AGING, GROWTH-RATE AND BREEDING SEASON PHENOLOGY OF WILD POPULATIONS OF CALIFORNIA QUAIL IN NEW ZEALAND

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(with a mathematical appendix by A. H. Carr)

The technique of aging some species of gallinaceous birds by means of the progress of the wing moult has most recently been investigated by Thompson & Kabat (1950), Genelly (1955) and Wallmo (1956). Nevertheless, some biological and mathematical assumptions involved in such studies need critical examination and this paper is offered in the hope that it may prompt such examination. It is the second in a series (for the first see Williams 1957) planned to deal with various aspects of a long-term study of the population dynamics and secular fluctuations of wild populations of California quail *(Lophortyx californicus)* in New Zealand.

THE AGING TECHNIQUES

To obtain an adequate idea of population structure and breeding season phenology one must be able to distinguish not only birds of the year from adults, but also to determine age distributions within these two major groups. In this species the separation of adults (birds of one year of age or more) from all others is a simple and accurate procedure based upon the possession of unmottled primary coverts by the old birds. Birds of the year, unlike the adults, may be subdivided on sight into three age classes distinguished by characteristic plumage states: (i) *chicks,* those in natal down or juvenile plumage and of mean age less than four weeks; (ii) *juveniles,* those undergoing post-juvenile moult of the primaries; and (iii) *immatures,* those that have passed through the post-juvenile moult, are in their first winter plumage and can be distinguished from adults most readily by their retention of mottled juvenile primary coverts which are not shed until the first post-nuptial moult.

Within all four age classes more detailed age distributions can be found, but only for the juveniles has a *direct* method been devised: Within their age range, which lies between about four and 25 weeks, individual ages may be determined by the progress of the post-juvenile moult of the primaries. For chicks, immatures and adults marking and recapture methods are at present being used.

When population studies were begun here no method for accurately aging juvenile California quail had been published though Genelly has published one since for the species in California. Rather than rely on
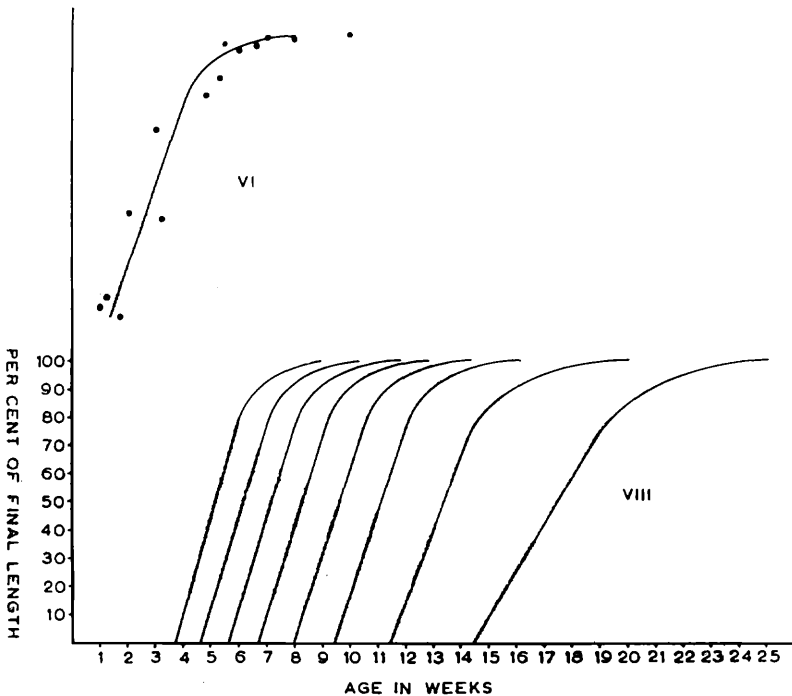
Fig. 1: *Age vs. moult of primaries in captive California quail.* For greater clarity experimental points have been omitted from the main curves. As a fair example, however, those for Primary VI are given separately above.

aging tables already published for bobwhites a beginning was made on a study of the moult of captive local California quail. Three broods were used—one in one year, two in another. The total number of survivors throughout the periods of study was 21—seven males and 14 females. Measurements from a number of obviously unhealthy birds that died during the course of the investigation have been disregarded in preparing the graphs, but those from apparently normally-developed birds that died have been included. (Obviously unhealthy birds have been found to be very rare in the wild.)

Progress of the moult with age was followed by measuring the length of the growing unflattened primaries from their tip to the point of insertion of the calamus into the skin. The graph showing the growth rates of the primaries was then prepared from points found by calculating, from all birds of the same age ("runts" excluded), the mean length of the remige at any one time expressed as a percentage of the feather's mean final length. Body weights obtained at the same time have been similarly treated. With moult rates and growth rates expressed in this way immediate comparisons may be made with those of other species or populations similarly expressed. Unfortunately,

TABLE NO. 1

True age (in days)	True age (in weeks)	No. of birds	Mean percentage growth of mean final length of primaries:							
			1	2	3	4	5	6	7	8
28	4.0	9	10							
35	5.0	11	46	16						
40	5.7	6	52	37	11					
49	7.0	6	91	55	39	13				
51	7.3	9	84	80	48	11				
56	8.0	15	95	88	49	25	10			
57	8.1	9		90	70	38	2			
63	9.0	6		95	91	54	24	4		
64	9.1	9		96	88	76	39	7		
69	9.7	9				82	42	10		
70	10.0	6	99	99	97	94	50	37		
77	11.0	6	100	100	100		82	65	6	
78	11.1	9				97	84	35	0	
90	12.9	8						80	27	
93	13.3	9				100	98	85	37	
94	13.4	6					100	98	60	
98	14.0	9						95	58	
103	14.7	8						96	81	0
105	15.0	15						100	84	12
112	16.0	8						98	91	18
120	17.1	9						100	95	39
126	18.0	15							91	72
133	19.0	6							98	74
140	20.0	16							96	87
161	23.0	6							98	94
175	25.0	21							100	100

much of the data given in the literature are expressed as actual measurements and weights which means that much recalculation must be done before valid comparisons can be made. Table No. 1 contains the data from which Fig. No. 1 was prepared. Table No. 2 gives, for each brood, the mean final length of each primary; and these, with their standard deviations, are included to show the degree of homogeneity of the experimental material.

The graph shows that the growth of the first winter primaries begins about 25 days after hatching and continues until about the 175th day. Furthermore, the intervals between the appearance of any two consecutive primaries tend to gradually lengthen from about six days with Nos. I and II to about 21 days with Nos. VII and VIII. The growth

TABLE NO. 2: Mean lengths of fully-grown first-winter primaries in captive California quail (to nearest millimetre)

PRIMARY NUMBER

Brood	Number in brood	1	2	3	4	5	6	7	8	
1	6	64	69	76	83	84	86	87	83	Mean
		3.16	4.34	5.52	2.37	1.97	1.18	1.97	2.76	S.D.
2	9	60	67	74	82	83	83	84	83	Mean
		3.70	2.69	3.70	2.36	1.35	1.01	1.85	1.48	S.D.
3	6	61	66	72	79	81	82	83	81	Mean
		2.69	2.69	2.69	2.36	2.36	3.03	2.81	3.16	S.D.

rates of the first six primaries (as measured by the slopes of the curves) are about equal and have been shown so in good conformity with the experimental data; that of No. VII is a little slower and No. VIII slowest of all. Juvenile primaries IX and X are normally not shed in the first year. Because growth rates of individual primaries begin to diminish after reaching about 75% of the final length only the earlier parts of the curves should be used for aging—especially in the field, where only *estimates* of percentage growth are possible when large numbers of birds are being handled. Accurate aging under these conditions can probably not be relied on after the birds have reached an age of about 21 weeks. Contrary to practice generally recommended by most other authors, estimates of the state of growth of the *two* youngest feathers are asked for from field operators rather than that of the youngest (or shortest—or missing) feather. One estimate then acts as a check against the other and errors are reduced when the means of both are taken, as Thompson & Kabat have already shown. During weeks 22-25, when only primary VIII is growing and has entered upon the last and slower stages of its growth, field estimates may be expected to decline in accuracy.

The progress of the moult in these local California quail is, in general, little different from that found for American bobwhites *(Colinus virginianus)* by Petrides & Nestler (1943) or for scaled quail *(Callipepla squamata)* by Wallmo or, as far as can be ascertained from his less-detailed study, for California quail by Genelly; though the onset of the moult in the local birds seems a little advanced and its completion delayed. The slopes and shapes of the growth curves of the individual primaries, not drawn in the original publications of either Wallmo or Petrides & Nestler, are similar to those in Fig. 1, and the degree of reliability of the aging technique is about the same; that is, the great majority of birds may have their hatching date fixed to within about three to four days either way of the true date—as can be seen for this study from Table No. 3.

Whether the primary moult and growth rate is the same for captive and wild birds is extremely difficult to decide directly for it is almost impossible to obtain a satisfactory number of truly wild quail of known age that are subject to continual retrapping. (Dr. C. H. Blake informs me that in doves there *is* a difference in the rate of progress of the primary moult between wild and captive birds.) An indirect way of testing the validity of transferring the application of the technique from the one type of population to the other is afforded by the reaging of retrapped *wild* juveniles: The progress of the moult between the first and second (or subsequent) trappings should be very close to that required by the theory derived from the study of the captive population. I have found, as did Wallmo, that the agreement is satisfactory and close enough for the purpose for which the phenological data are to be put—see Table No. 4. The main point to be reassured on is that any differences that may exist are consistent from year to year.

So far there are no indications that this is not so. The methods used by Thompson & Kabat to test the reliability of the technique among wild birds (i.e. by comparing the age indicated by each of the two youngest primaries on a single bird or by comparing the state of

TABLE NO. 4: Reaging of 24 retrapped wild juveniles

Age *expected* from known interval between first and last trapping (aging at 1st trapping assumed correct).
10½ 11½ 12½ 10 12 11½ 12 10½ 10½ 9½ 9½ 9½ 9½ 6½ 5½ 10 7½ 8½ 7 7½ 8½ 9 8

Age *found* from state of moult at the last trapping.
10½ 12 9½ 11 11 9½ 9 9 9 7½ 9½ 6½ 9½ 7 7½ 7 7½ 8½ 8 8½

All ages taken to the nearest half week

If a bird was retrapped more than once, the last occasion was used so that the longest possible interval could be used for testing the validity of the method. Intervals between trappings ranged from ½ to 3½ weeks.

TABLE NO. 3:   Theoretical age vs age indicated by
primary wing moult in captive birds

Number	True Age	Mean age of group calcd from primaries	Standard Deviation	Maximum Individual Discrepancy	Diff. between Cols 3 & 2
	in days	in days		in days	in days
11	35	38	3.78	10	+3
6	40	44	1.58	5	+4
6	49	53	2.76	7	+4
9	51	51	3.03	5	0
15	56	56	5.16	10	0
9	57	57	5.39	11	0
6	63	67	2.76	7	+4
9	64	65	6.06	13	+1
9	69	67	3.03	8	−2
6	70	75	2.76	7	+5
6	77	82	1.97	7	+5
9	78	75	3.37	9	−3
8	90	88	3.16	2	−2
9	93	89	3.37	10	−4
6	94	99	1.97	7	+5
9	98	96	4.00	8	−2
8	103	99	4.92	9	−4
15	105	106	6.15	10	+1
8	112	107	5.97	14	−5
9	120	118	3.37	8	−2
15	126	127	2.93	5	+1
6	133	130	4.34	9	−3
16	140	142	7.88	14	+2
6	161	161	5.52	8	0

The age of individual birds in each group was taken as the mean of that calculated from each of their two most-recently-replaced primaries which usually agreed to within two days and seldom disagreed by more than four. However in the later stages of growth in primaries VI, VII & VIII the ages indicated by the two feathers concerned could differ by as much as 12 days.

feather-growth between birds apparently belonging to the same brood) demonstrate both consistency and reliability; but they, too, still leave undecided the question whether moult rates calculated from captive birds give *true* ages when applied to wild ones. However, more light is thrown on this question if growth rates calculated from weights of wild and captive birds are compared: (As a check on the reliability of the operator all juveniles aged in the field are weighed. It is very seldom indeed that a weight is returned seriously at variance with that to be expected from the moult data. When, however, this does occur it is assumed that there has been a miscount of the primaries, for simple weighing errors are far less probable. Of course, some of these few birds may be "runts." Nevertheless, no attempt at correction is made—that particular bird is not used in the preparation of pheno-logical graphs or tables.) When a comparison of growth rates is made, as in Fig. 2, that for captive quail appears consistently slower than that for wild ones. However, what is not apparent in this graph is that the captive birds are consistently and significantly lighter in weight throughout as well, as Genelly has also found. Now one thing soon
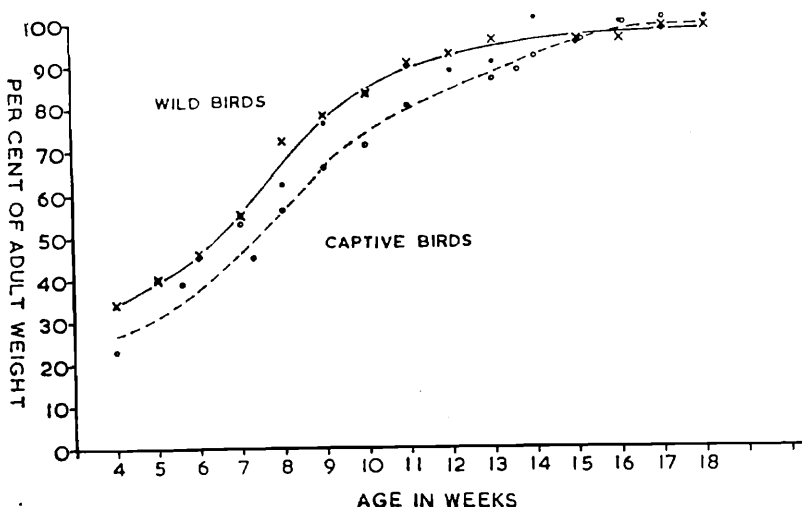
Fig. 2: *Increase in live body weight vs. age.* In wild birds x = males and
● = females. Both sexes had to be combined in the captive quail. Mean number
of observations for each point on the wild bird curve is 28 (range 2-78); for the
captive birds it is 14 (range 6-24).

became very clear in the course of the growth and moult studies in the
captive quail, and that was that birds of the same age (in fact from
the same brood) that were markedly different in weight were also
markedly different in their states of moult. In such cases quite fictitious
age differences of up to a week were common and occasionally, in a
few extreme instances, such a difference could amount to as much as
nearly three weeks. In all but one of these the large variations occurred
in "runts" dying early; and the lighter the bird of a known age the
younger it would appear to be. Thus, as the difference between the
final weights of 21 captive and 149 wild late juveniles (the age range
in each category being from 16-25 weeks) is about 30 grams, we would
perhaps expect the moult rates to be different too—slightly retarded
in the lighter and captive population. (It is interesting that no signifi-
cant difference has yet been found between the growth rates of either
wild or captive cocks or hens, nor between birds from the central North
Island and those from Central Otago in the South Island where the
weight differences between the late juveniles is about 13 grams for
males and 17 grams for females and remarkably constant from year
to year. And finally, no significant difference has so far been detected
between the growth rates of wild birds in different years, which is
not totally unexpected as the weights of the fully-grown quail are so
constant from year to year. The subject of weights is still being studied
and will be discussed fully at a later date.)

Since (a) the advance of the moult as found by retrapping wild
juveniles is very close to that expected to have occurred in the known
interval when the rate found from captive birds is used as the standard,
and (b) growth rates observed for wild birds are so nearly constant
under so many different conditions, then there appears good justification

for the following assumption: That is, whatever may be the precise relationship of the state of wing moult to age in the two types of population (wild and captive), the one may be used to assess the other without causing any serious error in the results.

Rare aberrations in the wing moult have appeared during the course of this study: captive and wild birds have been found moulting primaries Nos. IX and X after the growth of the first eight winter primaries. A captive bird has been found with *eleven* primaries and a few wild quail from one locality with an apparent full complement of *nine*. In two of the original total number of captive birds (27) a primary already grown in was either shed or pulled out and then regrown out of sequence. There is no instance of this known among wild birds. In a few juveniles and immatures—captive or wild—nearly all of the mottled primary coverts have been either shed or become faded, always the more distal. This is contrary to expectation since the coverts would be replaced from proximally outwards—as in the primaries. An alternative explanation would then be that mottling may not always occur on the most distal first winter primary coverts. Only one likely case of mottled primary coverts being retained into the second year is known in spite of the fact that many hundreds of quail trapped and banded as juveniles or immatures have been retrapped or recovered and examined in the following year. (Thompson & Kabat have also discussed irregularities in the post-juvenile moult of bobwhites.) Actual *errors* made by field operators and keepers of shooting diaries in the aging of quail by means of the primary coverts have been looked for in the return of banded birds of known age and checked by the examination of shooting bags in the field. Such errors have been found to be negligible. Co-operators found to be unreliable have been discarded. Those errors that remain are likely to be consistent from year to year and place to place and will show their effect in a slight underestimate of the proportion of young birds in the population because the shedding or fading or lack of mottling that sometimes occurs among the primary coverts as already described will result in these birds being classed as adults.

APPLICATIONS OF THE AGING TECHNIQUES

(i) The ability to separate with almost 100 per-cent accuracy birds of the year from adults by means of the presence or absence of mottled primary coverts enables us, with certain provisos, to obtain an index of population size each year. Briefly, I have found that changes in population size from year to year are clearly reflected in the changes in the proportion of young to old birds as calculated from early autumn trapping or the return of winter shooting diaries. In a publication in preparation the result of study over twelve years of population fluctuations in California quail in New Zealand (in which the use of this index plays an important part) will be discussed. (ii) By being able to age juvenile quail by means of the progress of the wing moult we are enabled to study apparent sex differences in juvenile mortality (Williams 1957), and, as we have already seen, determine growth rates. (iii) In addition, if we can be sure of taking a representative sample of the population we can determine the phenology of the hatching period and from it the phenology of the breeding season as a whole.

DATING EVENTS IN THE BREEDING SEASON

The average clutch-size for California quail in New Zealand is 13.3 eggs, the incubation time 22-23 days and the rate of laying is equal to, or very slightly less than, one egg per day. On an average then, laying begins about five weeks before the hatching date. If a representative sample of the population of young birds in an area is taken at such a time that none of the juveniles has completed its moult and hatching is complete then it should be possible to build up a picture of the events of the breeding season just passed, as has been done, for example, in Fig. 3. That such a system as this can be used for California quail is particularly fortunate, for nests are notoriously hard to find in any appreciable numbers and so the more ideal method of dating breeding season events—from actual nest records—is denied us. On the other hand, in the case of passerines or species with nidicolous young, this more direct method is the one used. Nevertheless, a method of aging juvenile birds similar to that described in this paper would be a very useful adjunct to actual observation of the fate of nests in nidicolous species; and in theory, at least, a comparison of the two methods of fixing the duration and intensity of events within the breeding season could give a measure of juvenile mortality over the first few months.

Trapping results and simple observation show that in most years young quail begin to appear in New Zealand about the end of October, though they do not become really noticeable in numbers until some weeks later. After mid-February newly-hatched chicks are uncommon in most seasons and probably owe their appearance to the renesting of pairs that had previously been unsuccessful. If the breeding season is taken to extend from the laying of the first egg to the hatching of the last then the season in New Zealand is about five months long. Trapping usually begins during the last week of February and continues throughout March. Hence, with an accurate retrospective reach of the aging method of approximately 21 weeks, the whole of the breeding season is subject to sampling; and from this sampling and aging raw hatching date frequency graphs can be prepared as in Fig. 4. A number of these have been prepared and they indicate that most hatching occurs in December and January. In most, if not all, previous studies of this kind—and in the present one as well—chicks (i.e., birds

TRAPPING

HATCHING

INCUBATION

LAYING

| 20 | 27 | 3 | 10 | 17 | 24 | 1 | 8 | 15 | 22 | 29 | 5 | 12 | 19 | 26 | 2 | 9 | 16 | 23 | 2 | 9 | 16 | 23 | 30 |

OCT   NOV   DEC   JAN   FEB   MAR
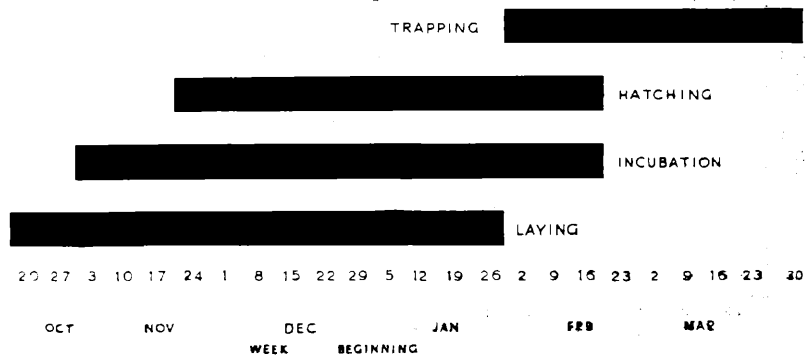
WEEK   BEGINNING

Fig. 3: *Phenology of California quail breeding season in central North Island 1956/57.*

that have not yet begun the first primary wing moult) have not been included in the population sample because no method has yet been devised for aging them directly, though doubtless this should be possible. Direct account could be taken of these chicks by first of all making sure the trap design is such that they would be efficiently caught and retained and secondly by using a feather clipping system that would permit of retraps being identified and aged retrospectively if retrapping occurred after the age of four weeks had been attained. It is, of course, impossible to leg-band chicks because of their small size.

As they stand the raw histograms are in need of correction for they take no account of the age-class 0-4 weeks nor of mortalities proportional to age, for the older the age-group sampled the longer has it been subject to the forces of mortality and the smaller must then be its surviving numbers at the time of trapping. Or, in other words, the earlier-hatched birds are not represented in the sample or the histogram in their correct proportions. Nevertheless it is the uncorrected figures that have been used in most phenological studies to date, even though mortality during the first month or two of life is considerable. This mortality after hatching is something about which more must be learned as it appears to show a fair amount of variation from year to year and place to place. Its importance is therefore obvious. A measure of its exactions has been made for the Central North Island for the year 1957 and from it corrections have been applied to the hatching date histogram for the same area and year, as can be seen in Fig. 5.

The mortality estimate was made as follows: Sight counts of complete broods were obtained during the period of hatching and afterwards and the age of the broods estimated according to the birds' behaviour, coloration and size. (see Table No. 5). Fig. 6 shows the reduction of mean brood size with increasing age during one season.
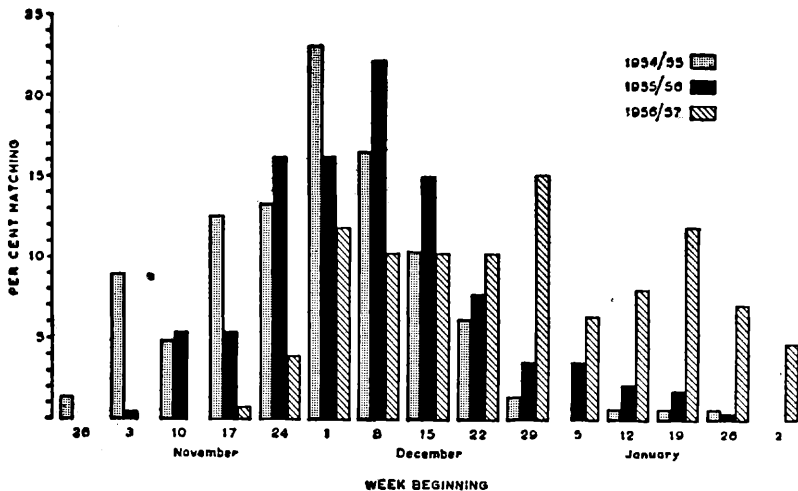

Fig. 4: *Hatching date histograms, South Island (uncorrected)*. Number of birds involved, 1954/55: 143; 1955/56: 222; 1956/57: 127.

TABLE NO. 5: Brood count observations in Fig. 6

Number of observations	Approximate age of chicks	Mean number in brood	Standard error
12	1 week	8.6	4.0
12	2-3 weeks	7.3	4.5
17	4 weeks	6.4	2.8
37	6-7 weeks	6.0	3.7
18	8-9 weeks	5.1	3.2

The resultant curve is fairly smooth and indicates an approximate mortality of 50 per cent between hatching and five weeks of age which increased to over 60 per cent at 10 weeks. (An extension of the mortality curve can be made from calculations based on shooting diary returns from reliable sportsmen who keep a tally of the various age and sex classes if it is assumed—as seems reasonable, Williams 1957—that a reliable sample of the population as a whole is obtained thereby. These calculations, expressed as the total number of young per adult female, have then to be corrected for continuing adult mortality which is regarded as occurring at a constant rate throughout. For the validity of making this last assumption see Hickey 1952 and Lack 1954. Another correction would have to be incorporated if the contribution made by shooting to the overall mortality was appreciable. This does not seem to be the case in the Central North Island where the quail population is a very large one and only lightly shot each year.) It is from the mortality rate calculated from this curve—or rather its complement,
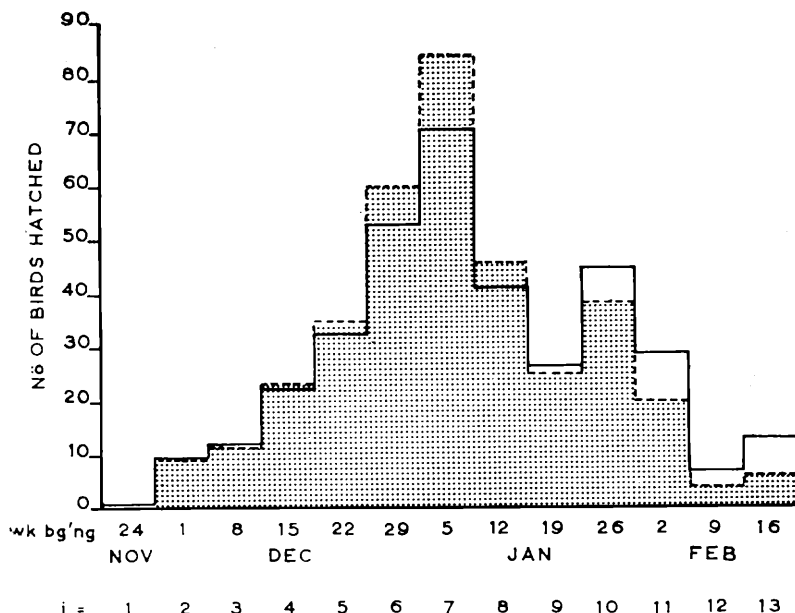

Fig. 5: *Hatching date histograms, North Island 1956/57.* Hatched area—frequencies observed (H[1]); unhatched area—estimated frequencies (h[1]) scaled to same total.

the survival rate *s*—that the corrections have been made to the hatching
date histogram constructed from the raw data. Their application does
not greatly affect the general form or apparent length of the hatching
period in this instance, though the subsidiary peak at week No. 10
(26th Jan.-1st Feb.) is strengthened and now seems significant. It can
be provisionally put down to the appearance of young birds resulting
from renesting and similar peaks at about the same time appear in the
Central Otago histogram for the same year (Fig. 4). For the statistical
treatment underlying the corrections made to the North Island histogram
the appendix should be consulted.

Corrected (or even uncorrected) histograms such as these will enable
breeding season phenologies to be compared from place to place and
year to year. There are not enough accurate figures to allow any com-
parisons to be made, at present, between different years in the Central
North Island; but by using graphs prepared from raw data comparisons
can be made between different years in Central Otago, South Island.
In Fig. 4 such graphs for the last three seasons there are shown, and
although the figures upon which the 1956-1957 histogram is based
come from only 127 juveniles sampled over a wider area and longer
period than in the two previous seasons, it is clear—as was in any case
obvious from general field observation—that the onset of the breeding
season was not only delayed by about two weeks in relation to the
earlier ones but its peak was delayed by about three weeks too. It is
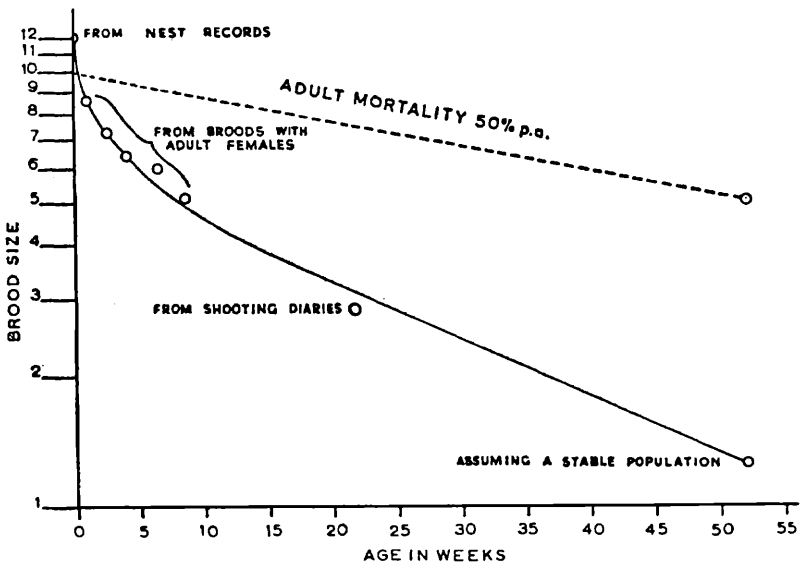doubtless significant that throughout most of New Zealand the late

Fig. 6: *Juvenile mortality (and immature mortality) from various sources, North
Island 1956/57*: Though a stable population was assumed for calculation of the
final point, in fact the population in this year almost certainly increased over
that of the year before. Hence adult and immature mortality rates would have
been about equal.

spring and early summer of this year were far wetter than usual (even heavy falls of snow occurred in parts of Otago in early December) though January, the month in which most chicks were about, had normal weather.

Comparisons such as these and those between the survival rate of young in different years will be part of the essential information needed for any comprehensive study of the population dynamics of a species. For example, once the main events of the breeding season have been fixed in time with some accuracy then we are obviously in a good position to try to correlate these events and the survival rates of young with other factors and with the annual fluctuations.

ACKNOWLEDGMENTS

SUMMARY

(i) As a preliminary to a study of fluctuations in California quail populations in various parts of New Zealand over a number of years it was necessary to be able to age juveniles so that events in the breeding and post-breeding seasons could be fixed with some accuracy. The method based upon the progress of the appearance and growth of the first winter primaries was chosen and, by using three captive broods of known age, a graph has been prepared from which birds may be aged in the field.

(ii) Among these captive birds the growth of primary I begins, on an average, about 25 days after hatching and that of primary VIII (usually the last to appear in the first year of life) ends on about the 175th day. Although captive birds can thus be aged fairly accurately between the limits 3½ weeks to 25 weeks, accurate aging *in the field* (where large numbers of birds have to be handled and only *estimates* of state of feather growth are feasible) can probably be relied upon only between the limits 4 to 21 weeks. The hatching date is given to within ±3-4 days.

(iii) The method satisfies some tests for self-consistency and it seems justifiable to apply the curves found for the rate of feather-growth for captive birds to populations of wild birds so that their age may be estimated. However, since among captive quail the progress of the moult is correlated with increase in body-weight and there are consistent differences between rates of increase in body-weight among captive and wild quail, it is reasonable to suppose that there is also a difference in moult-rate (that of wild birds being more rapid). The difference is apparently small.

(iv) No difference has so far been demonstrated between the sexes as far as the moult and growth rate of the primaries are concerned.

(v)   A few aberrations in the wing moult are described. Most of these are known only from captive birds.

(vi)   When the progress of the primary wing moult is used for aging, the state of growth of the *two* youngest feathers should be used: not just that of the youngest. Estimates of extent of growth of the feathers should be expressed as a percentage of the final length to be attained rather than as an actual measurement in millimeters.

(vii)   There is need for the development of a technique for directly aging (and trapping a representative sample of) birds less than four weeks of age. At present this can be done only indirectly by a marking and recapture method.

(viii)   From hatching date histograms it is clear that the breeding season in New Zealand lasts for about five months with the peak of hatching usually about early December. Since the mean clutch size is 13.3 eggs, the laying rate about one per day and the incubation period 22-23 days, then laying must begin about five weeks before hatching.

(ix)   Breeding season histograms constructed from raw data should be corrected for the absence of the age class 0-4 weeks and for continuing mortality among this and other age classes. One method of estimating mortality among young birds is by following the diminution in mean brood size with advancing age. Once the mortality—or survival—rate has been calculated in this way it can be applied to correct the raw histogram. An example of how this may be done is given in the body of the paper and in the appendix. Chick, juvenile or, in effect, first-year mortality should be calculated for each main area yearly for there is reason to believe that it is an important variable in the population dynamics of the species.

(x)   As in studies of a similar nature in other species, certain assumptions have to be made unless there is evidence to the contrary that they cannot apply. Among such assumptions or likelihoods are: that there is no age or sex bias in trapping, that there is constant age—specific mortality, that different techniques of sampling all give representative samples of the population as a whole and so on. None of these should be taken for granted if there is any method of putting them to the test and none of the ways of estimating adult or first-year mortality used in this paper should be regarded as a satisfactory substitute for estimations of those mortalities made from returns from an adequate and long-term banding program. Such returns have not yet been obtained for California quail in New Zealand.

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APPENDIX

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Method of Correcting the Hatching-Date Histogram, Fig. 5

Table No. 6 is a two-way classification of the 363 juveniles trapped in the Central North Island in 1957. The breeding season is divided into weeks, the first week beginning on 24 November 1956 (the earliest estimated hatching date.) Then $n(i,j)$ denotes the number of juveniles trapped in the j'th week which are estimated to have hatched in the i'th week. The histogram in **Fig. 5** represents the marginal frequencies $H(i) = Sn(i,j)$ over j, the number of *trapped* juveniles estimated to have hatched in the i'th week.

But the relative frequencies $h(i)$ with which birds actually hatched in the wild population during these weeks must be rather different, since the sampling procedure allowed juveniles which hatched late in the season, or were ageable during weeks in which trapping was particularly intensive, to have undue influence on their marginal classes $H(i)$. The estimated values of these true frequencies $h(i)$ scaled to the same total of 363, are shown in Fig. 5 and Table No. 7.

To make this correction to the marginal frequencies $H(i)$ for mortality and for uneven trapping, it is supposed that the observed frequencies $n(i,j)$ are distributed as independent Poisson variates with respective means $h(i).ks^{j-i-4}.t(j)$ in the range i = 1 to 13, j = 11 to 20, subject to j-i = 4 to 21, with the notation:

$h(i)$ = actual number of birds hatched during the i'th week, on an indeterminate scale
k = probability of a chick surviving from hatching to 4 weeks of age
s = average probability of a juvenile surviving from one week to the next, from ages 4 to 21 weeks
$t(j)$ = probability of a juvenile alive in the j'th week being trapped in that week
$T(j)$ = $Sn(i,j)$ over i = number of juveniles trapped in the j'th week.

The Maximum Likelihood equations for the $h(i)$ and $t(j)$ are
$h(i) = H(i)/S[t(j)ks^{j-i-4}]$, summing over j
$t(j) = T(j)/S[h(i)ks^{j-i-4}]$, summing over i

with $Sh(i) = SH(i) = 363$ as a suitable constraint. Summation is within the range specified above. For values h_1 to h_7 the full range j = 11 to 20 is appropriate, and the solutions have the simple form $h(i) = c.H(i)s^i$ (c a constant,) representing a correction for mortality alone; but to obtain h_8 to h_{13} it is necessary to solve the M.L. equations by iteration, starting with $h(i) = H(i)$ and disregarding k.

The juvenile weekly survival factor s may be estimated from independent data.

Table No. 6 Classification of 363 juvenile C. quail trapped
in the Central North Island in 1957.

Trapping week (j)

		11	12	13	14	15	16	17	18	19	20	H(i)	h(i)
	1						1					1	1.1
	2	8	1									9	9.7
	3	6	3	1					1	1		12	12.3
	4	2	6	5			4			1	5	23	22.5
	5	7	5	4	10	2	1	1	2	1	2	35	32.5
Estimated	6	2	18	9	15	11		2	2	1		60	52.9
Hatching	7		15	11	15	4	17	7	8	2	5	84	70.4
Week (i)	8	—	2	1	5	5	6	10	5	10	2	46	41.2
	9	—	—		4	6		2	6	7		25	26.7
	10	—	—	—		10	6	2	2	18		38	45.0
	11	—	—	—	—	5	3	4	7	1		20	28.7
	12	—	—	—	—	—		4				4	7.0
	13	—	—	—	—	—	—		2	3	1	6	13.0
T(j)		25	50	31	49	43	38	32	36	49	10	363	

Table No. 7 Regression values N(i,j) corresponding to Table No. 6

	11	12	13	14	15	16	17	18	19	20
1	.1	.2	.1	.1	.1	.1	.1	.1	.1	.0
2	1.0	1.6	.9	1.2	.9	.8	.6	.7	1.0	.2
3	1.3	2.2	1.2	1.6	1.2	1.1	.9	1.0	1.3	.3
4	2.6	4.2	2.3	3.0	2.4	2.0	1.6	1.8	2.5	.5
5	4.0	6.3	3.5	4.6	3.6	3.1	2.5	2.8	3.8	.8
6	6.7	10.9	6.0	7.8	6.2	5.3	4.3	4.8	6.5	1.3
7	9.4	15.2	8.3	11.0	8.7	7.5	6.0	6.7	9.2	1.9
8	—	9.4	5.1	6.8	5.3	4.6	3.7	4.1	5.6	1.2
9	—	—	3.5	4.6	3.6	3.1	2.5	2.8	3.9	.8
10	—	—	—	8.2	6.4	5.6	4.5	5.0	6.8	1.4
11	—	—	—	—	4.3	3.7	3.0	3.4	4.6	.9
12	—	—	—	—	—	1.0	.8	.9	1.2	.2
13	—	—	—	—	—	—	1.5	1.7	2.3	.5

Fig. 6 shows the decline in mean brood size with advancing age. Nest records from throughout New Zealand over a number of years indicate that the average number of chicks hatched from the mean clutch of 13.3 eggs is 12. (Ideally a mean hatching figure for the Central North Island for the 1956/57 breeding season is required, but there are insufficient records to give this. In any case clutch size and hatchability among game birds are properties of the population not likely to vary *greatly* within New Zealand from year to year, and see, for example, Middleton 1935—*G. R. W.*) The sighting of apparently complete broods with a female provides the data for five more points. The age classes, based on recognisable physical characteristics, are given in Table No. 5.

A seventh point may be obtained from the ratio of juveniles to adult females (308.82 = 3.76:1) given in reliable shooting diaries from the same area, the season extending in 1957 from early May to mid-July. From the mode hatching week (i= 7) to the middle of the shooting season (the 28th week in this sequence) is 21 weeks. At present it appears (from calculations based on juvenile/adult ratios from shooting diaries in eight consecutive years—*G. R. W.*) that annual adult mortality is about 50%, being hardly affected by shooting, and we may therefore suppose that 75% of breeding females survived to the mid-shooting season. The average brood survival at 21 weeks is thus the juvenile/adult-female ratio multiplied by 75%: 3.76 x 0.75 = 2.82 out of the original 12. (The assumption must be made at present that all adult females in the shooters' diaries had succeeded in raising broods in the 1956/57 breeding season.)

Available evidence suggests that the adult population in the Central North Island has varied little over the last four seasons, and the proportion of females among adults shot has been generally close to 40% (Williams *unpubl.* and 1957). To replace adult losses for the next hatching season an average of 1.25 birds per brood must survive a full year, if all adult females are assumed to breed. From a smoothed curve through these eight points, the value of s (the average weekly survival factor from 4 to 21 weeks of age) is estimated to be about 0.95.

The information matrix is easily computable, but too large to be inverted, and there appears to be no satisfactory means of approximating the variances of the h(i). However, since the terms H(i) are independent Poisson variates, the form of the solutions for h_1 to h_7 suggests that the variance of each h(i) is probably approximately equal to the parameter itself. The secondary peak at h_{10} therefore appears to be significant.

While these estimated parameters h(i) may be expected to give a truer picture of the hatching season than the uncorrected H(i), a chi-square value of 176 for 32 degrees of freedom (after suitable grouping of low-frequency rows and columns) shows that there is still need for a more refined model than the present one. When a suitable model is chosen, proper design of the trapping programme can of course considerably lighten the computation.

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