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SARTOR O. WILLIAMS III, New Mexico Dept. of Game and Fish, State Capitol, Santa Fe, New Mexico 87503. Received 22 April 1988, accepted 6 Sept. 1988.

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Factors affecting the termination of breeding in Nuttall's White-crowned Sparrows. - A number of factors are known to affect the length of birds' breeding seasons, including intrinsic geographical factors, such as photoperiod and latitude (Miller 1960, MacArthur 1964, Ricklefs 1966, Wyndham 1986), and ecological factors, such as altitude and climate (Davis 1933, Skutch 1950, Immelmann 1971). Factors influencing the length of the breeding season can operate by affecting either the timing of the initiation or the termination of breeding or both. Climatic conditions are generally thought to affect the timing of the initiation of breeding by affecting the availability of food resources for the birds (Lack 1950, Skutch 1950, Snow and Snow 1964, Immelmann 1971, Wyndham 1986). However, climatic conditions may also affect the availability of nest sites or nesting material, particularly in areas with extensive winter snowfall (Morton 1978, DeSante, unpubl. data). Climatic conditions may also affect the termination of breeding through a relationship with food supply, but possibly in a more indirect or anticipatory manner. In migratory species, for example, the termination of breeding may occur well in advance of the time when food resources begin to diminish, presumably to allow the birds adequate time and an adequate food supply to raise their young to independence, complete their prebasic molt, and store fat for migration. In non-migratory birds, certain of these necessities may be somewhat relaxed, but the termination of breeding must still to some extent be controlled by the availability of food

In situations where the environment provides predictive information as to the future availability of food resources (Immelmann 1973), the question arises as to what happens if the environmental cues lead to faulty predictions. If a predicted good food supply should suddenly fail, it seems obvious that the birds will either curtail breeding or fail in their breeding attempts if they persist. But what if a predicted failure of the food supply does not happen and food remains abundant? Wong (1983) presented circumstantial evidence to show that supplemental feeding with poultry mash extended the breeding season of Eurasian Tree Sparrows (*Passer montanus*) by two months at a site in Malaysia. Here we present data suggesting that a local superabundance of food will permit extended breeding by individual pairs that have access to that food resource.

Coastal central California experiences a Mediterranean climate characterized by mild wet winters and warm dry summers. Along the immediate coast, where both the Point Reyes Bird Observatory's Palomarin Field Station and Golden Gate Park are located, the summer drought is ameliorated somewhat 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. Virtually all of the annual plants,

Year	Annual (winter) rainfall (cm) <sup>a</sup>	Number _ of nests	Mean clutch completion date for latest 10% of nests		Clutch completion date for latest nest	
			Date	Julian date	Date	Julian date
1979	67.16	9	28 June	179.00	28 June	179
1980	95.96	46	6 July	188.08	19 July	201
1981	63.40	42	30 June	181.20	8 July	189
1982	134.80	47	14 July	194.51	17 July	198
1983	151.69	44	12 July	192.50	20 July	201
1984	86.92	37	22 June	174.03	25 June	177
1985	79.20	32	30 June	181.40	8 Inly	189

TABLE 1
Timing of the Termination of Breeding of Nuttall's White-crowned Sparrows at the Palomarin Field Station

including both introduced grasses and native forbs, as well as many of the perennial grasses and shrubs, and even certain trees, such as California buckeye (Aesculus californicus), curtail primary production, dry up, turn brown and/or drop their leaves during the summer months. The timing of this browning of the landscape varies with the amount of winter rainfall that the area received. This occurs because increased amounts of winter rainfall tend to increase soil moisture content, ground water supplies, and spring-fed stream and seep flows, all of which permit vegetative growth later into the summer. Furthermore, winters of heavy rainfall are often followed by heavy spring rains that extend later than usual, thereby further delaying the onset of summer dry-up.

Because many breeding birds feed their young on herbivorous insects, and because most herbivorous insects feed on green growing plant material, it should be expected that the onset of the summer dry-up would bring about an abrupt termination to breeding activity in passerine birds. In order to test this hypothesis, we analyzed data from 247 Nuttall's White-crowned Sparrow (Zonotrichia leucophrys nuttalli) nests monitored during an intensive 7-year study (1979–1985) of the breeding biology of this species at the Palomarin Field Station of the Point Reyes Bird Observatory. The timing of the termination of breeding was estimated by the mean clutch completion date of the latest 10% of the nests found each year, as well as by the clutch completion date of the latest nest found each year (Table 1). The clutch completion date for nests found after the clutch was already completed was assumed to be 12 days prior to hatching, the mean length of the incubation period for Palomarin White-crowneds. For nests that were found after the clutch was already completed and that were preyed upon before hatching, the clutch completion date was estimated as the median date of the range of possible dates, again assuming a 12-day incubation period.

Figure 1 indicates that the timing of the termination of breeding, as determined by the mean clutch completion date of the latest 10% of the nests found each year, was directly related to the amount of winter rainfall during the previous year (r = 0.820, P < 0.05), such that breeding extended later into the summer following winters of heavier rainfall. A similar relationship existed using the single latest nest found each year, although it was not statistically significant (r = 0.694, 0.05 < P < 0.10), no doubt because the smaller sample size (7 rather than 26 nests) magnified the individual variation among the birds themselves. Nevertheless, these results indicate that the timing of the termination of breeding in Nuttall's

<sup>&</sup>lt;sup>a</sup> Measured from 1 July of the previous year to 30 June of the present year.

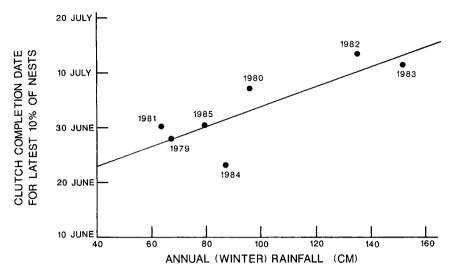


Fig. 1. Timing of the termination of breeding in Nuttall's White-crowned Sparrows as a function of the amount of annual rainfall during the preceding winter.

White-crowned Sparrows is a function of local weather conditions and is probably related, in an anticipatory manner, to the availability of food for their young. Petrinovich and Patterson (1983) documented significantly reduced reproductive success in Nuttall's White-crowned Sparrows in San Francisco in 1976, and attributed it to the severe drought conditions that year. This reduced reproductive success was likely caused, at least partially, by an early termination of breeding in response to the local browning of the vegetation.

It should also be noted that 1985 was characterized by rainfall during the previous winter (79.20 cm) that was somewhat below the 7-year mean (97.02 cm), and a termination of breeding (30 June; as determined by the mean clutch completion date of the latest 10% of the nests found) that was likewise slightly earlier than the 7-year mean (3 July).

Nevertheless, on 4 September 1985, Baptista was attracted by begging calls of a juvenile Nuttall's White-crowned Sparrow near the California Academy of Sciences, Golden Gate Park, San Francisco, California, some 33 km from the Palomarin Field Station. A brief search produced a spotted juvenile being attended by an adult. The adult soon flew away and was followed by the fledgling. The fledgling's tail was observed well and was judged to be no more than one-half of the tail length of the adult. The fledgling, therefore, could not have been out of the nest for more than 7 days, which would indicate that it fledged no earlier than 28 August.

On the following day, a spotted juvenile was again seen at the same spot accompanied by two adults. The juvenile continuously uttered begging calls and followed one of the adults, keeping within 15 cm of the latter as it foraged. Both the adults and the juvenile performed double scratches on the leaf litter. One adult (the female?) repeatedly pecked at objects on the leaf litter and three times inserted food items into the juvenile's bill. Baptista immediately moved to the location where the adult was gathering food and feeding it to the juvenile, and began sweeping the leaf litter aside. Large numbers of terrestrial amphipods (*Talitrus sylvaticus*) were observed jumping in all directions as soon as the leaf litter was disturbed.

These amphipods were inadvertently introduced into Golden Gate Park from Australia, probably with soil attached to exotic plants. Larger individuals of these amphipods reach 15 mm in length and appear to be important food items for local birds. On numerous occasions, Baptista has observed White-crowned Sparrows eating them.

On 9 September 1985, Baptista observed two spotted juvenile White-crowned Sparrows being attended by adults near the Conservancy of Flowers in Golden Gate Park. This second site is about 0.5 km from the first. These juveniles had longer tails than the first one observed, and appeared to be slightly older. Still, because their tails were not fully grown, they could not have fledged earlier than 26 August.

For Nuttall's White-crowned Sparrows raised in central coastal California, fledging dates of 26–28 August correspond to clutch completion dates of 4–6 August, 35–37 days later than the mean of the latest 10% of the nests found at Palomarin in 1985, and fully 27–29 days later than the latest nest found at Palomarin in 1985. Moreover, these dates are 15–17 days later than the latest nest ever found at Palomarin, that being in the summer of 1983, the summer following the excessive rainfall (151.69 cm) associated with the 1982–1983 El Niño Southern Oscillation (Philander 1983).

It might be argued that the lateness of the observed fledglings at Golden Gate Park was an artifact of the amount of time and effort spent in observation, and of the ease of observation in open park habitat as compared to the dense coastal scrub habitat at Palomarin. We do not believe this to be the case, however. Nearly every nesting attempt of a population of some 20–25 pairs of Nuttall's White-crowned Sparrows was monitored at Palomarin over several thousand hours of observation. We are confident that we did not miss any late nesting attempts at Palomarin during the rather dry summer of 1985.

Thus we suggest that the superabundance of the introduced *Talitrus* amphipods in Golden Gate Park provided a readily available extra food source enabling certain individual pairs of Nuttall's White-crowned Sparrows to continue successful breeding activities well beyond that of nearby local populations.

Acknowledgments.—The actual monitoring of the 247 nests at the Palomarin Field Station from 1979 to 1985 was accomplished by the many field biologist interns of the Point Reyes Bird Observatory. Geoffrey R. Geupel supervised the work of these interns and provided helpful comments on an earlier draft of this manuscript. Financial support for this work was provided by the membership of the Point Reyes Bird Observatory and by the Chevron Corporation. We thank the administration of the Point Reyes National Seashore for their cooperation. This is PRBO Contribution Number 388.

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DAVID F. DESANTE, Point Reyes Bird Observatory, 4990 Shoreline Highway, Stinson Beach, California 94970; AND LUIS F. BAPTISTA, California Academy of Sciences, Golden Gate Park, San Francisco, California 94118. Received 29 March 1988, accepted 10 Sept. 1988.

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Inbreeding in Ospreys.—James et al. (1987) cite the scarcity of reports of inbreeding in natural populations of birds and report a case of mother-son mating in the Merlin (Falco columbarius). This and a case of mother-son mating in the Eastern Screech-Owl (Otus asio) (Van Camp and Henny 1975:37) appear to be the only published reports of inbreeding in raptors. Here, I report a case of full-sibling mating in the Osprey (Pandion haliaetus).

This pair was first noted in 1981 during my study of a color-banded Osprey population on a series of wildlife floodings around Houghton Lake, Roscommon County, in the north-central Lower Peninsula of Michigan (Postupalsky 1977). Most nests there occur on manmade platforms described by Postupalsky and Stackpole (1974).

Both members of the pair were raised on the same platform nest on the Dead Stream Flooding (also known as Reedsburg Dam Backwater) on the Muskegon River 4 km west of Houghton Lake. The female hatched in 1973, the male in 1974. Their mother was banded as a nestling in 1965 on Fletcher Pond, Alpena County, 100 km northeast of her breeding site, and nested on the same nest for seven seasons, 1970–76. Her mate during the 1972–76 breeding seasons was a banded male. Considering that the survival rate of adult males in my study area is 84% (N = 239; Postupalsky, unpubl. data), and that by 1973–74 very few individuals banded only with a FWS band were left in the population (most were either unbanded, or also had color bands), the probability is very high (84–100%) that the same male was involved in both 1973 and 1974. Therefore, the members of the pair reported here were at least half-siblings, and very likely full siblings.

The female was first found nesting in 1976 on a platform (designated P-2) on the east side of Backus Creek Flooding, 6 km east of Houghton Lake and 21.5 km ESE of her natal site. She nested there for five seasons, 1976–80, with unbanded male(s). The male was first observed nesting on another platform (P-1) near the west side of the same flooding in 1978; his mate during 1978–80 was another individually marked female.

In 1981 the female at P-1 was missing and was replaced by the female from P-2, which had moved about 0.5 km across the flooding, and had formed a pairbond with the resident male at P-1, her younger brother. An unbanded pair took over the P-2 territory. The sibling