PREDICTION OF CALIFORNIA QUAIL POPULATIONS FROM WEATHER DATA

WILLIAM J. FRANCIS

A study of the effect of weather conditions on population fluctuations in California Quail (*Lophortyx californicus*) included an analysis of weather parameters and of quail population data over a 14-year period in the area near Shandon, San Luis Obispo County, California (Francis, 1965). A multiple regression analysis showed a remarkably close correspondence between certain weather parameters and the changes in quail populations as measured by the ratio of subadults (birds hatched the previous summer) to adults in the fall hunting samples. A forthcoming paper describes in some detail the methods of analysis and the biological basis of the reasoning involved in the selection of the particular weather parameters (see Francis, 1965). Pending publication of that report, it seems desirable to present at this time the method of calculating predicted production in California Quail. Population levels estimated from such calculations can provide a basis for studies of other factors affecting fluctuations, as well as being of direct utility in management.

The index of quail productivity which has been most widely used (*e.g.*, Sumner, 1935; McMillan, 1964) is the ratio of young to adult birds of both sexes in fall hunting bags. I further tested the validity of this index by an analysis of the sex and age ratios reported by McMillan (1964) from 1949 to 1962. My analysis showed that the ratio of subadult to adult birds was closely correlated ($r = 0.974$) with the estimated change in population.

I found that annual changes in quail productivity for the 14-year period could be accounted for almost entirely ($R^2 = 0.988$) by two weather parameters calculated from rainfall and temperature data as described below, plus one population parameter—the percentage of adults among the females in the previous year's hunting sample.

Greater production was realized with a higher percentage of adult females in the population, suggesting that adult females produced young more efficiently than subadults. The reality of the relation between production and the age of breeding females was supported by observations of confined, individually marked birds during 1963 and 1964. Four adult females (in the second or later breeding season) hatched a total of 82 chicks, while three yearling females (in the first breeding season) failed to hatch any chicks.

The most important factor was the calculated value of soil moisture at the end of April, computed from a running comparison of rainfall with potential evapotranspiration as defined by Thornthwaite (1948). The second weather factor, of less importance than either of the parameters discussed above, was the seasonal rainfall total from 1 September to 29 April. Although the simple correlation of the rainfall with quail productivity is positive, the partial correlation coefficient in multiple regression is negative. This is a consequence of the strong positive correlation between rainfall and the calculated soil moisture; production of quail was higher with an increased value of soil moisture, which occurred when rainfall amount was relatively high and favorably distributed; production was lower with rainfall in excess of that necessary for maximum soil moisture.

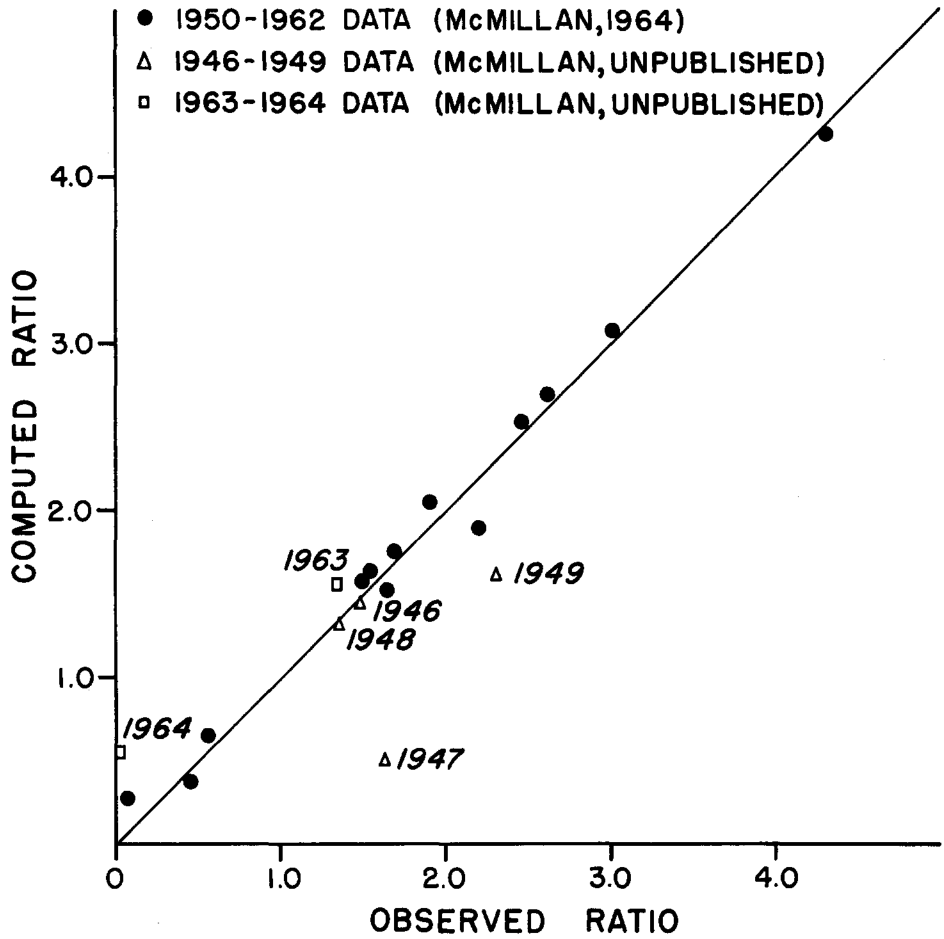

Figure 1. Comparison of calculated and observed values of the ratio of juvenile to adult quail in hunting samples from San Luis Obispo County, California (see text).

The regression equation, computed using the data on quail sex and age ratios reported by McMillan (1964), is as follows:

$$Q = 0.021A + 0.929M - 0.120P - 0.975 \tag{1}$$

where Q = Quail production as measured by the ratio of subadult to adult birds in the hunting season,

A = Percentage of adults among the female quail taken in the previous fall sample,

M = Moisture content of the soil in inches at the end of April as calculated from potential evapotranspiration and rainfall comparisons,

P = Precipitation total in inches from 1 September to 29 April.

Figure 1 illustrates how closely the expected quail productivity calculated from this equation fits the observed data (from McMillan, 1964). As a test of its predictive ability the equation was also applied to additional data from 1946–49, and

TABLE 1

POTENTIAL EVAPOTRANSPIRATION IN INCHES FOR A 10-DAY PERIOD, AS A FUNCTION OF FAHRENHEIT TEMPERATURES, UNCORRECTED FOR DAYLENGTH; SAN LUIS OBISPO COUNTY, CALIFORNIA[a]

Temp. F.	0	1	2	3	4	5	6	7	8	9
30	–	–	–	0.00	0.02	0.03	0.04	0.06	0.08	0.10
40	0.12	0.14	0.16	0.18	0.21	0.24	0.27	0.30	0.33	0.36
50	0.39	0.43	0.47	0.51	0.55	0.59	0.63	0.67	0.71	0.75
60	0.79	0.83	0.87	0.91	0.95	0.99	1.04	1.09	1.14	1.19
70	1.25	1.30	1.35	1.41	1.46	1.52	1.57	1.63	1.69	1.74
80	1.80	1.85	1.91	1.97	2.03	2.09	2.13	2.17	2.20	2.24

[a] Modified from Thornthwaite and Mather (1957).

to the data collected during the period of this study in 1963 and 1964 (McMillan, unpublished notes). The calculated values of Q for these years are compared in Figure 1 with the observed data. Only in 1947 is the difference greater than can be accounted for by the sampling error of the observed data and the standard error of estimate of the computed value. In that year (as in 1946, 1948, and 1949) the proportions in the age groups were not separated by sex. Thus, it was necessary to estimate A on the basis of assumptions which may not have been correct, and an additional error in Q could have been introduced in this way. It is also possible that the age data were correct but that factors other than those operating from 1949 to 1962 may have been important in 1947.

In spite of this single departure, the predictive value of the equation appears to offer a research and management tool of some utility in the area studied in San Luis Obispo County. In other areas, it should be possible to develop prediction equations of similar form, but this may depend on other variables than those found to be important on my study area. Determination of such equations requires a long series of data on fluctuations in populations (I would prefer a record of a length of about 20 years, instead of the 14 years used in this case, to improve statistical significance), and the application of comparable methods of analysis. The present paper is intended only to describe the application of the prediction equation (1), including the necessary tables to compute the weather factors.

Determination of A, the percentage of adults among the females, requires that both sex and age be recorded for the fall samples from hunting bags. A is then computed as the number of adult females, divided by the total number of females, times 100. Since the females normally constitute less than half the population, the sample size for satisfactory precision should be on the order of 500 birds (200 to 250 females). Such data have been obtained by McMillan (1964) by keeping records of the age and sex of all birds bagged during the quail hunts in which he participated; I have obtained samples of this order of magnitude by checking the birds taken by hunters on the opening day of the season on the Hunter Liggett Military Reservation in Monterey County (574 quail on 2 November 1963). Subadults are readily distinguished by the mottled upper primary coverts; these feathers are plain gray in the adults (Sumner, 1935).

Calculation of M, the soil-moisture storage at the end of April, requires data throughout the year on daily mean temperature and on precipitation amounts. In order to take into account the variability in the distribution pattern of rainfall, 10-day periods, beginning with 2 September each year, are taken as the basic units.

TABLE 2

CORRECTION FACTORS FOR POTENTIAL EVAPOTRANSPIRATION, FOR LENGTH OF DAY AT LATITUDE 36° N[a]

Date	Correction	Date	Correction
2–11 Sept.	1.06	1–10 Mar.	0.96
12–21 Sept.	1.03	11–20 Mar.	0.99
22 Sept.–1 Oct.	1.00	21–30 Mar.	1.03
2–11 Oct.	0.97	31 Mar.–9 Apr.	1.06
12–21 Oct.	0.94	10–19 Apr.	1.09
22–31 Oct.	0.91	20–29 Apr.	1.12
1–10 Nov.	0.88	30 Apr.–9 May	1.14
11–20 Nov.	0.86	10–19 May	1.17
21–30 Nov.	0.84	20–29 May	1.19
1–10 Dec.	0.82	30 May–8 June	1.20
11–20 Dec.	0.81	9–18 June	1.21
21–30 Dec.	0.81	19–28 June	1.22
31 Dec.–9 Jan.	0.82	29 June–8 July	1.21
10–19 Jan.	0.83	9–18 July	1.20
20–29 Jan.	0.85	19–28 July	1.18
30 Jan.–8 Feb.	0.87	29 July–7 Aug.	1.16
9–18 Feb.	0.90	8–17 Aug.	1.14
10–28 Feb.	0.93	18–27 Aug.	1.11

[a] Modified from Thornthwaite and Mather (1957).

For each 10-day period, mean temperature and total rainfall are readily calculated from daily values; rainfall data from Cholame (U.S. Weather Bureau Station No. 1743) and temperatures from Paso Robles (Station No. 6730) were found to be the most representative available in this area. These data are reported in inches and degrees Fahrenheit, and the equations and tables are constructed for the same units. It is also necessary to estimate or to assume a value for soil-moisture capacity and for the soil-moisture content at the beginning of the precipitation season on 1 September. For the study area in San Luis Obispo County, soil-moisture capacity was estimated at 7.00 inches, on the basis of soil surveys (Kotlar, 1939) and soil samples taken in the course of this study. Soil-moisture content on 1 September, determined from preliminary calculations, averaged 0.28 inch from 1949 to 1962, and this value may be used each year, or the computation may be carried out throughout the year to obtain a new value for 1 September of each year after the first. Neither the soil-moisture capacity nor the soil-moisture storage value for 1 September is critical in the calculations, and minor inaccuracies will not appreciably affect the computed value of M.

The procedure for computing the water balance from temperature and precipitation data involves the following steps for each 10-day period after 1 September.

Step 1. Enter table 1 with the mean temperature and find the uncorrected value of the potential evapotranspiration. (Note: Values in table 1 are adapted from Thornthwaite and Mather [1957] corresponding to the temperature regime of the study area, and cannot be used for other areas.)

Step 2. Multiply the value from table 1 by the correction factor given in table 2 for the time of year, to correct for the length of day at the latitude of the study area.

Step 3. Compare the precipitation with the corrected potential evapotranspira-

TABLE 3

SOIL-MOISTURE COMPUTATION FOR 19–28 FEBRUARY, 1964
(Paso Robles-Cholame data, San Luis Obispo County)

Soil moisture brought forward from previous period		1.74 inches
Mean temperature		48.1° F
Precipitation		0.07 inches
Uncorrected potential evapotranspiration (table 1)		0.33 inches
Correction factor (table 2)		0.93
Corrected potential evapotranspiration		0.31 inches
Water need	(0.31) – (0.07) =	0.24 inches
Water use	(0.24) × (1.74)/(7.00) =	0.06 inches
Soil moisture	(1.74) – (0.06) =	1.68 inches

tion from Step 2. If (1) the precipitation is greater, subtract the potential evapotranspiration and add the remainder to soil moisture up to a maximum of 7.00 inches; any excess is runoff and is disregarded. If (2) the potential evapotranspiration is greater, subtract the precipitation; the remainder is the water need.

Step 4. Water need is satisfied in part by the soil moisture carried forward from the previous period, in proportion to the degree of saturation of the soil. Calculate soil water use as follows:

$$\text{soil water use} = \frac{\text{soil moisture}}{7.00} \times \text{water need}.$$

Step 5. Subtract soil water use from the soil moisture brought forward from the previous 10-day period, giving the soil-moisture value for the current period.

Repeat the procedure for each 10-day period, using the soil moisture from the previous period for each Step 4 calculation (use 0.28 for the period 2–11 September). The soil moisture computed in this way for the 24th 10-day period (20–29 April) is the value of M to be used in equation (1). Although at first glance this appears to be a rather laborious computation, it requires only a few minutes at the end of each 10-day period to maintain a current balance. As soon as temperature and rainfall

TABLE 4

CALCULATION OF PREDICTED QUAIL PRODUCTIVITY INDEX (SUBADULT: ADULT RATIO) FOR 1963 IN SAN LUIS OBISPO COUNTY

Predicted ratio of subadults to adults in fall, 1963	
Percentage of adult females	$A = 24$
Soil moisture end of April	$M = 3.12$ inches
Precipitation total through April	$P = 7.17$ inches
$Q = 0.021A + 0.929M - 0.120P - 0.975$	
$= 0.504 + 2.898 - 0.860 - 0.975$	
$= 1.57$ subadults/adult	
95% confidence interval: 1.42 – 1.72.	
Observed bag of subadults and adults in fall, 1963	
Total adults	389
Total subadults	511
Ratio subadults to adults	1.31
95% confidence interval	1.15–1.50

data for the period are available, average the temperatures and sum the rainfall, find the potential evapotranspiration from tables 1 and 2, compare evapotranspiration with precipitation, and enter the new value of soil moisture in the record. A sample computation for a 10-day period (using actual data) is given in table 3 to illustrate the procedure.

The precipitation total is also kept current throughout the year, and the seasonal total as of 29 April is the value of P to be used. A and M have been computed as described above, and these three values are then substituted into equation (1) and the predicted Q is calculated. The following fall an observed value of Q is obtained from the data on sex and age ratios and compared with the predicted value in order to evaluate the accuracy of the prediction. Table 4 shows the computation for 1963.

SUMMARY

A method is presented by which the productivity (proportion of subadults in the fall population) of California Quail in San Luis Obispo County, California, can be predicted from the age-ratio of females, and two weather parameters: (1) the soil moisture at the end of April computed by the Thornthwaite evapotranspiration and water-balance method, and (2) the total seasonal precipitation from September through April. Tests on independent data verify the predictive value of the method.

ACKNOWLEDGMENTS

This report is based on studies carried out while I was a graduate student at the Museum of Vertebrate Zoology, University of California, Berkeley, California. Support of the Museum and of the Department of Zoology is gratefully acknowledged. Financial support was provided by a National Science Foundation Graduate Fellowship, and by a grant for research expenses from the Union Foundation Wildlife Fund. I am indebted to A. Starker Leopold for encouragement and guidance in this research, to William F. Taylor for assistance in the statistical analysis of data, to Ian I. McMillan of Shandon, California, for the opportunity to conduct studies on his ranch and for making his field notes available for my study, and to other faculty members and students of the university who assisted in various ways. W. R. Edwards, G. C. Sanderson, and Helen C. Schultz offered editorial suggestions.

LITERATURE CITED

Francis, W. J. 1965. The effect of weather on population fluctuations in the California Quail (*Lophortyx californicus*). Ph.D. dissertation, Univ. Calif., Berkeley.

Kotlar, E. 1939. Soils description report, property of McMillan, San Luis Obispo County, Calif. U.S. Dept. Agric. Plan of Soil and Water Conservation, 22 June 1939.

McMillan, I. I. 1964. Annual population changes in California quail. J. Wildl. Mgmt., 28: 702–711.

Sumner, E. L., Jr. 1935. A life history study of the California Quail, with recommendations for its conservation and management. Calif. Fish and Game, 21:167–256.

Thornthwaite, C. W. 1948. An approach toward a rational classification of climate. Geog. Rev., 38:55–94.

Thornthwaite, C. W., and J. R. Mather. 1957. Instructions and tables for computing potential evapotranspiration and the water balance. Drexel Inst. Tech., Lab. of Climatology, Publ. in Climatology, 10:185–311.

Museum of Vertebrate Zoology, University of California, Berkeley, California. (Present address: Illinois Natural History Survey, Urbana, Illinois 61801.) 17 June 1966.