986 with the previous 10 years for the HY/AHY ratio as determined from banding data during the 100-day period 10 May to 17 August for 51 species classified according to (5a) migratory behavior, (5b) habitat preference, (5c) nest location (next page), and (5d) foraging behavior (next page). Symbols and information presented are as in Figure 2.

4-year mean, but in neither case did the range of maximum or minimum temperatures fall outside the range of the previous 4 years.

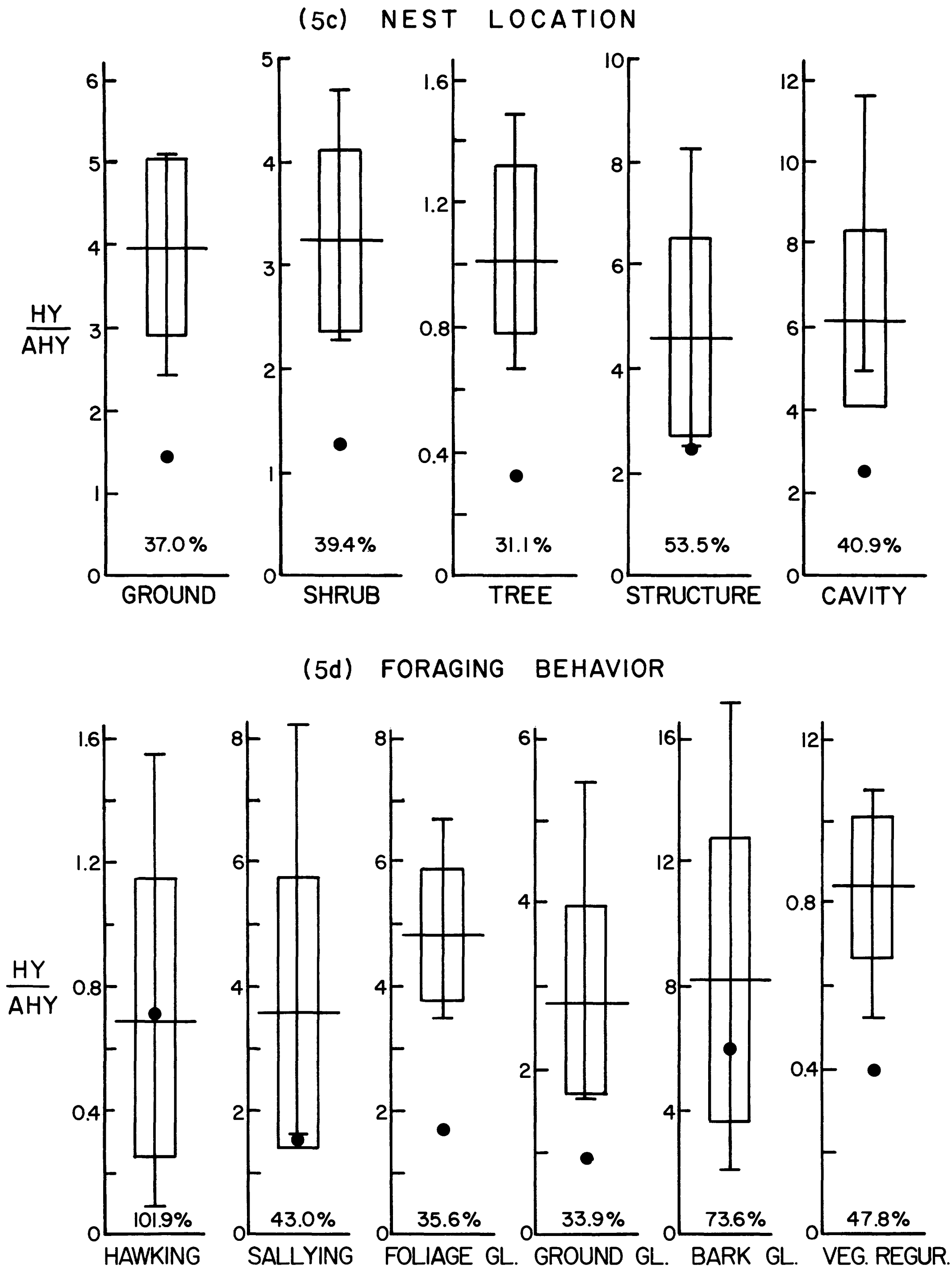
Finally, no major habitat changes have occurred in the past 11 years within at least 2 km of the study area (which lies inside the Point Reyes National Seashore), other than the gradual continuing natural succession of a portion of the disturbed coastal scrub. Furthermore, no direct application of pesticides, herbicides, or other chemical contaminants were known to have occurred in the past 11 years within at least 2 km of the study area.

THE 1986 REPRODUCTIVE FAILURE: INDIVIDUAL SPECIES AND SPECIES GROUPS

During the 10-year period 1976 to 1985, HY individuals of 31 of the 51 locally breeding species were captured in large enough numbers to allow meaningful comparisions with 1986 (Table 1). Significant decreases in the number of HY birds banded occurred in 1986 for 22 of these 31 species. In contrast, significant increases in the number of HY birds banded occurred in 1986 for only three species (Hairy Woodpecker, Northern Flicker, and Steller's Jay), while nonsignificant changes (four decreases and two increases) occurred in 1986 for six species (Downy Woodpecker, Barn Swallow, Rufous-sided Towhee, White-crowned Sparrow, House Finch, and American Goldfinch). Furthermore, only four of the 20 rare species showed increases in 1986 in the number of HY birds banded. It appears, therefore, that the 1986 reproductive failure was characteristic of the great majority of individual species as well as being highly significant for all species combined.

For AHY birds, 26 of the 51 species had large enough sample sizes during the 1976 to 1985 period to permit meaningful comparisons with 1986 (Table 1). In striking contrast to the situation for HY birds, only four of these 26 species showed significant decreases in 1986 in the number of AHY birds banded, while seven species showed significant increases in 1986, and 15 species showed nonsignificant changes in 1986 (11 decreases and four increases). Thus, no consistent increasing or decreasing trends in the number of AHY birds banded in 1986 were characteristic of the various individual species. This is in agreement with the fact that the total number of AHY birds banded in 1986 for all species combined did not differ significantly from the previous 10-year mean.

In order to provide further possible insights into the 1986 reproductive failure, species were grouped according to migratory behavior, habitat preference, nest location, and foraging behavior and the HY/AHY ratios of these groups were examined. (See footnotes to Table 1 for definitions of each of the groups.) Highly significant decreases in the HY/AHY ratio occurred in 1986 for all three groups of species classified by migratory behavior (Fig. 5a; the 1986 value was 6.73 SE from the mean of the previous 10 years for the 19 long-distance migrant species, 9.44 SE from the mean for the 13 short-distance migrant species, and 7.33 SE for the 19 resident species). These results indicate that if the 1986 reproductive failure was related to factors operating during the previous winter on the wintering grounds of the various species, these factors were not confined either to the vicinity of the Palomarin Field Station or to the tropics but



instead were very widely distributed. Alternatively, these results suggest that the factors involved were more likely operative during the breeding season at Palomarin.

Highly significant decreases in the HY/AHY ratio also occurred in 1986 for species characteristic of each of the major habitat types in the vicinity of the Palomarin Field Station (Fig. 5b;

the 1986 value was 6.20 SE from the mean of the previous 10 years for the 11 grassland species, 9.35 SE from the mean for the 13 scrubland species, and 11.58 SE for the 27 woodland species). The factors that contributed to the 1986 reproductive failure, therefore, were apparently not confined to any one habitat.

We created five nest location classifications in order to determine if the potential susceptibility to nest predators could have had an effect upon the severity of the 1986 reproductive failure. In particular, we felt that cavity nesters and, to a lesser extent, structure nesters should be less susceptible to nest predation than open-cup nesters that nest either on the ground or in shrubs or trees. Species in all five nest location groups, however, showed highly significant decreases in the HY/AHY ratio in 1986, although structure nesters (but not necessarily cavity nesters) were perhaps less severely affected (Fig. 5c; the 1986 value was 7.67 SE from the mean of the previous 10 years for the nine ground-nesting species, 7.32 SE from the mean for the 12 shrub-nesting species, 8.61 SE for the 13 tree-nesting species, 5.67 SE for the 13 cavity nesters, and 3.67 SE for the four structure nesters). This suggests that the factors causing the reduced reproductive success in 1986 were not primarily related to nest predation. The striking consistency across the various species groupings in the magnitude of the 1986 reproductive failure should be noted at this point. For all 11 groups of species classified according to migratory behavior, habitat preference, and nest location, 1986 produced, by far, the poorest HY/AHY ratio. For nine of these 11 groups, the 1986 HY/AHY ratio was only 24 to 41% of the previous 10-year mean.

Finally, we grouped the species according to their breeding season foraging behavior into six groups (Fig. 5d). These groups were developed not only to indicate the type of foraging behavior used by adult birds in the breeding season but also to reflect upon the type of food fed to nestlings. The 12 foliage-gleaning, 19 ground-gleaning, and 6 vegetation-regurgitating species showed highly significant decreases in the HY/AHY ratios in 1986 (being, respectively, 9.62, 5.37, and 8.23 SE from the mean of the previous 10 years). The 4 sallying species also showed a dramatic decrease in productivity in 1986, the HY/AHY ratio being 3.04 SE from the mean of the previous 10 years and thus falling well outside the 98% confidence interval, but barely inside the 99% confidence interval, of the mean. In sharp contrast to those four groups of species, two groups, the five hawking species (swallows) and five bark-gleaning species (woodpeckers, nuthatches, and creepers), showed no significant decreases in productivity in 1986, the HY/AHY ratio being, respectively, only 0.09 and 1.55 SE from the mean of the previous 10 years.

TIMING OF THE 1986 REPRODUCTIVE FAILURE

We next inquired when, during the season, the 1986 reproductive failure occurred. Was it evident from the very start of the season or did it occur sometime after the breeding season had begun? By comparing the 1986 HY capture rates during each of the ten 10-day periods between 10 May and 17 August with those of the previous 10 years, we found that 1986 started out as a perfectly normal year (Fig. 6a). Although the numbers of HY birds captured during the first three 10-day periods are always small, the numbers in 1986 were not significantly different from those in previous years, being some 95%, 109%, and 131%, respectively, of the previous 10-year mean. Beginning in the fourth 10-day period, however, highly significant decreases were detected in 1986 that increased in severity to a low of only 24% of average in the eighth 10-day period in late July. A slight recovery may have occurred in the ninth and tenth periods with decreases only to 34% and 37% of average, respectively. In summary, it was as if the peak of production that normally occurs from late June to mid-August simply never occurred at all in 1986, and numbers of HY birds remained roughly at early June levels.

It must be stressed here that the HY birds captured in our standardized battery of mist nets and shown in Figure 6a were, in the vast majority of cases, birds in juvenal plumage that were undergoing juvenal dispersal. They had fully grown tails and were independent of parental

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FIGURE 6. Comparison of 1986 with the previous 10 years for the number of birds banded per 100 net hr during each of the ten 10-day periods between 10 May and 17 August. (6a) HY birds. (6b) AHY birds. Symbols and information presented are as in Figures 2 and 5.

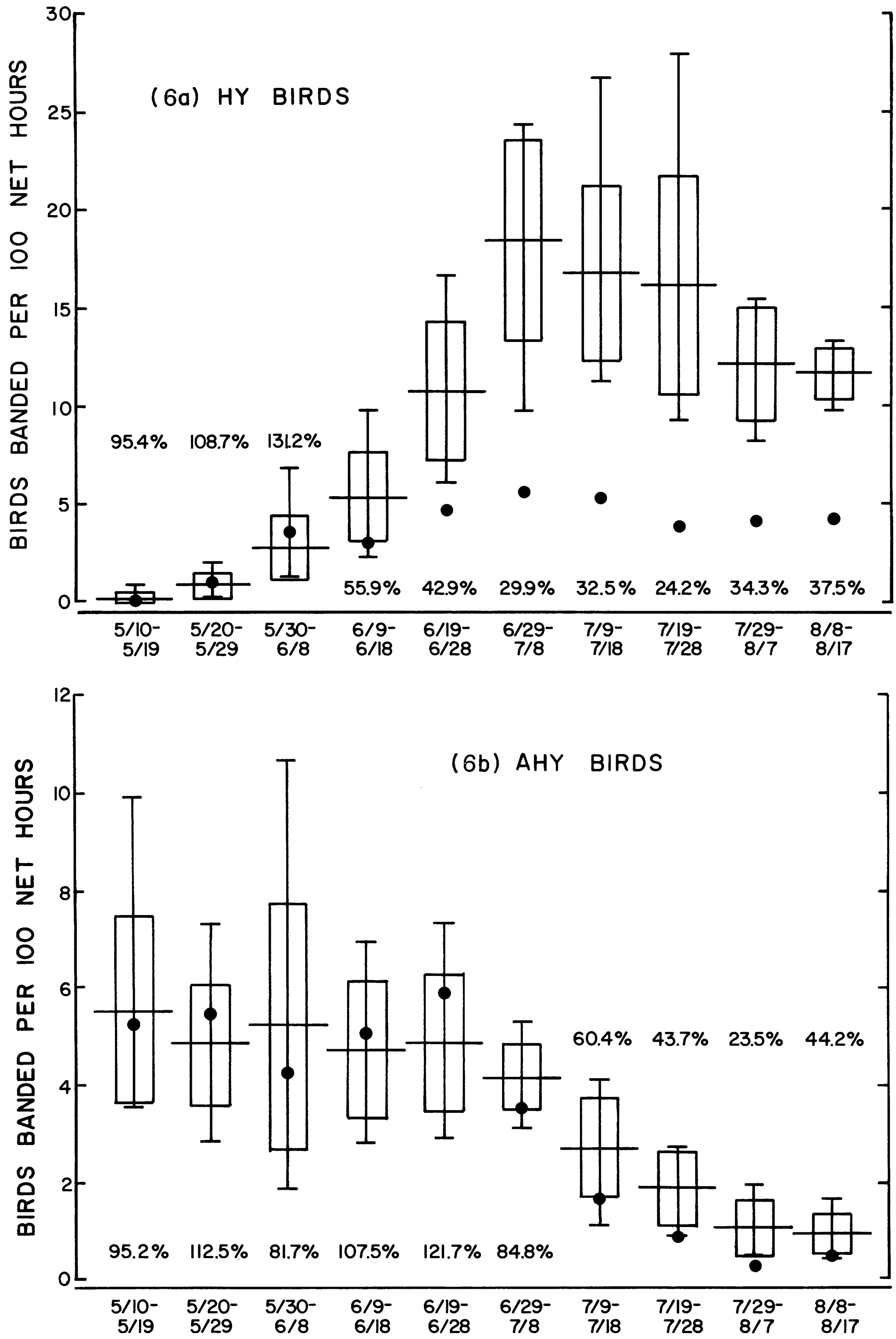
(6a) HY BIRDS
BIRDS BANDED PER 100 NET HOURS
30
25
20
15
10
5
0
95.4%
108.7%
131.2%
55.9%
42.9%
29.9%
32.5%
24.2%
34.3%
37.5%
5/10- 5/19
5/20- 5/29
5/30- 6/8
6/9- 6/18
6/19- 6/28
6/29- 7/8
7/9- 7/18
7/19- 7/28
7/29- 8/7
8/8- 8/17
(6b) AHY BIRDS
BIRDS BANDED PER 100 NET HOURS
12
10
8
6
4
2
0
60.4%
43.7%
23.5%
44.2%
95.2%
112.5%
81.7%
107.5%
121.7%
84.8%
5/10- 5/19
5/20- 5/29
5/30- 6/8
6/9- 6/18
6/19- 6/28
6/29- 7/8
7/9- 7/18
7/19- 7/28
7/29- 8/7
8/8- 8/17

TABLE 3. Adult birds banded at the Palomarin Field Station 9 July to 17 August. Comparison of 1986 with the previous 10 years.

Classification	1976–1985 Mean[1]	SE[2]	Range	1986	% 1986[3]/Mean	No. of SE[4]	CI (%)[5]
Long-distance migrants	25.15	2.46	15.95–40.07	11.40	45.3	−5.59	99.9
Short-distance migrants	31.72	3.82	15.01–55.04	13.98	44.1	−4.64	99
Residents	9.84	1.71	3.34–20.03	6.15	62.5	−2.16	90

[1] Birds banded per 1,000 net hr.
[2] Standard error of the mean.
[3] The percentage that the 1986 value was of the previous 10-year mean.
[4] The number of standard errors that the 1986 value was removed from the previous 10-year mean. Calculated as (1986 value − mean value for 1976 to 1985)/SE of the mean for 1976 to 1985.
[5] The largest confidence interval of the 1976 to 1985 mean that the 1986 value was outside of.

care. In this respect, they had been out of their nests for at least 3 weeks and, in many cases, much longer. Thus, if the reproductive failure that we began to detect about 10 June was caused by an unusually high mortality of nestlings, this mortality must have begun to occur sometime between about 10 May and 20 May. If it was caused by the failure of eggs to hatch, this failure must have begun to occur somewhat earlier, about 25 April to 10 May. If it was caused by the failure of birds to breed or of females to lay eggs, it must have begun even earlier, roughly in mid-April.

We also compared 1986 with the previous 10 years for the number of AHY birds banded per 100 net hr during each of these same 10-day periods (Fig. 6b). We found no significant decreases in the number of adult birds during the first 60 days of 1986, but highly significant decreases during the last 40 days of 1986, at the time when the capture rate of adult birds normally begins to drop off. This significant decrease in 1986 could have been caused by an atypical mortality of adult birds. It could also have been caused by an unseasonably early termination of breeding activities in these birds that, in turn, was caused by their prior reproductive failures. Such an early termination of breeding activity would tend to bring about two related events: an early initiation of prebasic molt in adults, and an early initiation of fall migration in adult migrants. Both of these events would tend to lower the capture rates of adult birds because birds are less mobile and thus less likely to be captured during molt, and because adults of migrant species tend to migrate through interior California and are scarce on the coast where Palomarin is located (Stewart et al. 1974). It is of considerable interest, therefore, that the capture rate of adult birds during the last four 10-day periods of 1986 (9 July to 17 August) was significantly less than that for the previous 10 years for both long- and short-distance migrants but not for residents (Table 3). This provides a strong indication that the early termination of breeding and the consequent early initiation of molt and migration, rather than an abnormally high adult mortality, was the cause for the significantly low late season adult capture rate in 1986.

DISCUSSION

The relationship between landbird productivity in central coastal California and annual (winter) rainfall during the previous season appears to be that productivity is low in years of extremely low rainfall, increases to a maximum in years of average or slightly above average rainfall, and decreases substantially in years of very high rainfall. From an evolutionary standpoint, such a relationship may not be unexpected. It suggests that local breeding populations have become adapted to "average" levels of rainfall and produce fewer young during extreme conditions.

How might winter rainfall affect avian productivity? As winter rainfall increases from drought conditions it will bring about an increase in primary vegetative production. This, in turn, will bring about an increase in the food resources available for raising young as well as an increase in the amount of vegetative cover available for hiding nests from nest predators, at least for ground and shrub nesting species. In addition, in a Mediterranean climate, increased winter and spring rainfall will extend the time into the summer that the vegetation stays green and productive and will thus allow for additional broods or renesting attempts later in the season. All of these factors should tend to increase avian production.

Extremely high levels of winter rainfall, however, may tend to cause high winter mortality among both resident and short-distance migrant species, thus decreasing the size of the breeding populations the following spring. Years of extremely high rainfall are often characterized by inclement spring weather (Figs. 4f, g) that can easily delay the onset of breeding and cause reproductive failures in first brood attempts. It is also conceivable that extremely high rainfall levels could directly impact food resources by negatively affecting the hatching, development, and growth of insects. All of these factors should tend to decrease avian production.

Landbird productivity in 1986, however, did not follow the pattern established over the previous 10 years. Rather, 1986 productivity was 62.3% below the mean for the previous 10 years. In this respect, it is interesting to note that the 1986 rainfall value of 118.97 cm predicts, according to the curve shown in Figure 3, a 1986 productivity value of 10.3 HY birds per 100 net hr, a value that is 110.4% of normal. The actual productivity value for the first 30 days of 1986 in fact averaged 111.7% of normal. Thus, the breeding season of 1986 started out in a perfectly predictable manner until something drastic happened a month or so into the season.

The severity of the factors that brought about the 1986 reproductive failure of landbirds at Palomarin can also be gauged by examination of Figure 3. The most severe drought that occurred in California this century occurred in 1976 and 1977. Accordingly, a drop in productivity of from 19.2% to 32.2% of the 10-year mean occurred during these years. Similarly, one of the highest winter rainfalls in California this century occurred during the Southern Oscillation/"El Niño" year of 1983 and corresponded to a drop in productivity of 20.4% from the 10-year mean. In sharp contrast, the 62.3% decrease in productivity that occurred in 1986 was two to three times as great as those caused by several of the most drastic climatic extremes experienced in California this century. The factors causing the 1986 failure must have been severe indeed.

What then did cause the dramatic decrease in productivity that occurred in most landbird species at Palomarin in 1986? Very simply, we don't know. Additional insight into the situation, however, may be obtained by investigating characteristics of the species that appeared *not* to be affected: the three species of woodpeckers, the swallows (at least the Barn Swallow), and a few other miscellaneous species. It is difficult, at first, to imagine what ecological characteristics swallows and woodpeckers could share that could have prevented them from suffering the reproductive failures that characterized most other species of landbirds in 1986. They both, however, feed their young largely on insects that are produced from detritus- or decomposer-based ecosystems, rather than from ecosystems based on primary production. Woodpeckers, for example, feed largely on grubs and beetles that feed on dying, dead, or decaying wood (Bent 1939). Swallows feed extensively on flying insects, especially Diptera, that often emerge from aquatic ecosystems (Bent 1942). In the neighborhood of the Palomarin Field Station, such aquatic ecosystems occur primarily in the flowing waters of several small, year-round or intermittent creeks, and are almost exclusively detritus-based ecosystems.

Along these same lines, the four flycatcher species partially depend upon flying insects that emerge from aquatic ecosystems. They also take substantial numbers of flying insects that emerge from terrestrial or arboreal primary production-based ecosystems. Nevertheless, their partial dependence upon nonprimary production-based ecosystems may account for their slightly less drastic productivity decline in 1986, as compared to foliage gleaners and ground gleaners (Fig. 5d). These same considerations tend to explain why structure nesters showed a less severe productivity decline in 1986 than species utilizing other nest locations (Fig. 5c): two of the four structure nesters are swallows while a third is a flycatcher.

Vegetation-regurgitating species may also have been slightly less severely affected in 1986 than most other species (Fig. 5d). It would appear that their ability to utilize primary production directly as a food supply for themselves and their young, rather than being entirely dependent upon consumers of primary production, may have helped these species to a small extent. Along these same lines, short-distance migrants seemed to have fared slightly less poorly in 1986 than either long-distance migrants or residents (Fig. 5a). This is readily explainable by the fact that fully 85% of the individual short-distance migrants banded during this study were of the six vegetation-regurgitating species.

Thus, it appears that the birds that were most severely impacted in 1986 were those species that forage and feed their young exclusively on insects that are produced within a primary production-based ecosystem. If this were in fact the case, we might expect that species that forage and feed their young extensively on caterpillars or other large larvae that eat new plant growth might be the most severely affected. Indeed, this seems to be the case. We captured *no* HY Warbling Vireos or Black-headed Grosbeaks at Palomarin during the entire 100 days in 1986 and have no indication that any young of these species were produced anywhere in the vicinity of Palomarin. The previous 10-year means for these two species were 24 and six HY birds respectively.

The five miscellaneous species that showed no significant reproductive decline in 1986 warrant some discussion. The House Finch's 1986 reproductive success was only 16.7% of the previous 10-year mean. This drastic reproductive decline was not statistically significant only because in some years the species does not occur or breed at Palomarin at all. Regarding the Steller's Jay, we can offer no comment.

The three remaining species, Rufous-sided Towhee, White-crowned Sparrow, and American Goldfinch, are three of the four latest breeders at Palomarin and regularly fledge young well into August. (The fourth late breeder, interestingly, is the Barn Swallow which also regularly fledges young in August and occasionally even into early September.) The facts (1) that none of these four species showed significantly reduced productivities in 1986, (2) that for each of these species we banded substantial numbers of young during the final two 10-day periods of 1986, and (3) that the 1986 productivity decline during these final two 10-day periods was somewhat less than that of the three immediately preceding 10-day periods indicate that a recovery of reproductive success may have begun during these last two 10-day periods, but that it could only be detected in species whose breeding seasons regularly extend late into the season. If this were indeed the case, then the factors causing the reproductive failure may only have been operative for about 50 days.

The next obvious question is whether or not the phenomenon described here was limited to the immediate vicinity of Palomarin or extended over a greater area of California. Data from the Harvey Monroe Hall Research Natural Area in the subalpine Sierra Nevada suggests that, for Dark-eyed Juncos at least, a major reproductive failure occurred on the west slope of the central Sierra Nevada (D. DeSante, unpubl. data). Nine previous years of data have shown that numerous flocks of from 30 to 150 HY juncos normally move up the west slope of the Sierra into the subalpine in mid- to late summer. In 1986, the largest flock of dispersing juveniles recorded in the Hall Natural Area was only four individuals. Other workers on the west slope of the Sierra also reported extremely low numbers of juvenile juncos as well as a nearly complete absence of juvenile Warbling Vireos and Black-headed Grosbeaks (D. Gaines, pers. comm.).

An intensive study of the nesting of Mountain and Chestnut-backed chickadees at the Blodgett Forest Preserve on the west slope of the northern Sierra Nevada revealed that these species experienced nestling mortality during the last 2 weeks of May 1986 that was very much higher than that of any previous year (D. Dahlston, pers. comm.). Notably reduced reproductive success in 1986 as compared to 1984 and 1985 was reported for *pugetensis* White-crowned Sparrows at the Lamphere-Christensen Nature Preserve on the north coast of California (C. J. Ralph, pers. comm.). Furthermore, preliminary analysis of migrant *pugetensis* White-crowned Sparrows on Southeast Farallon Island indicates that the HY/AHY ratio for fall migrants in 1986 was 0.50 compared to the previous 5-year average of 2.71 (PRBO, unpubl. data). *Pugetensis* White-crowned Sparrows have a limited breeding range from extreme southwestern British Columbia south, west of the Cascade Range in Washington and Oregon, to northern coastal California (AOU 1957). Thus, it appears that the 1986 reproductive failure documented here for Palomarin was not limited to central coastal California but extended widely over northern California to and including the west slope of the Sierra Nevada, and perhaps north through western Oregon and Washington as well.

Interestingly, preliminary results indicate that the productivity of landbirds on the east side of the Sierra Nevada, both in the subalpine (D. DeSante, unpubl. data) and in the sagebrush shrubsteppe near Mono Lake (D. Gaines, pers. comm.), and specifically for Mountain Chickadees in Modoc County (D. Dahlston, pers. comm.), was at relatively normal levels. Similarly, preliminary data on landbirds from the Channel Islands off southern California indicate relatively normal, or even good, reproductive success (C. Collins, pers. comm.). Landbird reproductive success, therefore, was not uniformly poor throughout all of California but varied geographically. We are currently following up these reports and investigating other reports in order to determine the full extent of the 1986 reproductive failure in western North America and elsewhere.

No obvious explanation, therefore, appears to exist for the unprecedented, drastic decline in the local production of landbirds at Palomarin and elsewhere in California in 1986. Given this situation, we surmise that the reproductive failure must have resulted from either a single very rare event or from a rare combination of not so uncommon events. One rare combination of events occurred during the period 13 to 16 February 1986, when a series of very heavy storms, in conjunction with unseasonably warm weather, deluged central California and caused widespread flooding. Night temperatures during the height of the storms were recorded in excess of 15°C. Nevertheless, it is not at all clear exactly how such a combination of events could have brought on the reproductive failure documented here, especially since the failure did not occur at the start of the breeding season but, rather, part way into it.

A second unprecedented rare combination of events occurred on 6 May 1986, when a rather cold rain coincided with the passage over coastal Washington, Oregon, and northern California of a radioactive "cloud" from the accident at the Chernobyl nuclear power plant in the U.S.S.R. We must stress at this point that there exists absolutely no direct evidence linking the reportedly very small amount of radiation dropped from the Chernobyl cloud to the reproductive failure documented here. Mere coincidence may be a possible explanation for the fact that the timing of the passage of the Chernobyl cloud coincided remarkably well with the timing of the onset of the reproductive failure at Palomarin, and that the geographical area over which substantial rainfall was coincident with the passage of the cloud appears, at first glance, to coincide with the geographical areas that experienced some reproductive failure. Furthermore, the species that tended to be unaffected by the reproductive failure were those that raise their young on insects that tend to be produced in detritus or decomposer, rather than primary production food chains. This suggests that the 1986 reproductive failure could have been caused by radioactivity precipitated from the Chernobyl cloud by rainfall, absorbed and incorporated into the primary production food chain by growing plants, concentrated in the food chain by insect consumers, and fed to nestling birds by their parents that foraged on these insects. Again, however, we must emphasize that this entire scenario is completely hypothetical, that the quantities of radioactivity that were reportedly released from Chernobyl are thought by some experts to be far too small to cause nestling mortalities (I. L. Brisbin, pers. comm.), and that the entire relationship of Chernobyl to the 1986 reproductive failure may be coincidental. Nevertheless, when such an unprecedented and drastic avian reproductive failure occurs without any obvious explanation, as we have documented here, any and all coincidences deserve further investigation.

ACKNOWLEDGMENTS

The detection of aberrant phenomena in natural processes, such as the 1986 reproductive failure documented here, depends upon the existence of long-term baseline data against which the aberrancy can be compared. It is with gratitude that we acknowledge the efforts of L. Richard Mewaldt, whose unswerving dedication to the importance of long-term biomonitoring played a major role in the establishment and continuation of the Palomarin Field Station. We are most indebted, however, to the members of the PRBO who, through their continuing financial assistance and numerous donations of time, energy, tools, and equipment, have made this long-term study possible. We especially thank Dorothy B. Hunt for her many generous financial contributions to the Palomarin banding program. We also thank the Chevron Corporation for timely financial assistance with the data analysis phase of this project, and the Point Reyes National Seashore for their cooperation.

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APPENDIX

SCIENTIFIC NAMES OF THE SPECIES MENTIONED IN THE TEXT

Band-tailed Pigeon (*Columba fasciata*), Mourning Dove (*Zenaida macroura*), Downy Woodpecker (*Picoides pubescens*), Hairy Woodpecker (*Picoides villosus*), Northern Flicker (*Colaptes auratus*), Olive-sided Flycatcher (*Contopus borealis*), Western Wood-Peewee (*Contopus sordidulus*), Western Flycatcher (*Empidonax difficilis*), Ash-throated Flycatcher (*Myiarchus cinerascens*), Tree Swallow (*Tachycineta bicolor*), Violet-green Swallow (*Tachycineta thalassina*), Northern Rough-winged Swallow (*Stelgidopteryx serripennis*), Cliff Swallow (*Hirundo pyrrhonota*), Barn Swallow (*Hirundo rustica*), Steller's Jay (*Cyanocitta stelleri*), Scrub Jay (*Aphelocoma coerulescens*), Mountain Chickadee (*Parus gambeli*), Chestnut-backed Chickadee (*Parus rufescens*), Plain Titmouse (*Parus inornatus*), Bushtit (*Psaltriparus minimus*), Red-breasted Nuthatch (*Sitta canadensis*), Brown Creeper (*Certhia americana*), Bewick's Wren (*Thryomanes bewickii*), Winter Wren (*Troglodytes troglodytes*), Golden-crowned Kinglet (*Regulus satrapa*), Western Bluebird (*Sialia mexicana*), Swainson's Thrush (*Catharus ustulatus*), Hermit Thrush (*Catharus guttatus*), American Robin (*Turdus migratorius*), Wrentit (*Chamaea fasciata*), European Starling (*Sturnus vulgaris*), Hutton's Vireo (*Vireo huttoni*), Warbling Vireo (*Vireo gilvus*), Orange-crowned Warbler (*Vermivora celata*), MacGillivray's Warbler (*Oporornis tolmiei*), Wilson's Warbler (*Wilsonia pusilla*), Black-headed Grosbeak (*Pheucticus melanocephalus*), Rufous-sided Towhee (*Pipilo erythrophthalmus*), Brown Towhee (*Pipilo fuscus*), Rufous-crowned Sparrow (*Aimophila ruficeps*), Black-chinned Sparrow (*Spizella atrogularis*), Savannah Sparrow (*Passerculus sandwichensis*), Grasshopper Sparrow (*Ammodramus savannarum*), Song Sparrow (*Melospiza melodia*), White-crowned Sparrow (*Zonotrichia leucophrys*), Dark-eyed Junco (*Junco hyemalis*), Red-winged Blackbird (*Agelaius phoeniceus*), Brown-headed Cowbird (*Molothrus ater*), Purple Finch (*Carpodacus purpureus*), House Finch (*Carpodacus mexicanus*), Pine Siskin (*Carduelis pinus*), American Goldfinch (*Carduelis tristis*).