THE BREEDING BIOLOGY OF CALIFORNIA QUAIL IN NEW ZEALAND

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INTRODUCTION

The breeding biology of *Lophortyx californicus* in North America has been described by Sumner (1935), Glading (1938), Howard and Emlen (1942), Genelly (1955), Raitt (1960) and Lewin (1963); in the Hawaiian Islands by Schwartz and Schwartz (1949) and in New Zealand by Williams (1952, 1959).

Much more local information has now been gathered and this paper is concerned mainly with annual and local variations in the onset and duration of events in the breeding season, and with annual variations in clutch size, nest success and the fertility and hatchability of eggs — all factors that might be expected to show correlation with population fluctuations previously described (Williams 1963) which are now known to be no longer cyclic (Williams 1966).

The following study was made in the central North Island, near the northern end of Lake Taupo, and in Central Otago in the South Island, within a 40-mile radius of the town of Clyde.

THE REPRODUCTIVE PERIOD

The progress of the breeding season was followed by using indices of reproductive development (testis length and diameter of pre-ovulatory follicles) directly correlated with cellular and physiological changes occurring concurrently in the gonads. All measurements were made on fresh birds from Central Otago that had been either accidentally killed during trapping or shot during the open season. Not enough birds were obtained for analysis of variation in onset of the breeding season caused by age differences. One fact obvious from Figures 1 and 2 is that quail first breed when about 12 months of age.

The testicular cycle

The left testis, generally the larger, was measured to the nearest half millimetre. In its resting state it has a mean length of about 4 mm. Growth begins in late August; the organ reaches full size in November, begins to regress in December and is back in its resting state by the end of February (Fig. 1). Assuming that the histological stages described by Lewin (1963) for quail in California, are correlated with the same lengths of testis elsewhere, i.e. that production of mature sperm begins when the testis reaches 7.5–8.0 mm. and ceases upon its regression to 8.0 mm. late in the breeding season, then both Lewin's (1963) and Genelly's (1955) Californian data indicate a period of formation of mature sperm of about three months and the local data, four months. These figures may over-estimate the duration of the males' true reproductive period, since mature sperms in sufficient number for fertilization may not be produced immediately.

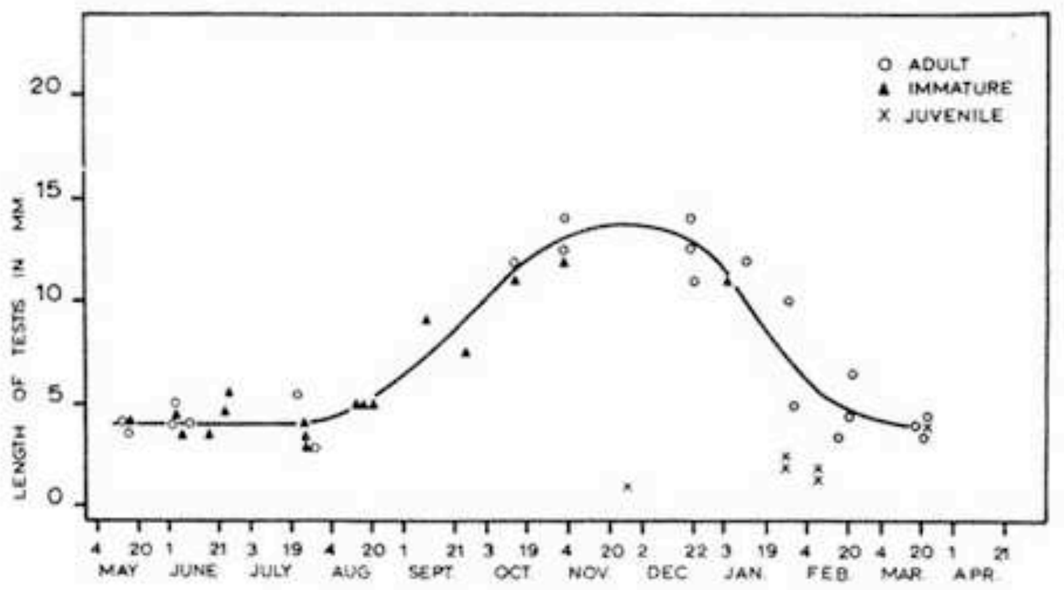

FIGURE 1. *Growth and regression of testes in California quail from Central Otago. Data from all years.*

Lewin had enough information to indicate whether there was likely to be any annual difference in the growth cycle of the testis. He found no evidence for it over three seasons and concluded that the cycle was independent of such variables as temperature and rainfall. Because males were producing mature sperm three weeks before the earliest egg was laid and for a week after the laying of the last, Lewin postulated that the cycle in males was an adjustment to the more variable timing of development in females.

Such data as I have indicate no difference in the rate of testis growth and regression between adults and immatures (i.e. birds coming into breeding condition for the first time). This agrees

Neither Raitt (1960) nor Generally have com-
Neither Raitt (1960) nor Genelly have comparable data for California quail but Raitt and Ohmart (1966) report a 15-week period of sperm — and egg — production in the closely-related Gambel quail (*Lophortyx gambelii*).

Mackie and Buechner (1963) stated that among chukar (*Alectoris graeca chukar*) in south-eastern Washington males began producing sperm, and females eggs at about the same time, but that the period of egg production exceeded that of sperm by at least three weeks. In this species spermatogenesis lasted about three months and oogenesis about four. There was no significant difference between adults and immatures in the time of onset or duration of gametogenesis.

For North American ring-necked pheasants (*Phasianus colchicus*) Kirkpatrick and Andrews (1944) found that rapid development of the testis, as measured by its weight and spermatogenesis, began at about nine months of age. In quail, with most hatching occurring in Central Otago at about mid-December or slightly earlier, a great increase in testis size would have to begin in September if both species matured at about the same rate; and this is what is found. Kirkpatrick and Andrews reported a second period of advanced growth of the testis between 81 and 144 days, followed by a spell of regression. Such was not apparent in either Lewin's study or my own.

The ovarian cycle

The pattern of the female reproductive cycle in Central Otago generally agrees with that found by Lewin who used — as I have done — the technique of measuring the diameter of preovulatory follicles. Local data show that the chances of finding an ovum about to be shed increase rapidly from August to a maximum at the end of October and begin to decrease rapidly in late December (Fig. 2). The duration of the laying period is not directly measured by this technique because a bird may have ovulated and perhaps even laid. This would not be apparent from the graph since the next largest follicle now remaining would be short of the point of shedding its ovum; and so unless the presence of a *post*-ovulatory follicle were observed, the bird would be classified as one which had not yet laid. Therefore Lewin's graph and mine do not fix the laying period precisely but only, perhaps, its minimum duration.

Lewin studied growth and regression of two other structures — the ovary and oviduct, both of which were weighed. All three techniques yielded similar results — laying began at about the end of

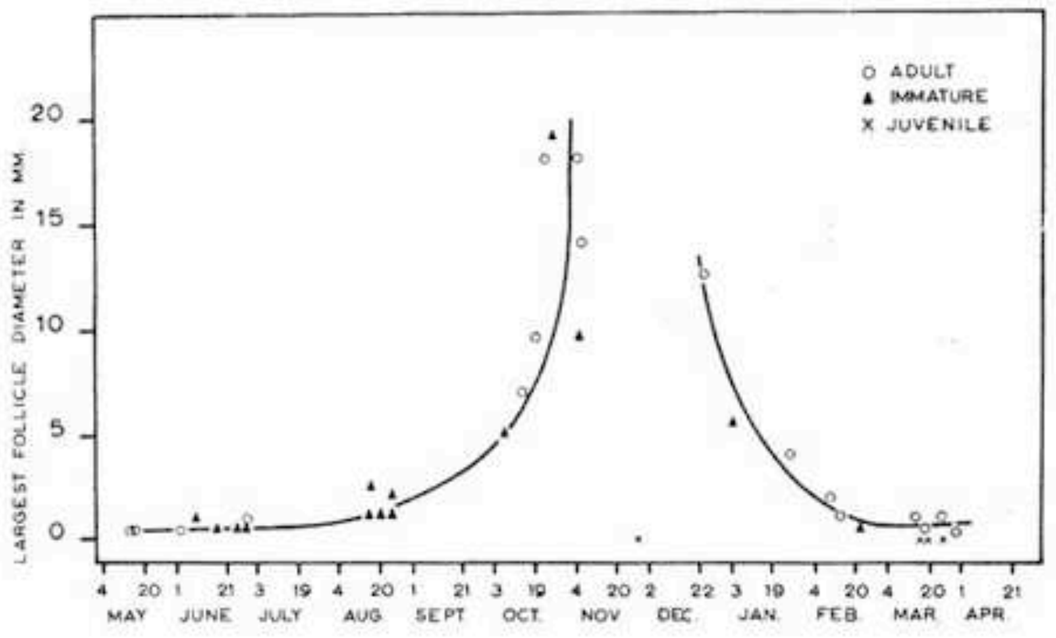

FIGURE 2. *Annual changes in diameter of ovarian follicles in California quail from Central Otago. Data from all years.*

April and ended in mid-June. Though his graphs gave this mean result (data from all three years were pooled), data from individual years showed that laying began on 24 April in 1954, 17 May in 1955 and 14 May in 1956. The corresponding dates for the end of the laying period were (reading from his Fig. 5) approximately 7, 4 and 16 June.

The duration of only about six weeks in 1954 (Lewin's longest period) seems too short; in 1955 it was barely three. The mean of the back-dating method (see below) for the two years for which there were data was about seven weeks. For Central Otago over a ten-year period the mean duration calculated by the same method was 13 weeks.

Genelly, in his two-year investigation, estimated the period to be 11 weeks. He classified hens as laying by using a combination of physical characteristics — weight in excess of 200 gms, condition of the cloaca, spread of the pubic bones and palpation of the abdomen. Raitt (1960), using palpation in a four-year study, reported an eight-week season but regarded the estimate as a minimum.

The occurrence of preovulatory follicles, in at least some of the Central Otago birds, of diameter 8–10 mm. when ova were about to be shed or had already been shed seems at variance with Lewin's growth curve for ovarian follicles (his Fig. 11). According to this, a follicle of 8–10 mm. is about five days short of ovulation; yet the rate of egg-laying in California quail is about one per day.

My data are insufficient to detect any difference in the rate of growth of immature and adult gonads among females; but such data as there are confirm Lewin's which suggested that, in spite of

differences in late winter and early spring, both age groups reached maturity together. Genelly presented evidence, based on only 30 birds over three seasons, that adults began to lay before immatures and quoted Lehmann's (1953) similar conclusions for bobwhite quail (*Colinus virginianus*). Raitt's results on California quail do not imply any clear difference; but he and Ohmart considered that adult Gambel quail tended to start laying earlier than young of the year.

Differences in the time of onset of laying between yearlings and those breeding for at least the second time have been reported for other species; e.g. for pheasants in New Zealand by Westerskov (1956), who found a consistent difference of about 13 days in both the start of laying and its peak of activity, and by Kluijver (1951) for great tits (*Parus major*). In this species adults tended to start laying up to five days before yearlings, but the differences were statistically significant in only five years out of nine. It may be that the type of season (i.e. favourable or unfavourable) has some influence. On the other hand Richdale (1949) found no such difference in yellow-eyed penguins (*Megadyptes antipodes*).

THE PHENOLOGY OF BREEDING SEASONS AND ANNUAL VARIATIONS

Dating of events such as laying and hatching periods within breeding seasons is important, for the year-to-year changes in their timing may influence reproductive success (e.g. Lack 1966). There are two methods for establishing the phenology of breeding seasons. The more direct involves careful, intensive and evenly-distributed observation of a large and representative sample of nests throughout, at least, the laying period. But quail nests are hard to find in statistically-useful numbers and there is no guarantee that those found comprise a random sample. The less direct method has therefore been used:—

Assuming that a representative sample of young is obtained by trapping and that none has completed the wing moult, the phenology of the breeding season may be reconstructed from the distribution of the hatching dates found by aging each bird from the state of moult of its primaries (Williams 1959, Raitt 1961, Taber 1963). Incubation and laying dates may be easily derived since they begin 22 and 35 days respectively before the corresponding hatching date. (Incubation takes 22 days and mean clutch size is 13 eggs, laid at approximately 24-hour intervals (Williams 1952, 1966)). Figure 3 compares the duration of the

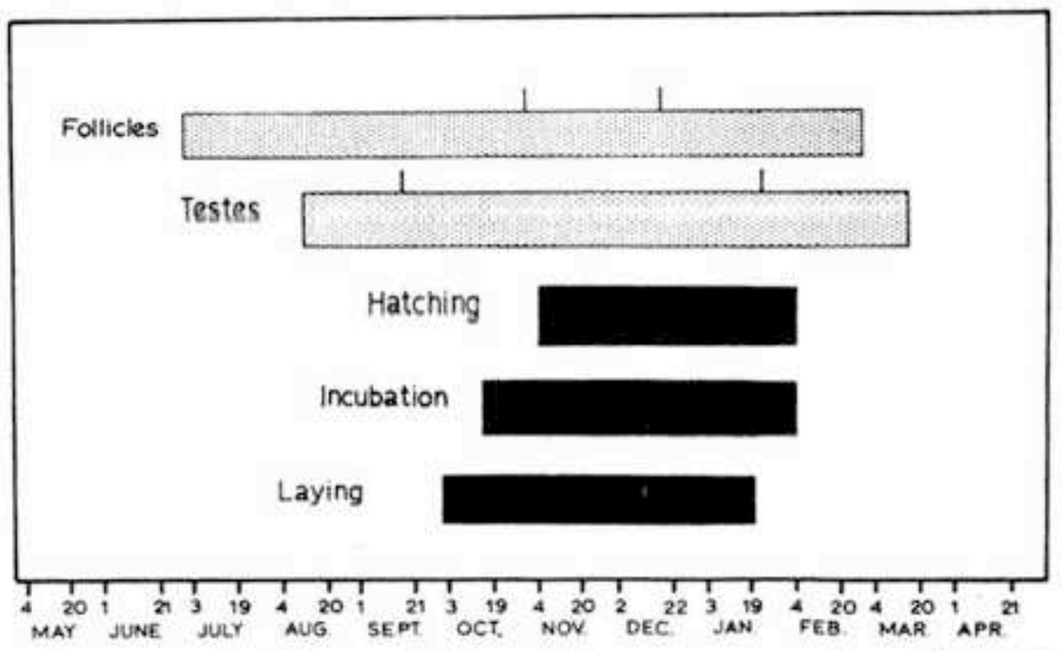

FIGURE 3. *General breeding season phenology in Central Otago as indicated by (a) growth of first-winter primaries of juveniles (solid bars) and (b) growth and regression of the gonads. Verticals on the follicle bar mark the dates at which most females were laying; those on the testis bar the dates between which length was 8 mm. or more.*

reproductive period in Central Otago as found by examination of the gonads with its phenology as calculated by back-dating. Agreement is satisfactory.

In Figures 4 and 5 hatching date distributions are given for ten seasons in Central Otago and for eight in the central North Island. Theoretically, corrections should be made each year to account for actual mean clutch size and mortality of young proportional to age (Williams 1959). Data necessary to make these are not available for most years so the distributions have to be used as they stand. Birds aged 0–4 weeks, which might be too small to be attracted to, or retained by, traps need not be corrected for because they are very scarce by the time trapping begins in mid-February.

TABLE 1. *Hatching period data, Central Otago.*

SEASON	STARTING WEEK No.	MEAN WEEK No.	DURATION IN WEEKS	No. OF YOUNG IN SAMPLE	TRAPPING AGE RATIO
1954–55	1	5.9	15	72	350
1955–56	2	7.4	14	219	387
1956–57	5	10.2	12	53	300
1957–58	5	12.5	12	51	60
1958–59	1	7.2	14	132	200
1959–60	2	7.1	13	205	440
1960–61	3	6.9	10	182	242
1961–62	1*	6.6	16	253	320
1962–63	1	6.6	13	313	459
1963–64	3	7.3	11	136	175
Means:		2.4±0.47	7.8±0.69	13.0±0.55	

Notes: Week No. 1 is that of 20–26 October
* One bird hatched two weeks before Week No. 1

Weather and breeding season phenology

That significant correlations should exist between various aspects of breeding- and population phenomena and weather seems incontrovertible. Difficulty lies in trying to find a logical starting point for an investigation among the complex inter-relationships of the many aspects of weather. Danger lies in having insufficient biological data, finding (by trial and error) a factor, however improbable, that does have a high correlation with the particular aspect being studied and then disregarding the biased method by which the correlation was obtained.

I have not tried to correlate events in the breeding season with minutiae of such variables as humidity, sunshine and frost. This is partly because preliminary examination of the data indicated that chances of finding any significant correlations were remote and partly because the lengths of the North and South Island series of breeding season data are probably insufficient. Furthermore, quail in Central Otago are obviously adapted to an environment different from that in the central North Island (or elsewhere). Such *detailed* findings as might apply in one region could not be anticipated to apply to another.

The main source of weather data has been the monthly summaries of the New Zealand Meteorological Service published in the New Zealand Gazette. There, after a brief general survey, rainfall, temperature, frost, sunshine and other records are given and the weather sequence during the month is described succinctly day by day. The maps of sunshine-, temperature-, and rainfall-departures from the monthly means have also been used. These are kept at the Weather Office in Wellington. I have here used departures from means because I believe that animals would be adapted to means of environmental factors rather than to their extremes.

Figure 4 and Table 1 show how very similar most Central Otago hatching periods are (and therefore, by implication, the rest of the breeding seasons too) in duration and in the time at which the peak and the mean hatching weeks occur; and this in spite of considerable variation in weather each year. The central North Island results (Fig. 5 and Table 2) are less uniform. Nevertheless, in five of the eight seasons, the mid-point of the mean hatching week lies between 28 December and 7 January and the other three between 15–20 January. In five of the seven seasons in which a peak week of hatching occurs it is either that

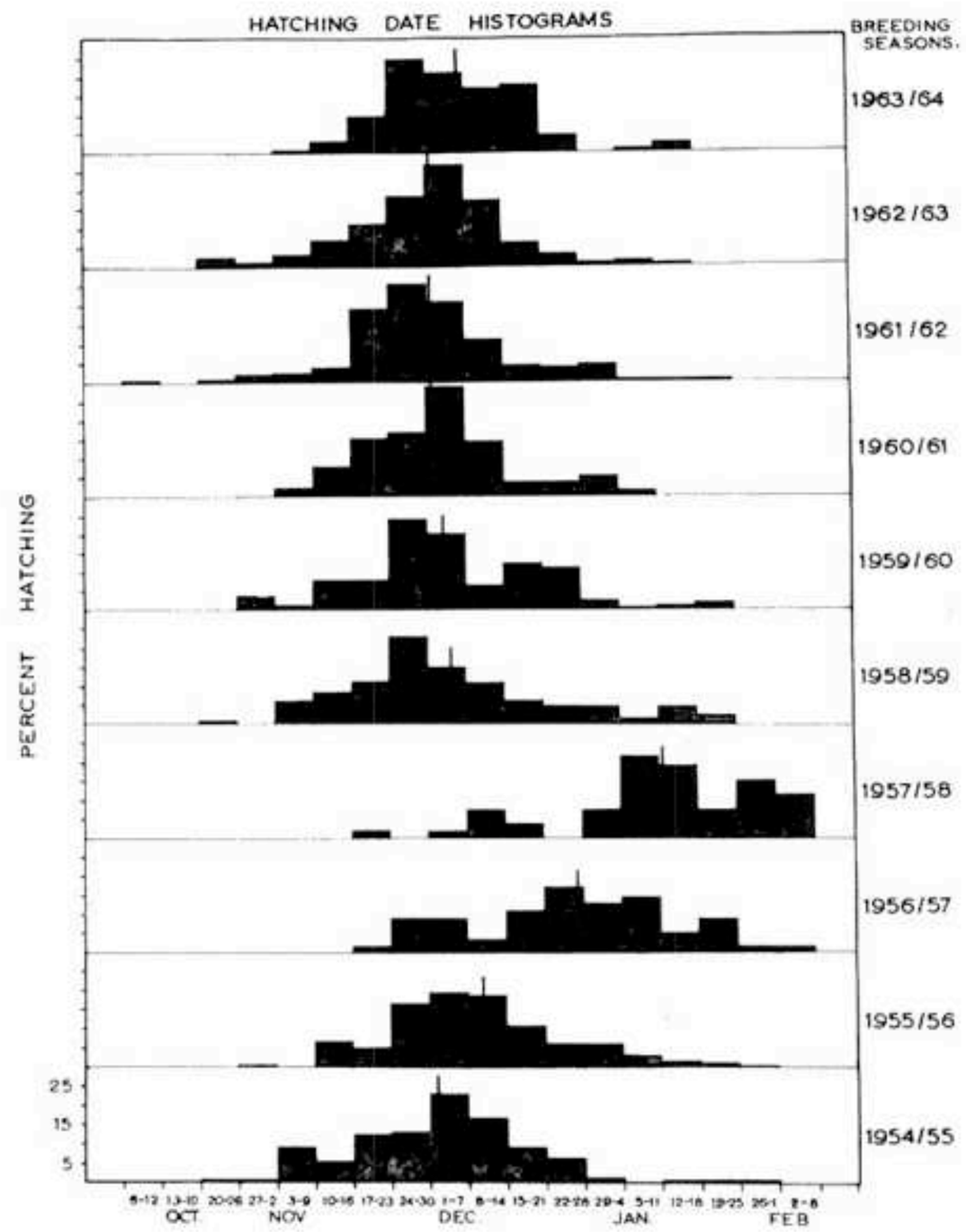

FIGURE 4. *Hatching date histograms, Central Otago. Vertical bars mark centres of mean hatching weeks.*

of 29 December–4 January or 5–11 January. In both districts, since the apparent variations in timing of the beginning and ending of the periods are frequently fixed by the capture of only one or two birds of a particular age, the magnitudes of these temporal differences are likely to be exaggerated.

TABLE 2. *Hatching period data, central North Island.*

SEASON	STARTING WEEK No.	MEAN WEEK No.	DURATION IN WEEKS	No. OF YOUNG IN SAMPLE	TRAPPING AGE RATIO
1956–57	6	13.0	13	150	400
1957–58	3	11.5	14	115	221
1958–59	4	10.4	11	81	156
1959–60	7	11.9	11	113	342
1960–61	6	10.7	10	71	159
1961–62	2	11.0	17	192	409
1962–63	10	13.6	10	71	107
1963–64	2	13.4	17	80	195
Means:	5.0±0.92	11.9±0.41	12.9±0.92		

Note: Week No. 1 is that of 20–26 October.

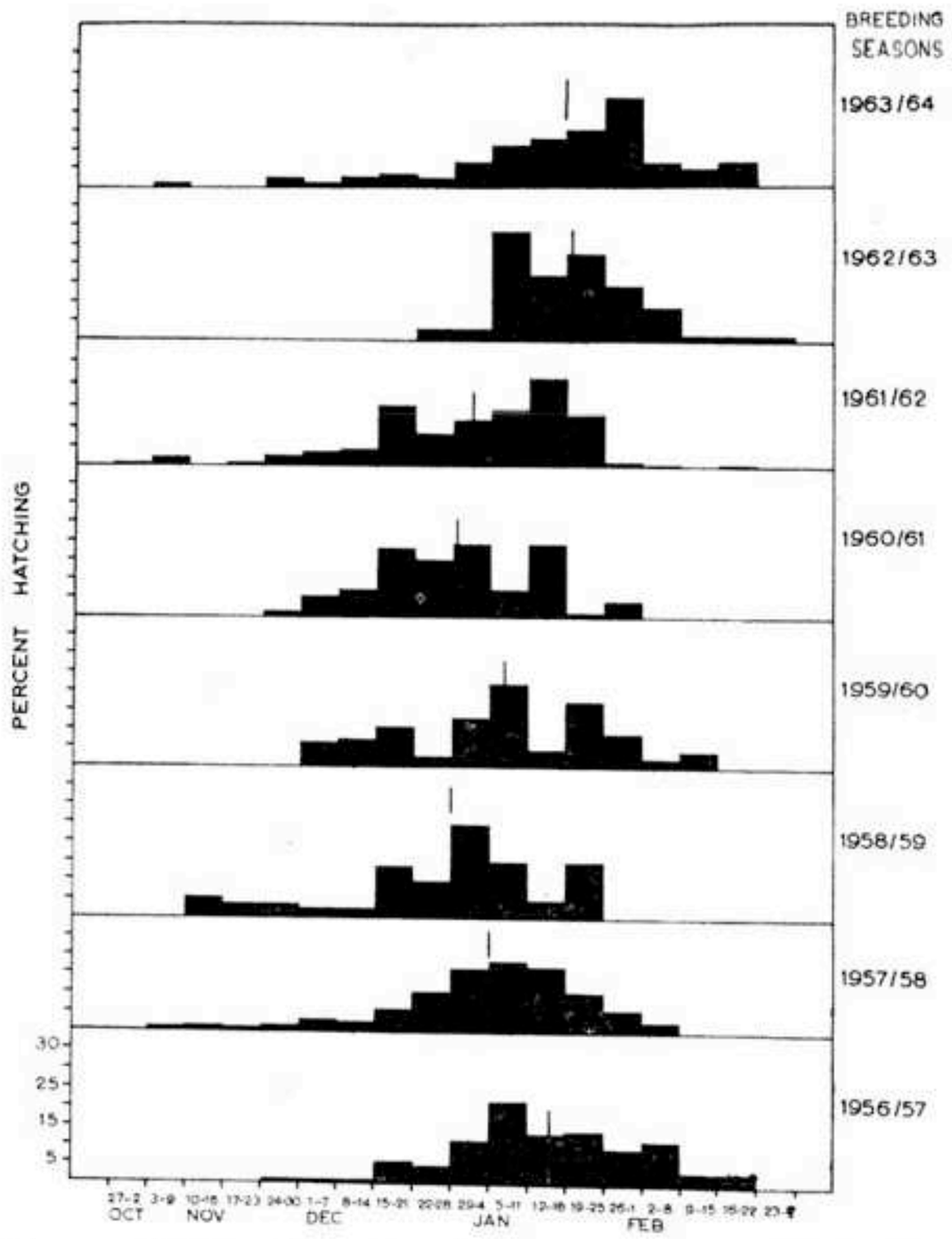

FIGURE 5. *Hatching date histograms, central North Island*

Nevertheless, in Tables 3 and 4 I have attempted an analysis of the effect of spring and early summer rainfall and temperature (the only two factors that, on inspection of the records, showed any likelihood of being significant) on the phenology of breeding seasons. For Central Otago there is some indication that early seasons tend to follow warmer-than-average Octobers and Novembers, though this is not confirmed by the central North Island data. In both districts September weather appears unimportant. Rainfall greatly in excess of the monthly means during October–December seems as likely to cause heavy mortality among newly-hatched chicks as to delay the onset of the breeding season.

Connexions were sought between rainfall during the period April–September and the phenology of the subsequent breeding seasons in Central Otago. When none was found (Williams 1966) this aspect of the investigation was abandoned after preliminary examination indicated that the same result was to be expected from the North Island data.

Relying on data from 27 birds over three years Lewin attempted to correlate variations in onset of the breeding season with annual variations in rainfall and mean daily temperature in spring. He concluded that heavy rain and mean daily temperature below 55°F. (13°C.) delayed ovarian development, whereas testicular development seemed independent of these variables. His conclusion may be correct but its experimental basis is slender.

Lack (1966) claimed there was a strong correlation between the temperature in March and April (northern spring) and the date of laying by great tits and suggested that temperature itself, or some factor linked with it, affected not merely breeding behaviour but also the growth of the gonads. He compared the "warmth sum" (the sum of the °C. above freezing point of the average temperature for each day from 1 March to 20 April) with the mean date of the first egg laid each year. His Figure 5 certainly shows a correlation between these two but it is not very convincing for warmth sums below approximately 325°C. Kluijver (1951), in a similar study,

TABLE 3. *Weather and the onset of Central Otago breeding seasons.*

	Temperature departure from the mean (°F.)			Rainfall departures from mean (%)		
EARLY SEASONS	Sept.	Oct.	Nov.	Sept.	Oct.	Nov.
1954–55	0 to +1	0 to +1	+3 to +4	—50	— 50	— 50
1958–59	0	+2	+2 to +3	—50	0	— 50
1961–62	—1 to —3	+3 to +4	+1	+50	— 50 to — 75	+ 50
1962–63	0 to +1	+1 to +2	0 to +1	—33	0 to + 50	— 25
"NORMAL" SEASONS						
1955–56	+1 to +3	+2 to +3	—1 to +1	—33	— 25 to — 50	0 to — 25
1959–60	+1 to +2	—2	+1 to +2	—33	— 25 to — 50	0
LATE SEASONS						
1956–57	+1 to +2	+1	0 to +1	—25	0 to — 25	+200 to +300
1957–58	+1 to +2	—1 to —2	—1 to +1	—50	+ 50 to +200	+200 to +300
1960–61	0	+2 to +3	0	+50	— 25 to — 50	— 25 to + 50
1963–64	0	+2	—2 to —3	0	0	— 50

Note: 0 = Mean temperature or rainfall
—25 = 25% less than the mean monthly rainfall, etc.

reported a similar result and later (1952) stated that his correlation was one without a causal relationship.

Using less precise data — mean hatching week and a warmth sum calculated from the mean of the daily maxima and minima from three weather stations in Central Otago (Alexandra, Cromwell and Hawea) for the period 1 September–20 October — I was unable to find any suggestive correlation (Fig. 6). I would not claim, as a result, that a correlation between warmth sum and mean hatching week might not be found if other dates were chosen or if, each year, events in the breeding season were followed directly instead of by backdating. On the other hand, spring temperatures are so much higher in Central Otago than in Holland or Oxford that such a correlation should not, perhaps, be expected.

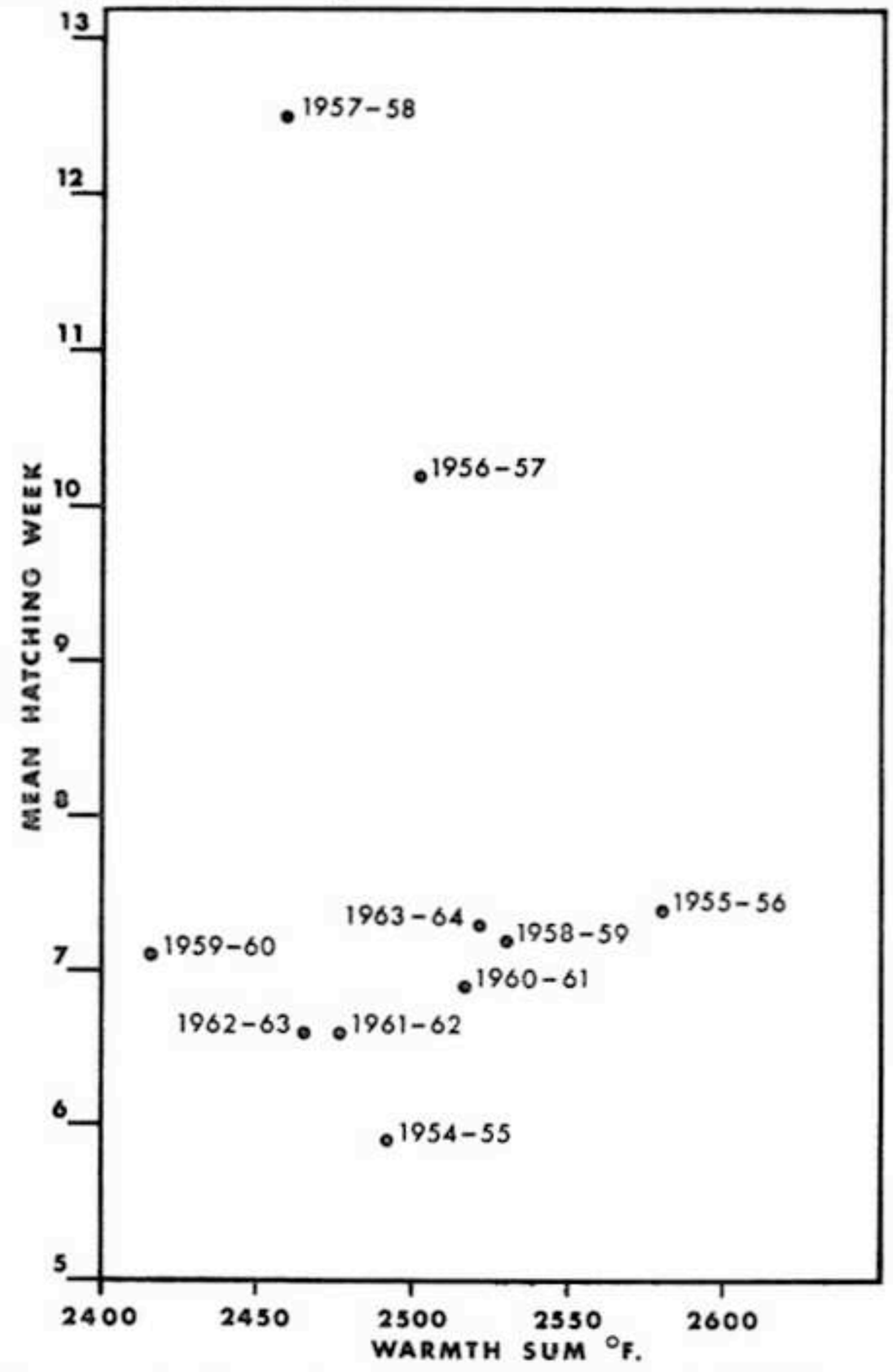

FIGURE 6. *Warmth-sum (in °F.) for period 1 September–20 October and mean hatching week, Central Otago.*

DIFFERENCES IN PHENOLOGIES BETWEEN CENTRAL OTAGO AND CENTRAL NORTH ISLAND

That central North Island hatching (and therefore breeding) seasons should start consistently later than those in Central Otago and have later periods of peak activity (Figs. 4 and 5) runs counter to the general rule that, under normal circumstances, breeding seasons should be later in all particulars with increasing latitude. The difference should be about 25 days for every ten degrees (Baker 1938). The question arises: Is the difference between Central Otago and the central North Island real and, if so, to what might it be attributed?

Westerskov (1956) found the expected relationship between latitude and onset of breeding for pheasants in New Zealand and used for his comparisons direct observations of egg-laying in two groups in approximately the same latitudes as the central North Island and Central Otago respectively, a difference of about eight degrees. The difference between the peaks of the two laying periods (data from only one season?) was approximately 21 days and that between starting dates approximately 14 days. The birds were game-farm animals; and one might reasonably expect that, under the circumstances of living in a protective environment, most modifying differences, except that of latitude, would be considerably reduced, leaving that of latitude paramount. Flux (1966) reported a difference of about a month in the expected direction between the start of the breeding seasons of song thrushes (*Turdus philomelos*) and blackbirds (*T. merula*) separated by about five degrees (and a considerable altitude) in New Zealand. But the peaks and the ends of the seasons occurred at very similar times. Gurr (1954), on the other hand, did not find that blackbirds in Dunedin bred at a time significantly different from that in some other parts of New Zealand.

For the two wild quail populations in about the same latitude as Westerskov's pheasants the difference, over all available years, between the means of the hatching periods was 4.1 weeks (week 7.8 in Central Otago and 11.9 in the central North Island). This difference is not only in a direction contrary to that expected but is also statistically significant ($t_{23}=6.56$, $P=0.001$).

Because the magnitude of any errors needed to give a result so much at variance with that expected would have had to be so great that it could hardly have escaped detection, it is simpler and more reasonable to assume the difference is

real and to try to discover a cause. Mean temperature appears an unlikely candidate, for that of the central North Island is generally higher than that of Central Otago. For growth rates of young to be involved those of Central Otago would need to be higher than those of the central North Island. Though the maximum growth rate (in body weight) of young Central Otago birds is greater (Williams 1966) their final body weight is also greater and it is unlikely that the difference between the two rates (even if faithfully reflected in that of the moult), would be enough to account for the difference between the two phenologies.

The difference may eventually be explained in terms of Lack's (1966) suggestion that the immediate factor determining the start of breeding is the obtaining by the female of enough food for egg formation.

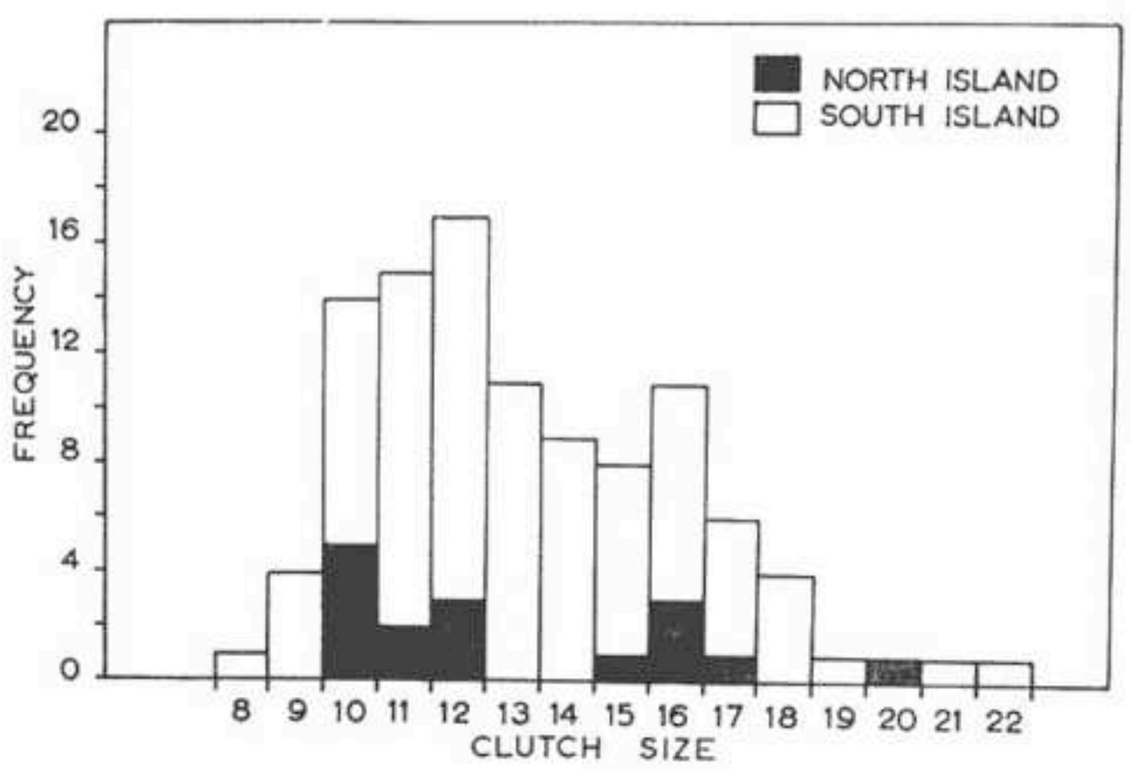

FIGURE 7. *Clutch size of California quail in Central Otago and the central North Island. Data for all years.*

CLUTCH SIZE

Taking as a complete clutch the number of eggs in a nest that has not been added to in 48 hours, I have records of 103 complete clutches in Central Otago over all years. Mean clutch size is 13.7 ± 0.27 with a range of 8–22. For 16 North Island clutches the mean is 13.00 ± 0.77 with a range of 10–20. (See Table 5 and Fig. 7.) Lewin gives a mean clutch size for Californian birds as fourteen. This was estimated from three different sources: a mean of 13.7 from 16 clutches, a mean of 11.0 from 40 clutches (Glading 1938), and a mean of 14.2 from an unstated number. Since the mean of the first two sources combined is only 11.8, his overall mean of 14 would require the unstated number to exceed 600. Considering the variations given by Lewin and the amount of annual variation possible in both New Zealand and California, a significant difference between mean clutch sizes in the two countries seems unlikely. Any difference arising from that of latitude (Lack 1954) if present, is in any event, likely to be small: the mean latitude for the New Zealand quail range is about 41° S., that of the Californian about 37° N.

Change in clutch size with advance of the season

Initial laying dates have been calculated for 52 nests, either from knowledge of the progress towards completion of the clutch or from hatching dates of clutches of known size. With data from relatively few nests available in any one year I have had to combine the Central Otago data for all years (see Table 6). This means that the results have to be interpreted cautiously. As they stand they indicate a steady falling-off in clutch size throughout the five-month period, though the differences between the means are not significant. This decline with advance of the season has been reported for other species, for example, for partridges (*Perdix perdix*) by Jenkins (1961) — an excellent study showing the annual frequencies of clutch size distributions at semi-monthly intervals; for American goldfinches (*Spinus tristis*) by Stokes (1950) — another excellent account; for the great tit by Kluijver (1951) and Lack (1956, 1966); for the house sparrow by Summers-Smith (1963) and for the California quail by Glading (1938), who found a mean clutch size of 12.2 for 26 nests between 1 May and 15 June and a mean of 8.5 for 15 nests begun between 16 June and 16 July.

In the present study it is extremely unlikely that first nestings and re-nestings of individual birds have been included or second clutches (i.e. those resulting from successfully breeding once and then re-laying), for double brooding apparently does not usually occur in California quail (also see Emlen 1939)* nor in some other game birds, for example, ruffed grouse (*Bonasa umbellus*) (Bump *et al.* 1947), partridges (Jenkins 1961), bobwhite quail (Stoddard 1946) and chukar (Mackie and Buechner 1963). Locally,

* A more recent paper by McMillan (1964) does record double-brooding, but only as a result of exceptional rainfall in a very arid area; and Francis (1965) has reported double broods in captive quail.

TABLE 4. *Weather and the onset of central North Island breeding seasons.*

	Temperature departures from the mean (°F.)				Rainfall departures from mean (%)			
"NORMAL" TO EARLY SEASONS	*Oct.*	*Nov.*	*Dec.*	*Jan.*	*Oct.*	*Nov.*	*Dec.*	*Jan.*
1957–58	—1 to —2	0 to +1	—1 to —2	+1 to +2	0 to + 50	0 to + 50	0 to + 50	0 to — 50
1958–59	+2 to +4	+1 to +2	+1 to +2	+3	0 to + 50	0 to — 25	+200 to +400	+100
1959–60	0 to +1	+1	+2	+1 to +2	0 to +200	0 to — 50	—25 to — 50	—50
1960–61	+2	0	—1 to —3	0 to +1	—25	0 to — 50	—25 to — 50	0
1961–62	+2 to +4	+1 to +2	+3 to +4	+3 to +4	—25 to — 50	—25 to — 50	0 to — 25	0 to + 50
LATE SEASONS								
1956–57	+1 to +2	0	+1	0 to +1	0 to + 50	0 to + 50	0 to + 50	—50 to — 75
1962–63	+2 to +3	+1 to +2	0 to +1	0 to +1	0 to + 50	+50	+150 to +300	—25 to — 50
1963–64	+1 to +2	—1 to —2	—1	—2 to —3	—10 to — 50	—25 to —100	0	—25 to —100

Note: 0 means mean temperature or rainfall.

—25 means 25% less than mean monthly rainfall, etc.

TABLE 5. *Breeding season data, Central Otago (nests of known fate).*

SEASON	1949–50	1953–54	1954–55	1955–56	1956–57	1957–58	1958–59	1959–60	1960–61	1963–64	Mean
Clutch size	11.7±0.83	13.1±0.83	13.6±0.73	14.0±0.85	14.2±0.71	11.8±0.65	12.4±0.61	13.3±0.63	14.0±1.27	10.7±0.72	13.2
(No. in sample)	(7)	(14)	(19)	(10)	(12)	(3)	(11)	(19)	(4)	(3)	
% Nest success	57.1	14.3	87.5	40.0	83.3	0	100.0	78.9	—	0	62.6
	(7)	(7)	(8)	(5)	(6)	(2)	(3)	(19)	(0)	(2)	
% deserted	14.3	71.4	0	20.0	16.6	50.0	0	5.3	—	50.0	18.7
	(7)	(7)	(8)	(5)	(6)	(2)	(3)	(19)	(0)	(2)	
% predated	28.6	14.3	12.5	40.0	0	50.0	0	0	—	50.0	18.7
	(7)	(7)	(8)	(5)	(6)	(2)	(3)	(19)	(0)	(2)	
% hatchability	74.1	84.7	97.7	88.0	100.0	—	100.0	99.4	—	—	96.0
	(31)	(13)	(87)	(25)	(68)	(0)	(37)	(135)	(0)	(0)	
% fertility	83.0	91.4	98.8	88.0	97.1	100.0	100.0	92.0	—	—	93.8
	(47)	(35)	(87)	(25)	(70)	(24)	(37)	(176)	(0)	(0)	
Mean hatching week	—	—	5.9	7.4	10.2	12.5	7.2	7.1	6.9	7.3	—
Subsequent shooting age ratio (young per adult female)	49	85	195	268	164	53	175	181	171	93	—

TABLE 6. *Variation of clutch size with advance of the season (all years).*

LAYING DATE	FREQUENCIES OF CLUTCH SIZE											MEAN	S.E.
	9	10	11	12	13	14	15	16	17	18	18+		
1–30 Sept.	0	0	1	0	0	1	0	2	0	0	0	14.3	1.02
1–31 Oct.	1	2	3	3	1	1	0	1	1	2	1(22)	13.5	0.89
1–30 Nov.	1	2	4	3	4	2	3	0	1	0	0	12.6	0.37
1–31 Dec.	0	2	1	2	2	0	1	1	0	0	0	12.4	0.74
1–31 Jan.	0	2	1	0	0	0	0	0	0	0	0	10.3	0.55
TOTALS:	2	8	10	8	7	4	4	4	2	2	1	12.8	

more observations of change in clutch size with time are needed, especially observations within one particular year. But there is little doubt that the trend will be confirmed.

The implication is that, all other things remaining equal, the later the breeding season within a particular locality the less successful will it be; a general conclusion also reached by Lack (1966). When mean clutch sizes of a species are being compared from place to place and from year to year account should obviously be taken, whenever possible, of at least the mean hatching dates of the season. Such data are only very rarely available. For annual mean hatching dates in New Zealand see Tables 1 and 2.

Annual variation in clutch size

Over ten years mean annual clutch sizes for Central Otago have ranged from 10.7 to 14.2 (see Table 5). Differences between years are not significant (some years have very small sample sizes), nor are there any statistically-significant correlations between annual mean clutch sizes and either breeding season phenologies or estimates of productivity such as age ratios found either at trapping in March or during the shooting season (Williams 1966). However, higher clutch sizes at least tend to be associated with higher age ratios and vice-versa, as Lack (1964) found for the great tit in a 17-year study and Jenkins, Watson and Miller (1963) for the red grouse (*Lagopus l. scoticus*) in Scotland over a five-year period. In my own study, even if the differences between all annual mean clutch sizes were significant, inspection will show that these differences could not alone be responsible for the annual differences in mean age ratios. I agree with the conclusions reached by Jenkins after a four-year investigation of population control in partridges: "With high nest losses and, particularly with a high mortality rate among newly hatched chicks, the small differences noted in clutch size [only 15.5 to 16.6] have rather little importance from the viewpoint of population control".

NEST SUCCESS

The criteria used for determining this statistic show considerable variation. Among the possible are:—

(i) The percentage of totally successful nests (i.e. those from which all young hatch).
(ii) The percentage of nests from which at least one egg has hatched.
(iii) The percentage of nests from which at least one egg has hatched of all those nests in which the clutch was known to be complete.
(iv) The percentage of nests from which at least one egg has hatched of all those nests in which not only was the clutch known to be complete but whose ultimate fate was also known.

Of all the possibilities (ii) seems to be the one in commonest use and was the one used by Glading to obtain a figure of 18% for California quail in a study lasting only one season. Though not explicitly stated, Jenkins, Watson and Miller apparently used (iv) for their red grouse. This should be the measure of nest success used whenever possible, though it is the hardest to obtain. Only complete clutches should be used since nests abandoned or destroyed during laying are likely to be replaced and so will be unimportant in any determination of subequent population size. Only nests of known fate should be used otherwise nest success is underestimated since nests of unknown fate are, in effect, classed as unsuccessful. Comparisons of nest success such as those made by Hickey (1955) lose most of their value because of lack of consistency in the standard, as Hickey himself recognized. I have used the term "nest success" instead of the more usual "nesting success" because the meaning seems more precise, implying the success of the nest and its contents rather than success in making a nest and depositing eggs in it.

Over all years nest success in Central Otago was 62.6% (Table 5). Expressed on a monthly basis it reached an apparent peak in November (Table

7); and although, once again, the smallness of the sample warns that the results must be interpreted cautiously, they parallel Glading's which indicated that nest success was at a maximum at a corresponding time.

TABLE 7. *Percentage of complete clutches of known fate from which at least one egg hatched.*

	Sept.	Oct.	Nov.	Dec.	Jan.	Undated
Number of nests	4	14	17	9	3	12
% successful	50.0	50.0	76.5	44.4	66.7	75.0

Causes of nest losses

Of the 103 nests with complete clutches in Central Otago, the ultimate fate of 43 is unknown. Of the remaining 59 we have just seen that 37 were successful. Eleven were deserted, generally as a result of examination early in the incubation period or through other disturbance by man or dog. The remaining 11 were destroyed either by predation of hen or eggs, or by such agents as fire, agricultural activities and, in one instance, robbery by man. Predators were known to be or assumed to be either feral domestic cats or such introduced carnivores as ferrets, stoats or hedgehogs. With relatively few records there is little justification for any further quantitative discussion of the causes of desertion or destruction.

Worth mentioning is the suggestion by Jenkins, Watson and Miller that among red grouse in certain years variations in behaviour, perhaps arising from psychological changes dependent on density-governing factors, may affect a bird's liability to desert its nest or neglect its young.

FERTILITY OF EGGS

In Central Otago there is no common trend or correlation between annual estimates of egg fertility and any population index. Fertile eggs are defined as those from which chicks have hatched or in which dead embryos have been found. In this investigation estimates of annual percentage of fertility are likely to be minima since any untrained observers in the nest recording scheme could be expected to overlook embryos dying in the earliest stages of development either through desertion, accident or genetic causes. The annual range was between 83.0% and 100%, the mean for all years being 93.8% (see Table 5).

Data on annual fluctuations in fertility are not common in the literature. Jenkins, in his study, reported that few partridge eggs proved infertile: of 41 that failed to hatch and were examined, only three — all from the same clutch — did not contain embryos. And over three seasons losses through infertility and death of embryos combined did not exceed 10%. In their red grouse investigation Jenkins, Watson and Miller found 28% of 94 unhatched eggs were infertile in two years of population decline but that none out of 78 examined was infertile in three of the good years.

In general, fertility of game bird eggs is high: Stoddart (1946) found only 5.26% addled or infertile out of 2,874 bobwhite quail eggs examined over four years. Middleton (1935) recorded that, over a number of years in England, 93% of nearly 60,000 common partridge eggs hatched. Of the remainder he remarked, "some are infertile, but others have been arrested in development during incubation or contain chicks which have died in the shell when ready to hatch". In New Zealand, Westerskov found 96% of eggs of wild pheasants were fertile, those from captive birds being only 89% so.

HATCHABILITY

Another variable affecting population recruitment is hatchability. This is to be distinguished from nest success which is affected by circumstances beyond the eggs themselves and the embryos they contain. By hatchability is meant the proportion of fertile eggs hatching from successfully incubated nests; it is, in effect, a measure of viability of the embryo — a property one might well expect to show some correlation with population density, being perhaps congenitally determined, as implicit in the ideas of Chitty (1960) and Pimentel (1961).

Because of the difficulties encountered in this study in obtaining a large amount of breeding season data, it has not always been possible to usefully separate information on hatchability as here defined from hatchability plus egg fertility. In the following brief discussion on annual variations in hatchability and changes in this property with advance of the breeding season, infertile eggs are included, since observers other than myself have not always distinguished between these and embryos dead in the shell. As far as annual variations are concerned there is no clear connexion between apparent hatchability and population level (Table 5) except that hatchability was low in two of the trough years. However, it was not significantly higher in the breeding season immediately preceding the 1956 peak than it was in the season that ushered in the 1954 "low".

Within the breeding season the trend of the change in hatchability is parallel with that of clutch size though the values for each month are not significantly different from each other (Table 8).

TABLE 8. *Variation of hatchability plus fertility of eggs with advance of the season (Central Otago all years).*

	Sept.	Oct.	Nov.	Dec.	Jan.	Overall
No. of eggs	30	79	163	50	21	343
% hatch.	100	92.4	88.3	88.0	80.8	89.8

Glading reported that 163 chicks hatched from 181 eggs during one season, a hatchability of California quail, in the sense used in Table 8, of 90.1%.

Jenkins, Watson and Miller calculated hatching success as the percentage of eggs hatching after deduction of losses through desertion and faulty incubation. Losses from predation had already been subtracted from the total number laid in each season. Hatching success so calculated (which apparently included infertile eggs and dead embryos) showed an annual variation over five years from 70% to 95% (mean 82.4%) and was at its lowest in the year of smallest population.

Lack (1954) discussed hatching success but calculated success from data combining "(a) proportion of nests totally destroyed, (b) proportion of eggs failing to hatch in nests where at least some hatched". His percentages of success were, of course, generally low, as would be expected from such treatment in which unhatched eggs include losses through accident, predation, desertion, infertility and embryo mortality. His discussion emphasizes the overall differences in early mortality between nidicolous and nidifugous species but does little else.

CONCLUSION

Apart from an unexplained difference in timing, contrary to that expected, between the breeding seasons of California quail in the central South and North Islands, seasons are little different in their most important aspects from those in other countries where the species occurs.

Population fluctuations (as measured by age ratios) are not closely correlated with annual variations in climate, breeding season phenology or with the different components of reproductive rate. However, the absence of at least some correlations may result from paucity of some necessary data.

Whether density-dependent mortality induced, for example, by food shortage beyond the breeding season, has brought about regulation of numbers — a situation Lack (1966) suggests is usual among birds — is a topic to be discussed elsewhere.

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