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MORTALITY RATES IN TWO POPULATIONS OF CALIFORNIA QUAIL IN CENTRAL OTAGO, NEW ZEALAND

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Two populations of California quail (*Lophortyx californicus* (Shaw))—one subject to fairly heavy shooting pressure, the other protected—were studied over a number of years to determine the effect of hunting on mortality rates. Both populations were situated in similar habitats in Central Otago. The shot population was at Poison Creek near Queensberry, the protected population at Cairnmuir near Cromwell, about 20 miles away.

Access to both was under some control: shooting at Poison Creek was by permission only and on condition that a full record was kept of the day's bag and all bands returned to the landowner. There is no reason to believe that unauthorized hunting was appreciable or that bands were not returned. Access to the birds at Cairnmuir was under close surveillance and although 29 out of 990 banded in approximately 11 years were recovered by shooting, clearly most, if not all, of these had emigrated from the area occupied by the covey beforehand.

Mortality rates at Poison Creek were calculated in three ways: (i) from bands recovered from shot birds, using these to construct a composite dynamic life table as explained by Hickey (1952); (ii) from capture-recapture data, using a stochastic model devised by Jolly (i.e. 1965); and (iii) from capture-recapture data, using known survivors to construct a composite dynamic life table (Raitt & Genelly 1964).

Mortality rates at Cairnmuir were determined by using only two methods—(ii) and (iii) above. The few bands returned from birds killed in ways other than by shooting were insufficient in numbers for any useful analysis.

In any studies involving the capture and marking of animals and the taking of subsequent samples three conditions should be proved: (i) the method of capture yields a random sample, (ii) subsequent samples are also random, and (iii) between the first capture and marking and any subsequent recapture marked animals have dispersed randomly among unmarked.

These three conditions are notoriously difficult to prove and many elegant statistical methods have been devised to detect sampling bias. One problem is particularly intractable —that of detecting bias in an animal's first encounter with a trap. I have tried to approach the problem of sampling bias indirectly: I shall show in another paper that frequency of recapture among adult quail follows a Poisson distribution and is therefore random. If trapping does not affect an animal's subsequent behaviour towards a trap there will probably be no bias on the first encounter. Some supporting evidence, admittedly crude, is afforded by the fact that adult sex ratios, whether calculated from first trappings or from shooting data, are not significantly different from each other. Two independent methods of sampling are unlikely to be equally biased. Trapping, then, probably always yields a random sample among adult quail.

Analysis of recapture data for young quail indicates that they are caught for the second time rather more frequently than would occur by chance. But though the recapture of young may be biased, indirect evidence similar to that above suggests unbiased behaviour on first encounter with a trap: sex ratios of immatures at first capture are not significantly different from those obtained by shooting.

I have no evidence that banded quail become randomly dispersed among marked birds but observation does not suggest any segregation. Comparisons between the different methods of calculating mortality rates—or their equivalents—have been confined to two classes, all males and all females, regardless of age. The other combination, all adults and all immatures, permits only a more limited treatment since immature quail become adult at the end of their first year and so recoveries or recaptures beyond the first twelve months of life refer to adults. To give a life table for animals banded as immatures and to calculate mortalities from it as though the animals were immature throughout their lives is both unrealistic and misleading, but is sometimes done.

Where relevant, mortality rates calculated for each of the four age and sex classes (adult or immature males and females) will be mentioned. Details for these calculations will appear elsewhere.

THE HUNTED POPULATION

(1) *Mortality calculated from Jolly's stochastic model.*

Jolly's method has some advantages over most deterministic methods: (a) there is no need for intervals between trapping periods to be equal, or (b) for trapping effort to be equal on each occasion; and (c) there are no implications that the environment has been constant from one trapping period to the next, or (d) that survival rates are constant between one trapping period and the next. However, there is the usual assumption that trapping samples are random. This appears so for adult quail, but may not be strictly true for immatures.

To calculate probabilities of survival (and therefore mortality) between trapping periods we need to know only the following and the rest is simple arithmetic:

(a) The total number of animals caught, n_1, in trapping period *1*.

(b) The number of marked animals in the sample, m_1.

(c) The number of animals released after trapping, s_1.

(d) The number of animals marked in previous periods, not caught in period *1* but caught subsequently, Z_1.

(e) The number of animals released in period *1* and caught subsequently, R_1.

TABLE 1. *Mortality calculated from stochastic model: all males, Poison Creek.*

Trapping period I	Marked birds caught m_i	Total no. caught n_i	No. released s_i	No. previously marked, not caught period I but later Z_i	No. released in period I and caught later R_i	No. marked in the population M_i	$M_i - m_i + s_i$	Probability of survival from period I to $I+1$
Mar. '54	0	43	43	0	20	0	43.00	0.8079
Aug. '54	12	54	54	8	19	34.74	76.74	1.5924
Mar '55	13	78	78	14	10	122.20	187.20	0.0899
Aug. '55	1	5	5	19	6	16.83	20.83	4.2909
Mar. '56	19	183	183	5	13	89.38	253.38	0.7235
Mar. '57	10	65	65	8	3	183.33	238.33	0.2518
Mar. '58	4	56	56	7	7	60.00	112.00	0.1647
Mar. '59	13	61	60	1	11	18.45	65.45	0.2941
Mar. '60	11	132	132	1	16	19.25	140.25	0.2581
Aug. '60	9	18	17	8	5	36.20	44.20	1.1186
Mar. '61	9	91	91	4	9	49.44	131.44	0.4127
Aug. '61	2	19	19	11	4	54.25	71.25	0.3844
Mar. '62	12	120	118	3	23	27.39	133.39	0.6282
Aug. '62	9	24	22	17	5	83.80	96.80	0.4511
Mar. '63	17	130	128	5	24	43.67	154.67	0.8625
Aug. '63	11	34	34	18	5	133.40	156.40	—
Mar. '64	23	90	90	–	–	—	—	—

NOTES.
1. No. of marked birds in the population (M_i) is obtained from the expression $(s_iZ_i/R_i) + m_i$.
2. Probability of survival from period I to $I+1$ is obtained from the expression $(M_i+1)/(M_i - m_i + s_i)$.
3. Mean probability of mortality March to March, 0.68 (see text).
4. M=Maximum likelihood estimate of the number of marked animals in the population.

The relevant calculations and results for all males are shown in Table 1. In calculating probability of dying (1−probability of survival) in the March to March intervals I have not used the few periods where $P_{survival} > 1$. The mean figure of 0.68 was therefore obtained from periods 5-6, 6-7, 7-8, 11-13 and 13-15. Death and emigration from the area are not distinguishable. The mean probability of death for all females from March to March was 0.70.

Jolly's model also makes it possible to estimate population size but this will not be considered here.

(2) *Mortality rates calculated from bands recovered by shooting.*

Hickey (1952), Farner (1955), Balham and Miers (1959) and Frith (1963) have discussed the terminology and the major assumptions made in using band returns to estimate mortality rates. Once again, death and emigration are inseparable.

For quail, the banding period lasts about three weeks, sometime between mid-February and the end of March. Hence the birds have at least 8 weeks to settle down and disperse before hunting begins.

TABLE 2. *Mortality of all male California quail banded and shot at Poison Creek, 1954 to 1964 inclusive.*

Year banded	Number banded	Recoveries in years following banding 0–1	1–2	2–3	3–4	Total shot
1954	43	8	4	0	1	13
1955	66	17	2	1		20
1956	164	39	13	3		55
1957	58	11	3	0		14
1958	61	12	0	3		15
1959	51	4	7	0		11
1960	124	26	7	1		34
1961	82	11	3	3		17
1962	111	25	13	1		39
1963	116	14	7			21
1964	67	12				12
Totals	943	179	59	12	1	251

% bands recovered in each succeeding year following banding

$$\frac{179}{943} \quad \frac{59}{943-67} \quad \frac{12}{876-116} \quad \frac{1}{760-111}$$

$$18.99 \quad 6.74 \quad 1.58 \quad 0.15 = 27.46$$

Mortality rate for each recovery interval

$$\frac{18.99}{27.46} \quad \frac{6.74}{27.46-18.99} \quad \frac{1.58}{27.46-18.99-6.74} \quad \text{etc.}$$

$$= 69.2 \quad = 79.6 \quad = 91.4$$

Weighted mean = 72.6

$$\text{Expectation of further life} = \frac{2-m}{2m} \quad \frac{2-0.726}{1.452} = 0.88 \text{ year.}$$

NOTE. The difference in the number banded in certain years in this table and for the same years in Table 3 results from the inclusion of birds banded in August in the capture-recapture data. Such birds cannot be included in the analysis of shot birds.

Table 2 shows the results for all males. I have used Bellrose and Chase's (1950) method of calculating mortality rates. Farner's (1955) method of obtaining a weighted mean mortality rate has been used in the composite dynamic analyses. The mortality rate for the 0-1 recovery interval is the same as the weighted mean for a time specific analysis of the same data.

For all females the mean annual mortality rate is 67.5% and expectation of further life, 0.98 year. The mean rates for the various age and sex classes are: adult males 68.1%, adult females 68.2%, immature males 74.2%, immature females 66.8%. The mortality rates for immature birds are not those for chronological age 0-1, but those for recovery interval 0-1 when the birds are 0.5 to 1.5 years old. This is because sampling by shooting does not begin until June when the birds are about six months old, and immature mortality rates are approximately those of adults.

(3) *Mortality rates from capture-recapture data using known survivors (deterministic method).*

Raitt and Genelly (1964) calculated mortality rates by following the decline in succeeding cohorts in a population of California quail subjected to regular trapping. The number of survivors at each trapping period was taken to be the birds recaptured then, plus any which escaped recapture at that time but were recaptured later. Then, for any cohort, if A was the number banded in the first trapping period and B, C, D, E . . . were the numbers of known survivors in succeeding years, the mean percentage survival rate for the cohort was . . .

$$\frac{B + C + D + E + F \ldots . + N}{A + B + C + D \ldots . + M} \times 100;$$

and of course, percentage mortality rate = 100 − survival rate.

Since immatures are such only for their first year of life, their percentage survival rate was calculated as $\frac{100B}{A}$ for each cohort. The rest of the "immature" cohort was thereafter used as additional data for calculating adult survival. Figures from succeeding cohorts were summed to yield a composite dynamic life table and mean rates calculated from it.

Raitt and Genelly assumed that the trapping effort resulted in a relatively constant ratio of sample size to population size and that emigration equalled immigration. Though not explicitly stated they obviously took all the other usual assumptions for granted as well.

Their data may be more expeditiously handled in a way similar to the shooting recoveries in Table 2 above. Corrections are thus made for survival series necessarily incomplete because of insufficient lapse of time since banding. Immature mortality rate is calculated as before, i.e. from recoveries made in the 0-1 year interval.

My recalculations of their results give mean annual mortalities of 71.6% for all birds, 69.9% for adults and 72.3% for immatures. The age of their immatures was apparently two months when banded.

TABLE 3. *Known survivors from capture-recapture data of all male California quail banded at Poison Creek, 1954 to 1963 inclusive.*

Year banded	N	Recoveries in years following banding 0–1	1–2	2–3	3–4	4–5	5–6
1954	85	27	16	5	2	1	0
1955	69	8	1	1	1	0	
1956	164	12	5	3	1	0	
1957	55	3	2	1	0	0	
1958	52	7	2	0	0	0	
1959	48	8	0	0	0	0	
1960	130	13	5	0	0		
1961	99	10	3	1			
1962	123	19	4				
1963	136	18					
Totals	961	125	38	11	4	1	0
% Known survivors in each succeeding year class		125/961	38/825	11/702	4/603	1/473	
		13.00	4.61	1.57	0.66	0.21	= 20.05
Mortality rate for each recovery interval, %		64.8	65.4	64.3	75.9		

Mean = 65.6
E_x = 1.04 year

Table 3 embodies the data for all Poison Creek males, giving 65.6% mean annual mortality. For all females mortality is 77.1%, for adult males 67.7%, adult females 71.9%, and for the immatures 63.3% and 82.7% for males and females respectively.

(An even more rapid, and perhaps more valid, method of calculating mortalities from the capture-recapture data is by using the actual number of birds recaptured in each trapping period without allowing for birds known to be alive then but not caught until later. One is then making the reasonable assumption that the chance of retrapping members of any particular age group in any given trapping period is directly proportional to their numerical representation in the population. Calculations based on this method slightly reduce estimates of mean annual percentage mortality rates, e.g. that of adult males at Cairnmuir from 46.9 to 43.8. However, for comparison I have retained Raitt and Genelly's method.)

THE PROTECTED POPULATION

(1) *Mortality calculated from the stochastic model.*

Table 4 gives the data for all males for the period October 1953 to October 1964. As with the Poison Creek material I have not used the few values for P $_{survival} > 1$ for calculating the March to March probabilities of mortality. The mean estimates are 0.55 for all males and 0.67 for all females. (August to August mortalities for both populations yield means of 0.51 for males and 0.63 for females from Cairnmuir, and 0.66 and 0.69 respectively for the Poison Creek males and females.)

(2) *Mortality rates from capture-recapture data using the deterministic method.*

Table 5 shows the capture-recapture data for all known survivors among males. The period covered is 1958 to 1964 inclusive because there were no regular February-March trapping periods before 1958. Mean annual mortality rates are 45.4% for all males, 61.5% for all females, 46.8% for adult males, 54.3% for adult females, 51.1% for immature males and 75.4% for immature females.

TABLE 4. *Mortality calculated from stochastic model: all males, Cairnmuir.*

Trapping period *1*	Marked birds caught m_1	Total no. caught n_1	No. released s_1	No. previously marked not caught in period *1* but caught later Z_1	No. released in period *1* and caught later R_1	No. marked in the population M_1	$M_1 - m_1 + s_1$	Probability of survival from period *1* to *1* +1
Nov. '53	0	55	53	0	28	0	55	0.7291
Feb. '54	10	35	35	18	22	38.64	63.64	0.9351
Apl./May '54	27	40	40	13	16	59.50	72.50	0.8855
Sept./Oct. '54	13	18	16	16	5	64.20	67.20	0.5179
May '55	12	39	38	9	15	34.80	60.80	1.1485
Aug. '55	13	31	31	11	6	69.83	87.83	0.5059
July '56	13	55	55	4	7	44.43	86.43	0.1774
Mar. '58	8	45	44	3	18	15.33	51.33	0.6602
Mar. '59	14	55	54	7	19	33.89	73.89	0.5059
Mar. '60	13	48	45	13	24	37.38	69.38	0.7754
Aug. '60	23	45	44	14	20	53.80	74.80	0.5564
Feb. '61	23	46	44	11	26	41.62	62.62	1.0060
Aug. '61	22	41	41	15	15	63.00	82.00	0.7302
Feb. '62	10	45	42	19	16	59.88	91.88	0.7686
Aug. '62	20	47	47	14	13	70.62	97.62	0.3232
Mar. '63	22	76	74	4	31	31.55	83.55	0.7245
Aug. '63	28	62	61	12	21	62.86	95.86	0.5725
Mar. '64	23	52	51	10	16	54.88	82.88	0.5792
May '64	27	39	39	7	13	48.00	60.00	—
Aug. '64	17	19	18	3	0	—	—	—
Oct. '64	3	4	4	–				

NOTE. Mean probability of mortality March to March, 0.55 (see text).

TABLE 5. *Known survivors from capture-recapture data of all male California quail banded at Cairnmuir, 1958 to 1963 inclusive.*

Year banded	No. banded	Surviving in years following banding 0–1	1–2	2–3	3–4	4–5	5–6
1958	36	15	10	5	4	2	1
1959	41	12	8	4	1	1	–
1960	54	19	7	5	1	–	
1961	42	14	9	3	–		
1962	60	10	5	–			
1963	87	22	–				
Totals	320	92	39	17	6	3	1
% known survivors in each succeeding year class		92/320	39/233	17/173	6/131	3/77	1/36
		28.75	16.74	9.83	4.58	3.90	2.78
Total %=66.58							
Mortality rates		43.2	44.3	46.6	40.7	58.7	
Mean = 45.4%							
E_x = 1.72 years.							

DISCUSSION

At Poison Creek approximately one-third of all birds banded are eventually shot. This estimate is arrived at as follows. Some 1087 quail had been banded up to the end of 1960 and, of these, 325 (29.9%) had been returned by sportsmen up to the end of the 1964 shooting season. It is unlikely that any more of the 1954-60 bands will now be recovered and sent in. In addition, according to the shooting diaries, about 12% of birds shot down are not retrieved. Counting these as deaths (an overestimate), about 364 banded birds have been accounted for. An allowance has next to be made for bands recovered by sportsmen but not returned; 5% for Poison Creek is probably another overestimate. Thus, up to about 382 quail have been shot of the 1087 banded to the end of 1960; that is, in round numbers, probably less than 35%. Since there is no reason to suppose that banded birds are any more or any less likely to be shot than unbanded, the estimate of about one-third applies to the Poison Creek population as a whole.

At Cairnmuir shooting mortality is negligible; there is no reason to think that any of the 3% of quail from this population recovered by shooting have been other than emigrants.

A fairly satisfactory measure of agreement exists between the returns of the various methods of calculating mortality rates for each of the two populations (Table 6). The differences between Cairnmuir and Poison Creek are therefore probably real and presumably reflect the effect of shooting in the one district and its absence in the other. Accordingly, mortality rates at Poison Creek are higher for all age and sex groups than are those at Cairnmuir.

TABLE 6. *Mortality estimates for Cairnmuir and Poison Creek.*

		Cairnmuir	Poison Creek
Stochastic	All males	0.55	0.68
	All females	0.67	0.70
Capture-recapture (deterministic)	All males	44.7	64.8
	All females	61.1	77.6
	Adult males	46.2	65.9
	Adult females	54.5	76.2
	Imm. males	79.5	91.8
	Imm. females	69.8	86.6
Shooting	All males	—	74.0
	All females	—	70.8
	Adult males	—	68.8
	Adult females	—	70.2
	Imm. males	—	74.4
	Imm. females	—	72.2

In spite of the clear differences there is no independent evidence that the Poison Creek population is consistently declining or the one at Cairnmuir consistently increasing. If the populations are not changing and the mortality differences are maintained, then the higher mortality at Poison Creek must be compensated for in some way. Evidence is lacking on potential adjustments to clutch size, fertility or hatching success; but at the time of the March trapping there was a higher mean proportion of young at Poison Creek than at Cairnmuir (see Table 7). This suggests a better survival of young to this time at Poison Creek, but the difference between the two means is not significant, $t_{10} = 1.14$.

TABLE 7. *Age ratios at trapping in March.*

	% Young 1954	1960	1961	1962	1963	1964	M
Cairnmuir	15.9	42.5	30.7	66.3	61.7	44.8	43.7
N =	63	87	88	83	133	105	
Poison Creek	44.3	62.6	51.0	54.2	68.2	42.0	53.7
N =	79	235	147	212	223	169	

It is interesting to compare mortality rates in New Zealand with those in California. Hickey (1955) recalculated the mean annual mortality rate from Richardson's (1941) shooting recoveries over a number of years and obtained a value of 72%, confirmed by Sumner

(1935) in a study lasting one year. Raitt and Genelly's population not subject to shooting had a mean mortality rate of 72% over six years. All these are close to the Poison Creek results of 70% for all shot birds banded in March, 70% for all shot birds banded in August (not discussed here because there were only 32 recoveries), 71% for all Poison Creek birds by the deterministic capture-recapture and 0.66 by the stochastic method.

The Cairnmuir mean mortality rate for all birds by the deterministic capture-recapture method is 50% and by the stochastic method 0.54.

No American data appear to have been published on sex specific mortality rates in California quail.

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