

REPRODUCTIVE CONSEQUENCES OF AN EXTREME DROUGHT FOR ORANGE-CROWNED WARBLERS ON SANTA CATALINA AND SANTA CRUZ ISLANDS

KATHRYN M. LANGIN,¹ T. SCOTT SILLETT,² JONGMIN YOON,¹ HELEN R. SOFAER,¹ SCOTT A. MORRISON,³ AND CAMERON K. GHALAMBOR¹

¹*Department of Biology, Colorado State University, Fort Collins, CO 80523; langink@rams.colostate.edu*

²*Smithsonian Migratory Bird Center, National Zoological Park, Washington, DC 20013*

³*The Nature Conservancy, San Francisco, CA 94105*

Abstract—Bird populations on the California Channel Islands are adapted to a Mediterranean-type climate with extended dry periods and considerable annual variation in rainfall. The winter of 2006–2007, however, was outside the normal range in southern California and ranked as one of the driest on record. Here we report how these drought conditions affected the reproductive output of a small songbird, the “dusky” orange-crowned warbler (*Vermivora celata sordida*), on Santa Catalina and Santa Cruz islands in the spring of 2007. Warblers on Catalina Island began establishing territories in February, yet they did not commence breeding activities until mid-April. Even then, only 5 of 45 females built nests and only 1 female laid eggs. The young in that nest ultimately starved; thus, the reproductive output of our study population on Catalina Island was zero. This contrasts starkly with the population on Santa Cruz Island, where all individuals studied attempted to reproduce and began nesting in mid-March. Nevertheless, only 11% of Santa Cruz Island warbler pairs fledged young due to high nest predation. Taken together, our observations from the two islands reveal marked differences in the consequences of severe drought and in the factors that limit the reproductive output of terrestrial birds on the Channel Islands.

INTRODUCTION

Climatic extremes can have a profound effect on community processes. The productivity of plants, the demography of animals, and their phenology relative to one another are all influenced by local and regional weather patterns (Stenseth et al. 2002; van Asch and Visser 2007). In the case of birds, variation in climate has been linked to variation in the timing of reproduction (Wilson and Arcese 2003; Visser et al. 2006), breeding productivity (Boag and Grant 1984; Gaston et al. 2006), and survival (Sillett et al. 2000; Mazerolle et al. 2005), with subsequent effects on population numbers (Boag and Grant 1981; Jones et al. 2003). Most of these responses to climate variability have been attributed to bottom-up processes, or the influence of organisms at lower trophic levels (e.g., insects) on the demography of organisms dependent on them for food (e.g., birds; Newton 1998). However, a range of other factors, including variability in phenological cues (e.g., temperature; Sherry et al. 2007) and top-down processes (i.e.,

predation; Ostfeld and Keesing 2000), can also drive demographic responses of wild populations.

In arid and semi-arid regions, water is a principal limiting factor and precipitation extremes can lead to drastic changes in primary productivity and community dynamics (Noy-Meir 1973). Organisms in these environments are adapted to withstand long periods of drought, and to respond opportunistically when precipitation gives rise to a greater availability of resources (Cody and Mooney 1978). Furthermore, because of the resource-limiting nature of these environments, secondary and tertiary consumers in arid regions tend to be primarily limited by bottom-up processes (Turner and Chew 1981), with demographic rates that are closely tied to variation in rainfall and food availability (e.g., Polis et al. 1997; Lima et al. 1999; Greenville and Dickman 2005). For example, widespread reproductive failure can be common in passerine birds when food is scarce during periods of drought (Boag and Grant 1984; Morrison and Bolger 2002), a phenomenon that appears to be

limited to birds breeding in arid and semi-arid regions (Bolger et al. 2005).

Here, we report how a severe drought affected orange-crowned warblers (*Vermivora celata sordida*) breeding on the California Channel Islands. The islands are located within a Mediterranean climate zone characterized by dry conditions during the breeding season and considerable annual variation in rainfall (Cody and Mooney 1978). The winter of 2006–2007, however, was outside the normal range and ranked as one of the driest on record (National Weather Service 2007). We monitored the breeding activities of orange-crowned warblers on Santa Catalina and Santa Cruz islands during the spring of 2007 and report substantial variation in the degree to which this severe drought affected warblers breeding on the two islands.

MATERIALS AND METHODS

We studied orange-crowned warblers on a 10 ha plot in Bulrush Canyon on Santa Catalina Island (33°20'N, 118°26'W; hereafter Catalina) and on an 18 ha plot in Coches Prietos Canyon on Santa Cruz Island (33°58'N, 119°42'W; hereafter Santa Cruz). The plots were delimited into 25–50 m grids with flagging tape to facilitate mapping of warbler territories and monitoring warbler breeding activity. Our work began on Catalina in 2003 and on Santa Cruz in 2005. Both plots were located within mesic drainages and were representative of high quality habitat for *V. c. sordida* on the islands, with vegetation that is dominated by island scrub oak (*Quercus pacifica*), lemonade berry (*Rhus integrifolia*), toyon (*Heteromeles arbutifolia*), and ceanothus (*Ceanothus* sp.).

We closely monitored breeding pairs within the study plots for the duration of the March–May breeding season, and in 2007 complete reproductive data were obtained for 45 pairs on Catalina and 18 pairs on Santa Cruz. Fewer territories were monitored on Santa Cruz because *V. c. sordida* are extremely cryptic there, perhaps due to the presence of the island scrub-jay (*Aphelocoma insularis*), a visually oriented nest predator (Curry and Delaney 2002). Most males (40 of 45 on Catalina, 16 of 18 on Santa Cruz) and some females (14 of 45 on Catalina, 4 of 18 on Santa Cruz) were marked with a unique

combination of three colored plastic and one aluminum USFWS leg bands to enable individual identification. We visited territories every 1–3 days to 1) map territory boundaries, 2) locate nests, 3) determine laying dates, 4) count eggs and nestlings, and 5) monitor nest fates. Nestlings that survived to day seven after hatch were weighed, measured, and banded.

On both islands, we measured food abundance by sampling arthropods on branch clippings taken from island scrub oaks (methodology as per Johnson 2000). This technique is appropriate for orange-crowned warblers because they are foliage-gleaning insectivores (Sogge et al. 1994) and, in the case of populations on Catalina and Santa Cruz islands, focus their foraging efforts on oaks (Ghalambor and Sillett, unpublished data). Every two weeks, 12 points were randomly selected throughout each study plot and a 30 x 30 cm branch clipping was collected from the nearest oak. Samples were placed in individual plastic bags and frozen for at least 24 hr. After carefully inspecting and collecting arthropods from the frozen vegetation, leaves were removed from stems and weighed (to 0.1 g). The arthropods were stored frozen until they could be separated into adult insects, Lepidopteran larvae, and spiders, and then dried in an oven (at 80°C) and weighed on an electronic balance (to 0.0001 g). We calculated arthropod biomass for each branch clipping in milligrams of dry mass per gram of wet vegetation collected.

On Catalina, we surveyed oaks for new growth in April 2007 to determine the extent of leaf-out. Each week, we randomly selected 30–50 oaks throughout the study plot and examined each for leaf growth. The percentage of oaks with new leaves did not vary across the four weeks of the survey; therefore, we pooled data for statistical analysis. A GPS location was determined for each oak, and we used ArcGIS (ESRI 2007) to calculate the percentage of oaks that had grown new leaves within 40 m of the center of each warbler's territory. A buffer size of 40 m was chosen because 20 m, the average radius of an orange-crowned warbler territory on the Catalina study plot, yielded too small a sample size for most territories.

Rainfall data were obtained from weather stations located in Middle Ranch on Catalina (33°21'N, 118°26'W; Catalina Island Conservancy)

and in the Central Valley on Santa Cruz (33°60'N, 119°43'W; Western Regional Climate Center). Data were available from both weather stations for 13 years during the period 1990–2007, although data were not available for Santa Cruz in some years. Because the Channel Islands receive the vast majority of precipitation from November to April, we report winter rainfall and define it as that which fell from November in year $x-1$ to April in year x .

We used general linear models and program JMP IN (SAS Institute 2003) for all statistical analyses. Data were transformed when necessary to meet model assumptions. However, we report all summary data as untransformed means \pm one standard error.

RESULTS

Climatic Conditions

Rainfall patterns on the Channel Islands are highly variable from year to year. Wet years on Santa Cruz tend to be wet years on Catalina (Fig. 1), although the former receives more precipitation over the course of most winters than the latter (Santa Cruz, 44.2 ± 6.9 cm, $n = 13$; Catalina, 36.0 ± 5.6 cm, $n = 13$; paired t-test, $t_{12} = 2.6$, $P = 0.02$). That was the case during the winter of 2006–2007, when Santa Cruz received 14.9 cm of rain from November to April and Catalina only received 9.1 cm, rainfall

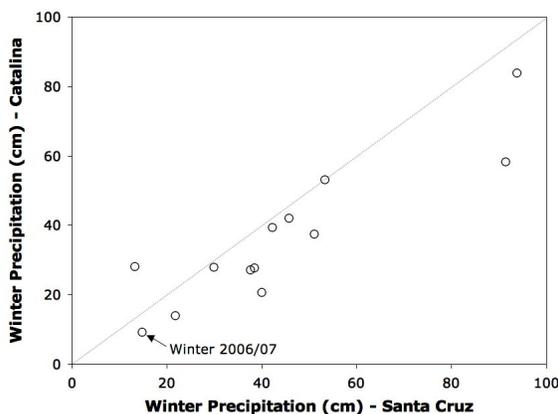


Figure 1. Winter precipitation (November to April) on Catalina and Santa Cruz islands for 13 years during the period 1990–2007 (data were not available for Santa Cruz in all years). Most of the points fall below the 1:1 line, indicating Catalina tended to receive less precipitation than Santa Cruz. Data are from the Catalina Island Conservancy (Catalina) and the Western Regional Climate Center (Santa Cruz).

Table 1. Number of orange-crowned warbler (*Vermivora celata sordida*) territories with nests, eggs, and fledged young on Santa Cruz and Santa Catalina islands during the 2007 breeding season, of the 18 and 45 territories that were monitored, respectively. Territories with unpaired males were not included. More females built nests and laid eggs on Santa Cruz than on Catalina (Fisher's Exact Test, $P < 0.0001$ for both), but there was no difference between islands in the proportion of territories that fledged young (Fisher's Exact Test, $P = 0.08$).

	Santa Cruz ($n=18$)	Catalina ($n=45$)
Nests	18 (100%)	5 (11%)
Eggs	17 (94%)	1 (2%)
Fledged young	2 (11%)	0 (0%)

totals that were well below the long-term average for both islands.

Warbler Reproduction

The drought of 2006–2007 affected orange-crowned warblers breeding on Catalina more so than those on Santa Cruz. On both islands, most male *V. c. sordida* established breeding territories by late February and paired with females by mid-March. The initiation of nesting activities, however, occurred much later on Catalina than on Santa Cruz. The first nest was found on March 17 on Santa Cruz, and the first egg was laid eight days later. In contrast, we found the first nest on Catalina on April 10 and the first egg 12 days later, amounting to a difference of 24 and 28 days, respectively, for nest detection and egg laying between the two islands. The proportion of females that attempted to breed also differed between islands. On Santa Cruz, all of the females whose territories were monitored built nests and 94% were confirmed to have laid eggs, whereas on Catalina only 11% of the females built nests and even fewer (1 of 45) laid eggs (see Table 1). Despite this stark difference in breeding attempts, reproductive output was similarly poor on both islands. Because of high predation rates on Santa Cruz (daily nest mortality: 0.09 ± 0.02 ; Sofaer et al., unpublished manuscript), only two territories were successful in fledging young. On Catalina, the only nest where eggs were laid failed due to the nestlings starving. Mean nestling mass in this nest was 4.5 g on day seven, much less than for nestlings on Santa Cruz in 2007 (8.4 g, $n = 1$ nest) and on Catalina from 2003–2006 (8.2 ± 0.1 g, $n = 71$ nests).

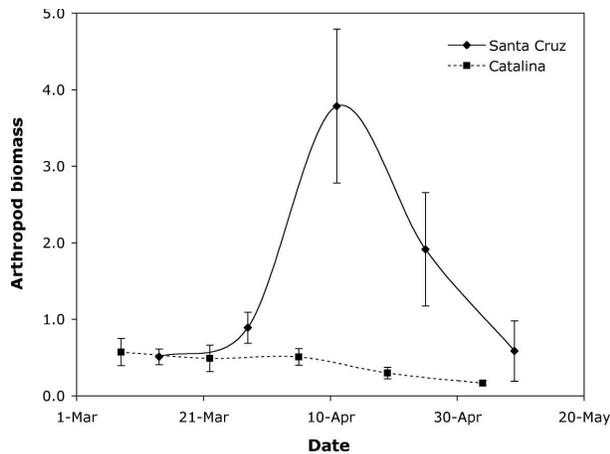


Figure 2. Arthropod biomass (in mg of dry mass per gram of wet vegetation; mean \pm SE) during the 2007 breeding season, as measured through branch clippings collected from island scrub oak (*Quercus pacifica*) bi-weekly on both islands ($n = 11$ or 12 for each point).

In the end, the mean number of young fledged per warbler pair on Santa Cruz in 2007 was 0.4 ± 0.3 ($n = 18$); no young were fledged on Catalina ($n = 45$).

Food Abundance

Orange-crowned warblers on Santa Cruz had more food available in 2007 than those on Catalina (Fig. 2). Arthropod biomass averaged 1.55 ± 0.31 mg of dry mass per gram of wet vegetation ($n = 59$) on Santa Cruz and 0.40 ± 0.06 ($n = 58$) on Catalina, a difference that was significant after controlling for sampling interval (two-way ANOVA, $F_{2,116} = 17.3$, $P < 0.0001$). The third sampling interval (see Fig. 2) also yielded significantly more arthropod biomass than the first and last ($F_{4,116} = 5.4$, $P = 0.0005$, Tukey's HSD), with no statistically significant interaction between island and sampling interval ($P > 0.05$). Most of the biomass during the breeding season was in the form of Lepidopteran larvae, the primary food item warblers feed to their nestlings (Sogge et al. 1994). Interestingly, this arthropod group made up a greater percentage of the total arthropod biomass on Catalina (65%) than it did on Santa Cruz (35%). Even so, the biomass of Lepidopteran larvae was nearly three times lower on Catalina (0.32 ± 0.06 mg/g vegetation, compared to 0.92 ± 0.23 on Santa Cruz). Warblers on Catalina did not compensate for the lack of food by defending larger territories. In contrast, their territories were much smaller on Catalina (0.11 ± 0.01 ha, $n = 45$) than on Santa Cruz (0.57 ± 0.10 ha,

$n = 18$; t-test, $t_{61} = 10.2$, $P < 0.0001$) and they bred at higher densities (4.5 and 1.1 pairs/ha on Catalina and Santa Cruz, respectively), a pattern that is consistent with previous years (Ghalambor and Sillett, unpublished data).

Oak Growth

On Catalina, only 34% of oaks had grown new leaves by April ($n = 158$) and we found considerable spatial variation in the degree of leaf-out (Fig. 3). The orange-crowned warblers that built nests did so on territories where at least 40% of oaks had grown new leaves. At the same time, females on many territories with $>80\%$ oak leaf-out did not initiate nesting activities. Although data are not available for Santa Cruz to make a formal comparison, we observed that in 2007 nearly all oaks in the study area had grown new leaves by April (personal observation). This suggests that in contrast with Catalina, availability of new oak leaves were not a limiting factor on Santa Cruz.

DISCUSSION AND CONCLUSIONS

Our data indicate that *V. c. sordida* breeding on Catalina experienced a much stronger impact of the 2007 drought than did warblers breeding on Santa Cruz. Warblers on Catalina bred nearly a month later than those Santa Cruz, and only 11% of females built nests and only 2% laid eggs. No young fledged from our Catalina study plot in 2007. All females on the Santa Cruz plot, in contrast, attempted to reproduce, although few were successful because of high rates of nest predation. In the end, the reproductive output of warbler pairs was similarly poor on both islands (<1 young fledged per pair, on average).

The events of 2007 stand in stark contrast to previous years on Catalina. From 2003 to 2005, nests were initiated as early as February and as late as March, and on average, warbler pairs fledged >2 young per year (Ghalambor and Sillett, unpublished data). In the extremely wet year of 2005 (62 cm of rain during the preceding winter), at least 15% of females attempted second broods. The 2006 breeding season was relatively dry (21 cm) and the timing of reproduction was similar to that observed in 2007, although in that year all monitored females attempted to reproduce and some were successful in

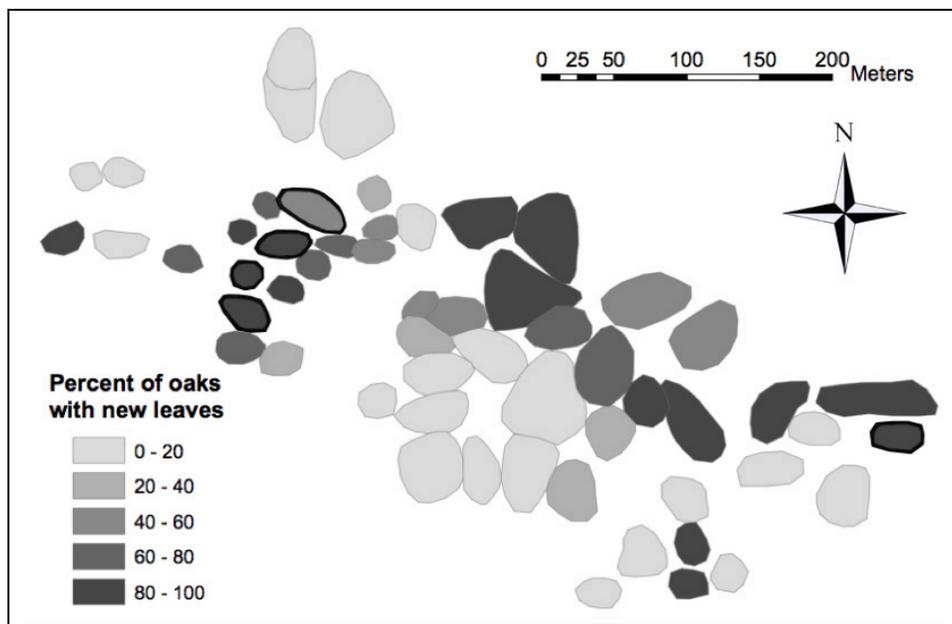


Figure 3. Spatial pattern of leaf growth for island scrub oak (*Quercus pacifica*) on the Santa Catalina Island study site in April 2007. Each polygon represents an orange-crowned warbler territory, and the shading denotes the estimated percentage of oaks that grew new leaves (see text). Nests were built on the territories outlined in black.

fledging young (0.7 young per pair; Ghalambor and Sillett, unpublished data). These patterns are consistent with a five-year dataset on rufous-crowned sparrows (*Aimophila ruficeps*) breeding in coastal sage scrub habitat on the California mainland. Bolger et al. (2005) reported a positive linear relationship between rainfall and reproductive output, which was attributed to a combination of limited food availability in drier years and reduced predation pressure in wetter years (Morrison and Bolger 2002). As in this study, they documented complete reproductive failure during the driest year.

The paucity of nesting attempts detected on Catalina in 2007 was not due to inconsistent survey effort. A four-person field crew has monitored the Catalina study site every year from 2003 to 2007, and two of the 2007 members had been part of the field crew in previous years (five breeding seasons combined experience). In addition, the field crew on Santa Cruz also consisted of four people and, in a much more challenging nest-finding environment, was still able to detect nesting activity for every focal pair. If anything, the data presented here for Catalina may be an overestimate of the proportion of females who attempted to breed on the island.

Bulrush Canyon is among the wettest drainages on Catalina, and the study site is located within prime habitat on the canyon bottom. We found no warbler nests on a nearby xeric ridge plot, and that habitat type is much more common across the island (Knapp 2005; Yoon et al., unpublished manuscript).

Rainfall was low on both islands during the 2006–2007 drought, although Catalina received only 60% of the small amount of rain that fell on Santa Cruz (see Fig. 1). Our data indicate that this precipitation difference had a clear biological effect: the degree of oak leaf-out and the abundance of food were much lower on the Catalina study plot. We suggest that these environmental factors were instrumental in determining the timing and number of nesting attempts. Orange-crowned warblers depend on the availability of Lepidopteran larvae to feed young during the energetically demanding nestling period, and larvae during that time are primarily obtained from newly grown oak leaves (Ghalambor and Sillett, unpublished data). Warblers on Santa Cruz started building nests well before the peak in food abundance (see Fig. 2), indicating that some other factor—for instance, oak leaf-out—provided the necessary cue to signify food availability during the nestling period. On

Catalina, few oaks grew new leaves and those that did were concentrated in patchy areas. Warblers that built nests on that island had territories that were located in areas where >40% of oaks had leafed-out (see Fig. 3), and even then individuals did not have enough food resources to successfully raise their broods to fledging, as indicated by the one nest that failed due to starvation. The warblers that did not lay eggs, therefore, appeared to do so because of a lack of food.

Compared to Catalina, warblers on Santa Cruz had enough food resources to breed, but nest predation appeared to limit their reproductive output. Both islands have nest predators (e.g., gopher snakes *Pituophis melanoleucus*, island foxes *Urocyon littoralis* ssp., and deer mice *Peromyscus maniculatus* ssp.), but Santa Cruz is the only Channel Island with a visually oriented predator of songbird nests, the island scrub-jay. Only two warbler pairs were successful in raising a brood to fledging of the 18 pairs monitored, and the vast majority of nests failed due to predation (23 of 27). Top-down processes, therefore, appeared to be a primary factor that limited the reproductive success of warblers on Santa Cruz during the 2006–2007 drought. The high rate of nest predation did not differ significantly from that observed during the 2005 breeding season (Sofaer et al., unpublished data), which followed an exceptionally wet winter, so it appears as though top-down processes predominate on Santa Cruz regardless of rainfall patterns.

Nest predation is likely higher on Santa Cruz because of both direct predation by scrub-jays and indirect effects on nest-site placement. Mainland populations of *V. celata* are ground nesters; however, populations that breed on the Channel Islands exhibit plasticity in the height at which they place their nests (Sogge et al. 1994; Peluc et al. 2008). On Catalina, they frequently build nests in vegetation off the ground and can do so up to 8 m in height. This plasticity in nest placement appears to be adaptive because ground nests suffer from the highest predation rates on Catalina (Peluc et al. 2008). On Santa Cruz, in contrast, *V. c. sordida* typically build nests within 0.5 m of the ground (Ghalambor and Sillett, unpublished data). It appears as though this behavior is due to the presence of jays because (1) the vegetation used to

build off-ground nests on Catalina (e.g., *Quercus*, *Rhus* spp.) is also present on Santa Cruz (Schoenherr et al. 1999), and (2) on Catalina warblers will build nests on the ground if they are exposed to an experimental jay presentation (Peluc et al. 2008). In addition to being a potential nest predator, therefore, scrub-jays may cause higher predation rates on Santa Cruz by inducing *V. c. sordida* to nest on or close to the ground, where they are at risk from mammalian and reptilian predators.

We note that the strategy of nesting lower in the presence of jays may have been rendered somewhat ineffective due to the presence of feral pigs (*Sus scrofa*) on the island. Pigs were introduced to Santa Cruz in the 1850s, and their rooting caused extensive damage to understory vegetation which in turn reduced the availability of concealed nesting sites for ground and shrub-nesting birds. Pigs were also likely predators of nests on the ground and in lower vegetation strata. By 2006, an eradication program had removed the pigs from the island (Morrison 2008), but drought conditions predominated between that time and the 2007 nesting season, so vegetation recovery was limited. It will be important to monitor warbler nest success in subsequent years, following rains and the recovery of understory vegetation, to assess whether rates of nest predation decline with the increase in understory structure.

Understanding biotic responses to climate variability and the relative importance of bottom-up versus top-down processes will be essential for predicting future impacts of climate change. Long-term projections for southern California point to a drying trend and increased variability in precipitation patterns (Cayan et al. 2008). Severe droughts such as the one experienced in 2006–2007, therefore, could be a more frequent occurrence in the coming century. We found substantial differences in the degree to which a severe drought affected *V. c. sordida* breeding on Catalina and Santa Cruz islands, along with the plants and arthropods upon which the warblers depend. Our results underscore the importance of comparative studies across the eight Channel Islands, particularly with regard to the factors that control phenology and limit productivity in terrestrial plants and animals.

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