Shaffer, M. 1987. Minimum viable populations: coping with uncertainty. In: Viable Populations for Conservation (edited by M. E. Soulé), Cambridge University Press, Cambridge, Great Britain, pp. 69–86.

Soulé, M. E. (editor). 1987a. Viable populations for conservation. Cambridge University Press, Cambridge, Great Britain. 189 pp.

Soulé, M. E. 1987b. Introduction. In: Viable Populations for Conservation (edited by M. E. Soulé), Cambridge University Press, Cambridge, Great Britain, pp. 1–10.

Soulé, M. E. 1987c. Where do we go from here? In: Viable Populations for Conservation (edited by M. E. Soulé), Cambridge University Press, Cambridge, Great Britain, pp. 175–183.

Thorne, R. F. 1967. A flora of Santa Catalina Island, California. Aliso 6:1–77.

Thorne, E. T., and E. S. Williams. 1988. Disease and endangered species: the black-footed ferret as a recent example. Conservation Biology 2:66–74.

U.S. Fish and Wildlife Service. 1989. Endangered and threatened wildlife and plants; animal notice of review. Federal Register 54(4):554–579.

Wayne, R. K., S. B. George, D. Gilbert, and P. W. Collins. 1991a. The Channel Island fox (*Urocyon littoralis*) as a model of genetic change in small populations. In: The Unity of Evolutionary Biology: Proceedings of the Fourth International Congress of Systematic and Evolutionary Biology, Volume II (edited by E. C. Dudley), Dioscorides Press, Portland, Oregon, pp. 639–649.

Wayne, R. K., S. B. George, D. Gilbert, P. W. Collins, S. D. Kovach, D. Girman, and N. Lehman. 1991b. A morphologic and genetic study of the island fox, (*Urocyon littoralis*). Evolution 45(8):1849–1868.

White, G. C., D. R. Anderson, K. P. Burnham, and D. L. Otis. 1982. Capture-recapture and removal methods for sampling closed populations. Los Alamos National Laboratory, LA-8787-NERP, Los Alamos, New Mexico. 235 pp.

Wilson, K. R., and D. R. Anderson. 1985. Evaluation of two density estimators of small mammal population size. Journal of Mammalogy 66:13–21.

Wood, J. E. 1958. Age structure and productivity of a gray fox population. Journal of Mammalogy 39:74–86.

The Fourth California Islands Symposium: Update on the Status of Resources
Edited by W. L. Halvorson and G. J. Maender. 1994. Santa Barbara Museum of Natural History, Santa Barbara, CA.

Effects of Precipitation and Density on the Abundance of California Quail on Santa Cruz Island

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Abstract. Lack of a detectable dependence of recruitment on density in hunted populations of California quail (*Callipepla californica*) led us to examine an unhunted population on Santa Cruz Island for this characteristic. We have estimated juvenile-to-adult ratios and an index of abundance near the beginning of August annually for the past 7 yr (1987–1993). Our sampling consists of 2 observers in each of 2 vehicles driving fixed transects and counting quail by age and sex for 3 dy. The juvenile-to-adult ratio depends positively and significantly on precipitation from January through March ($R = 0.87$, $p < 0.05$). With the effect of precipitation removed, the juvenile-to-adult ratio declines with adult density ($R = 0.69$, $p < 0.1$). Although sample size is low, these data indicate reproduction in California quail may be density-dependent.

Keywords: California quail; population dynamics; density-dependence; Santa Cruz Island.

Introduction

Although reproduction in California quail (*Callipepla californica*) has been shown to depend on physical environmental conditions in a variety of ways, no dependence on density has been demonstrated. From an analysis of the factors controlling quail population dynamics over 23 yr at a semi-arid site in central California, Botsford et al. showed in their 1988 study that reproduction did not depend on density. They proposed that the absence of density-dependence could be due to the fact that virtually all populations of California quail in California are hunted; hunting could maintain these populations below an abundance at which density-dependence would occur. We therefore sought an unhunted population of California quail to determine the nature of density-dependence in quail reproduction. The only viable candidate population in terms of both a current lack of hunting and future prospects for not being hunted was the population on Santa Cruz Island. This population had the added advantages that it was in a semi-arid climate zone, similar to other populations we had studied, and it was on an island, hence was a closed population.

Reproduction in California quail is affected by weather; however different populations are affected in different ways. Early summer rains destroyed California quail nests and chicks on the Modoc Plateau (Savage 1974) and wetting from rain and fog led to the deaths of chicks near Berkeley on the California coast (Raitt and Genelly 1964). Populations in semi-arid regions usually produce more chicks in seasons with higher rainfall. McMillan (1964), Francis (1967), and Erwin (1975) all reported that a population near Shandon, California, had higher production of juveniles in years with higher rainfall. Francis (1967) reported that the strongest correlate of juvenile production was soil moisture in April. For the years from which his model was developed this single variable accounted for 83% of the variance. However, it accounted for less of the variance in other years (Francis 1970; Leopold 1977). In our earlier study (Botsford et al. 1988) we found that soil moisture accounted for 38.4% of the variance, while total rainfall from December through April accounted for 74.1% of the variance.

Although California quail reproduction has been demonstrated to be both positively and negatively related to atmospheric and soil moisture, there has never been clear evidence that it is negatively related to population density, i.e., that it is density-dependent. Leopold (1977) reviewed the existing evidence for density-dependence. He noted that reproduction per individual was the same in the high density population on the McMillan ranch as in the adjacent lower density populations. However, densities were high on the McMillan ranch only during winter, when the quail were attracted by habitat enhancements and supplementary food. Barclay and Bergerud (1975) reported that recruitment was inversely correlated with spring density; but they did not report spring density, and there was no significant inverse correlation in September. Botsford, et al. (1988) showed that the relationship between juveniles and adults indicated a linear increase of juveniles with adults (i.e., no density-dependence).

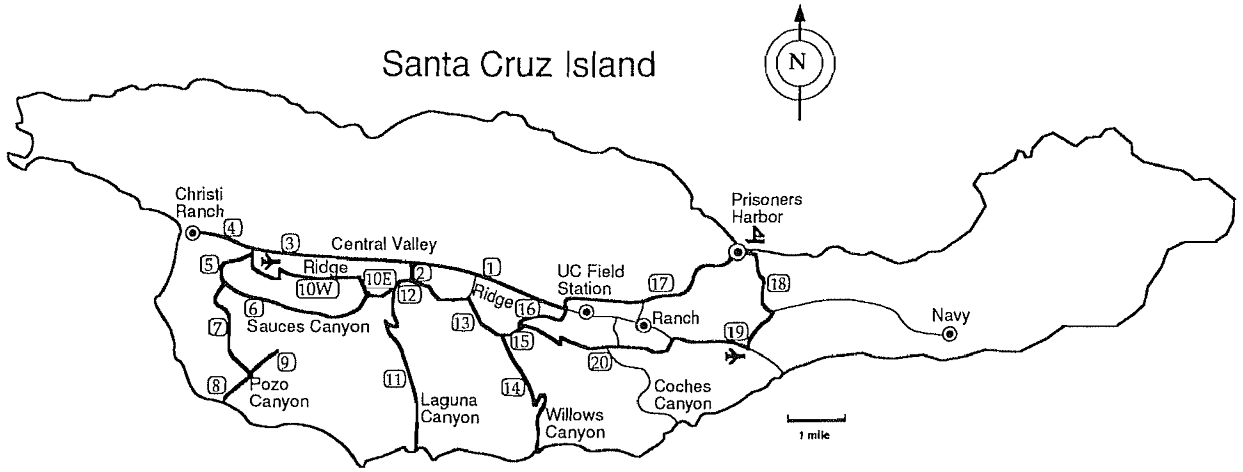

Figure 1. The roads driven during the study. The segments driven for each day of the annual census are given in Table 1.

Density-dependence in a population is important for both practical and theoretical reasons. For populations in general, it is the mechanism that keeps populations from unlimited abundance and extinction. Theoretically, it must be present in all populations. For management of hunted populations, knowing how population growth rates depend on density is important because, in simple terms, determining optimal harvest involves maintaining abundance just below the level at which density-dependence will decrease per capita reproduction and survival.

Materials and Methods

We censused abundance and juvenile-to-adult ratio of California Quail on Santa Cruz Island each August for 8 yr, 1987–1993. Data from a preliminary survey of quail on the island in 1986 are not included in the analyses presented here because our sampling protocol was not yet set. From 1987 to 1993, censuses took place over 3 consecutive days near 1 August. Each census consisted of 2 vehicles each with 2 observers (1 driving) traveling on specific road transects in a set pattern around the island during 3 mornings and 2 late afternoons (Fig. 1, Table 1). In addition, on the afternoon before each annual survey, all 4 observers conducted a census in a single vehicle as a calibration procedure to assure consistency between vehicles and years. All observers were professional wildlife biologists. The morning observations were made between 7:00 and 10:00 PDT and the late afternoon observations were between 17:00 and 20:00 PDT. The total length of the transects was about 230 km with a total observation time of about 32 hr each year. The number of quail seen, time of day and location on the transect were recorded. When they could be determined, we recorded the sex of each individual and the age of juveniles (birds hatched the current year) to the nearest week.

The primary purpose of each census was to determine the juvenile-to-adult ratio as an indication of reproduction per adult each year. Based on the preliminary survey of spatial distribution in 1986, the census routes were designed to sample the areas of highest abundance more frequently than areas of low abundance. This resulted in most of the road segments being driven multiple times each year. There was no need to attempt to control for counting the same birds multiple times on subsequent transects through the area, although care was taken not to count individuals more than once on the same transect.

Juvenile-to-adult ratios for each year were estimated as the ratio of the total number of juveniles observed to the total number of adults observed for sightings in which we could discern juveniles from adults. The total number of juveniles and the total number of adults were estimated by dividing up the estimated total number of quail according to the estimated juvenile-to-adult ratio. This method was used instead of using numbers of adults and juveniles identified as such because there were many more samples with total numbers. The total number of quail was estimated by summing the average number seen on each of the road segments. For data on precipitation, we used monthly rainfall recorded at the ranch on Santa Cruz Island.

Table 1. Road segments driven for each day of the annual census. Road segments are identified on Figure 1.

Vehicle	Run		Road segments
Cruzer 1	Day 1	PM	1-3-4-(4-3-1)
	Day 2	AM	1-3-4
		PM	5-7-8-9-(7)-6-10E-12-13-15-16
	Day 3	AM	16-15-14-(14)-13-12-11
		PM	17-18-19-20-16
	Day 4	AM	16-15-13-2-1
Cruzer 2	Day 2	AM	16-15-13-12-10E-10W-4
		PM	11-12-13-14-(14)-15-16
	Day 3	AM	1-2-12-10E-6-5
		PM	3-1
	Day 4	AM	17-18-19-20-16

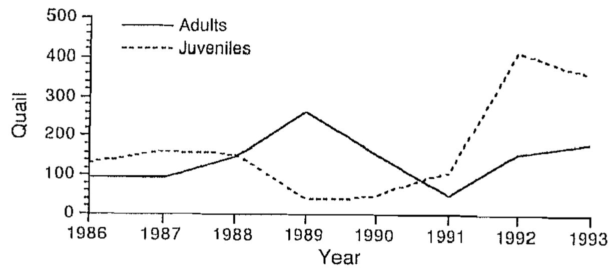

Figure 2. Estimated number of adults and juveniles sited each year. Data from 1986 (from a preliminary survey) are not used in the analyses herein.

Results

Abundance of both juveniles and adults varied substantially during the study (Fig. 2). Juvenile abundance generally declined until 1991, then increased dramatically. Adult abundance did not appear to be closely related to juvenile abundance. We examined the consistency between juvenile and adult data by computing the correlation between juveniles in 1 yr and adults in the next. The resulting correlation, $R = 0.389$ (n.s., $n = 6$) indicates juvenile abundance in 1 yr does not have a great effect on adult numbers in the following year. Factors such as adult survival being time-varying and first year adults being a small part of total abundance (i.e., high adult survival) would lead to low values of this correlation.

Juvenile and adult abundance appeared to be driven by the influence of precipitation on reproduction. Annual rainfall was lower than average until the last 2 yr of the study (Fig. 3). Average annual rainfall at the ranch from 1904 to 1993 was 503 mm. Rainfall was reasonably high in 1986, the year immediately preceding the study (805 mm) and slightly below average in the previous 2 yr (about 400 mm). For the years 1987–1993, juvenile-to-adult ratios were significantly correlated with precipitation in the previous February, and March (Fig. 4). Negative correlations in November, April, and May were due to single high rainfall events in relatively dry months. We used the sum of rainfall from January, February and March to represent the positive effect of rainfall on quail abundance in subsequent calculations. The correlation between juvenile-to-adult ratio and precipitation from January through March was 0.870 ($p < 0.05$) (Fig. 5).

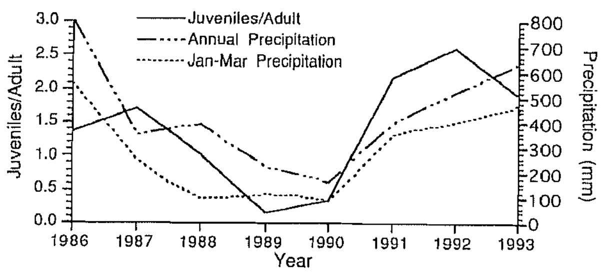

Figure 3. The ratio of juveniles to adults along with total precipitation and precipitation during what was considered to be the period of greatest positive effect of precipitation on reproduction (January–March). Data from 1986 (from a preliminary survey) are not used in the analyses herein.

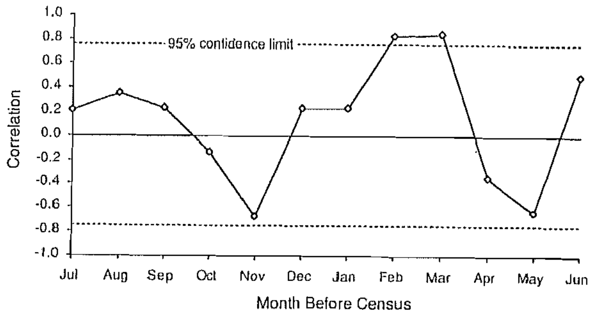

Figure 4. The correlation between juvenile-to-adult ratio and rainfall for months prior to the census.

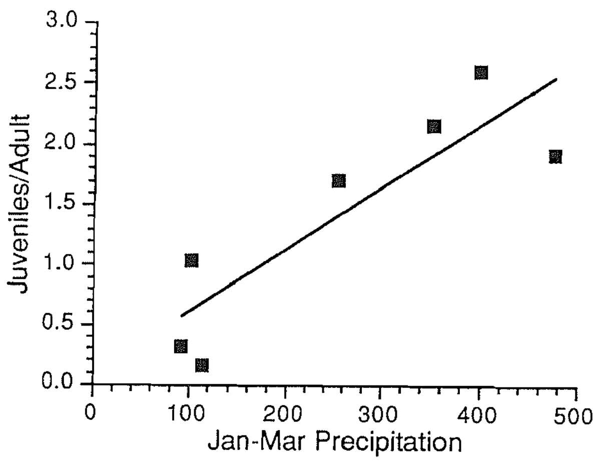

Figure 5. The relationship between juvenile-to-adult ratio and precipitation from January through March. The regression is $J/A = 0.0996 + 0.00518$ Precipitation (mm), $R = 0.870$, $p < 0.05$.

Reproduction also appeared to be influenced by adult density (Fig. 6). In the year of lowest adult abundance, reproductive rate was high, and in the year of highest adult abundance, reproductive rate was low, while for the years between those extremes in adult abundance, reproductive rate was evenly distributed between high and low values. To visually examine this relationship without the effect of precipitation in the data, we removed precipitation by subtracting the rainfall regression from the juvenile-to-adult data. The form of the density-dependent relationship remained similar after this transformation (Fig. 7). In spite of the lack of linear appearance the correlation between juvenile-to-adult ratio and adult abundance was $R = 0.69$ ($p < 0.10$).

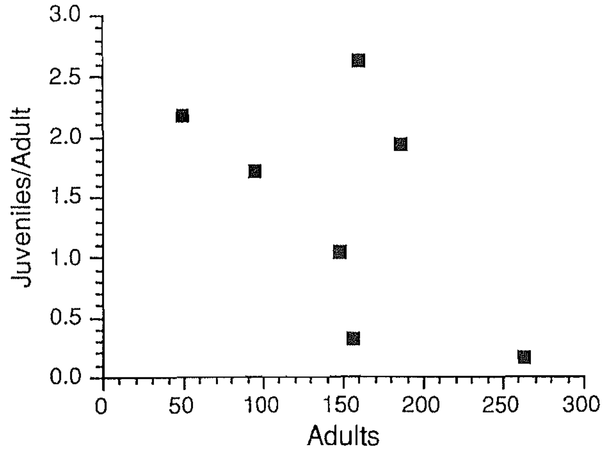

Figure 6. Evidence regarding density-dependence in reproduction: juveniles-per-adult vs adults.

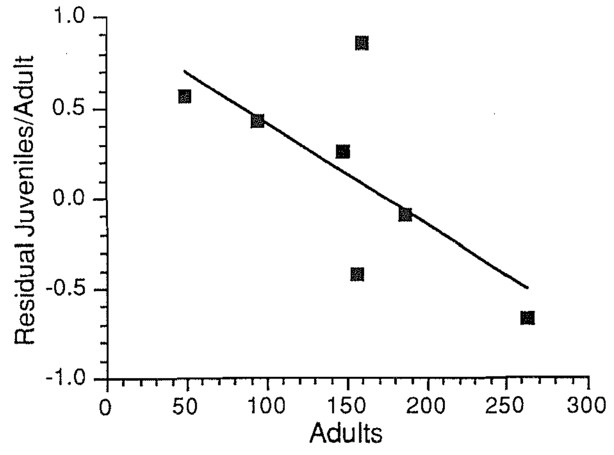

Figure 7. Juveniles-per-adult with the effects of precipitation removed, plotted vs adults. The regression is $J/A = 0.982 + 0.00564$ Adults, $R = 0.694$, $p < 0.10$.

To reflect the combined effects of precipitation and density on reproduction, we computed a regression of juvenile-to-adult ratio on both precipitation and adult abundance. The result, $J/A = 0.965 - 0.00481 \times \text{Adults} + 0.000237 \times \text{Precipitation (mm)}$, where $R = 0.932$, with probabilities of 0.139, 0.114, and 0.006 for the intercept, adults, and precipitation, respectively, reflects the relationships described above.

Discussion

Over the period of this study, the quail population on Santa Cruz Island responded to a prolonged drought followed by a return to normal precipitation conditions in ways that can be explained by the influences of precipitation and density on reproductive rate. Based on rainfall data, the population just prior to the study was probably near average abundance with relatively high reproduction in 1986. Reproductive rate declined from 1987 to 1989 due to low precipitation, then increased as precipitation increased in the later part (Fig. 3). Juvenile abundance declined through most of the study, then increased when rainfall increased toward the end of the study (Fig. 2). Adult abundance in 1989 was somewhat higher than would be expected on the basis of earlier juvenile and adult abundance, possibly due to unusually good juvenile and adult survival in the previous year.

The mechanisms underlying the dependence of reproduction on precipitation and density probably both involve varying levels of food. Years of higher precipitation probably involved greater forb abundance, and years of higher density probably involved less food per adult. Quail reproduction has been related to growth of forbs, particularly legumes (McMillan 1964; Francis 1970; Erwin 1975). Other factors proposed to affect quail reproduction in the past are probably not important. Lehmann (1953) proposed that California quail reproduction depended on adequate levels of vitamin A, but this was not borne out by Fletcher's (1971) feeding study. Leopold et al. (1976) proposed that reproduction in California quail could be inhibited by high estrogenic plant steroids, but Cain et al. (1987) found that extremely high levels were necessary to alter reproduction in scaled quail.

Although we have only 7 yr of data, the nature of the relationship between juvenile-to-adult ratio and adult abundance indicates density-dependence is present only at very high abundance. At intermediate levels of abundance, reproductive rate varies between high and low levels in response to rainfall. This behavior is consistent with the concept of density-vague population regulation in which density influences vital rates only at extreme values (Strong 1986).

Both the possibility that density-dependent recruitment was observed and the low correlation between juveniles and adults in the next year ($R = 0.389$) indicate this population may be at higher density than other populations. In our earlier study, of a more heavily hunted population, we obtained a value of 0.603 ($p < 0.05$) for this correlation (Botsford et al. 1988). The lower value could be caused by the fact that adults survive longer, making new recruits a smaller fraction of the adult population.

Interpretation of our results must be tempered by consideration of the low sample size and potential biases in our observational protocol. Although the relationships between juvenile-to-adult ratios and both precipitation and density were statistically significant, the low sample size allows the potential for heavy dependence on a few points. This does not appear to be a problem in the dependence of juvenile-to-adult ratio on precipitation (Fig. 5), but could be in the dependence on adult abundance (Fig. 7). Omitting either the point at low abundance or the point at high abundance would lead to a lower correlation. On the other hand, a density-vague relationship would involve some level of this statistical problem even at greater sample sizes.

Potential observational biases in our protocol do not appear to have had a great effect. The most significant potential bias is the effect of plant cover on sightability. Increased plant growth could reduce measures such as adult and juvenile abundance, which are indexed to observation effort, but would not affect juvenile-to-adult ratio. Plant cover appeared to be at a nominal level at the beginning of the study and declined with the drought. An estimated 37,000 sheep were removed from Santa Cruz Island between 1981 and 1987. After the removal, growth of some plant species increased, but the effect on sightability of quail is not known. Since most of our sightings were of birds feeding on or near the road, we expect the effect was minimal. A second potential bias is the effect of hunting. Recent recreational hunting of California quail by The Nature Conservancy on Santa Cruz Island has undoubtedly had an effect on density, and has probably had an effect on sightability. A third potential contributor to bias is the fact that although our sampling covers most of the quail habitat on Santa Cruz Island, it may not cover all, and some quail may migrate from unsampled locations.

In summary, we can conclude that precipitation affects this population in the same way that it affects others with similar habitat and climate. Our data also indicate that reproduction of California quail may be density-dependent, even though it may not appear to be in hunted populations (cf., Botsford et al. 1988). The robustness of the latter conclusion is limited by the low sample size.

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Literature Cited

Barclay, H. J., and A. T. Bergerud. 1975. Demography and behavioral ecology of California quail on Vancouver Island. Condor 77:315–323.

Botsford, L. W., T. C. Wainwright, J. T. Smith, S. Mastrup, and D. F. Lott. 1988. Population dynamics of California quail related to meteorological conditions. Journal of Wildlife Management 52:469–477.

Cain, J. R., R. J. Lien, and L. S. Beasom. 1987. Phytoestrogen effects on reproductive performance of scaled quail. Journal of Wildlife Management 51:198–201.

Erwin, M. J. 1975. Comparison of the reproductive physiology, molt, and behavior of the California Quail in two years of differing rainfall. M.S. Thesis, University of California, Berkeley.

Fletcher, R. A. 1971. Effects of vitamin A deficiency on the pituitary-gonad axis of the California quail, *Lophortyx californicus*. Journal of Experimental Zoology 176:25–34.

Francis, W. J. 1967. Prediction of California Quail populations from weather data. Condor 69:405–410.

Francis, W. J. 1970. The influence of weather on population fluctuations in California quail. Journal of Wildlife Management 34:249–266.

Lehmann, W. V. 1953. Bobwhite population fluctuations and vitamin A. Transactions of the North American Wildlife Conference 18:199–246.

Leopold, S. A. 1977. The California quail. University of California Press, Berkeley.

Leopold, A. S., M. Erwin, J. Oh, and B. Browning. 1976. Phytoestrogens: adverse effects on reproduction in California quail. Science 191:98–100.

McMillan, I. I. 1964. Annual population changes in California quail. Journal of Wildlife Management 28:702–711.

Raitt, R. J., and R. E. Genelly. 1964. Dynamics of a population of California quail. Journal of Wildlife Management 28:127–141.

Savage, A. E. 1974. Productivity and movement of California valley quail in northeast California. California-Nevada Wildlife 1974:84–88.

Strong, D. 1986. Density vagueness: abiding the variance in the demography of real populations. In: Community Ecology, (edited by J. Diamond and T. J. Case), Harper and Row, New York, New York, pp. 257–268.