

DEMOGRAPHY AND BEHAVIORAL ECOLOGY OF CALIFORNIA QUAIL ON VANCOUVER ISLAND

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A fundamental problem in ecology is to find the reasons for the relative stability of animal numbers. Given that the intrinsic rate of increase (r_m) is positive in all species, why over long periods of time is the net rate of increase (r) usually zero? One important stabilizing mechanism in some populations of birds is the phenomenon of inversivity (Errington 1945); that is, the rate of summer gain is inversely proportional to the spring density of adults. Inversivity appears to be a function of survival of the young between years rather than due to annual changes in fecundity (Hickey 1955).

We studied the demography and behavior of California Quail (*Lophortyx californicus* Shaw) on southern Vancouver Island from 1969 to 1972. The purposes of the study were (1) to describe the demographic parameters of the population; (2) to determine if inversivity occurred; and (3) to determine, if possible, the underlying mechanisms that could cause changes in survivorship between years.

The specific null hypothesis that we tried to refute was that there was no intrinsic difference in the behavior of adults between annual cohorts that might relate to chick survival. This hypothesis was suggested by some recent studies of tetraonids which showed that the intrinsic quality and behavior of adults varied between cohorts and/or in space, and was correlated with survival (Jenkins et al. 1963, Watson 1965, Bergerud 1970, Theberge 1971, Mossop 1971). Other workers who have documented the occurrence of inversivity in the Phasianidae have either not discussed possible underlying factors (Bennitt 1951, McMillan 1964), or have postulated that inversivity results from phenotypic social stress between pairs in spring (Kabat and Thompson 1963). No one yet has investigated the possibility that the quality (environmentally induced or genetic) of adults might vary between annual cohorts antecedent to spring pairing and be a common factor both in changes in density and the intrinsic viability of the young.

There are two general hypotheses of population regulation that involve social behavior. Christian and Davis (1964) have postulated that at high density social stress causes endocrine changes which affect survival and reproduction. Chitty (1960, 1967) has proposed a genetic-behavioral mechanism in which selection occurs for aggressive individuals at high density, resulting in reduced recruitment and a decline in numbers.

The California Quail appears to be a good species for such a study since it is noncyclic, nonmigratory and has a rate of turnover of about 70–80% annually (Sumner 1935, Emlen 1940, Raitt and Genelly 1964). In addition, quail can be trapped and are sedentary, which facilitates censusing. Conversely, a disadvantage is that quail are socially tolerant. Coveys with 30 birds are common. The birds are least tolerant in the spring when they form pairs. Thus the spring period may be important if regulation is accomplished through social behavior. We investigated the aggressive behavior of adult males in spring and of chicks in early summer. Only the latter, assuming negligible maternal influence, could discriminate between intrinsic and environmental aspects of behavior, as any differences in behavior between coveys would probably result from genetic differences.

STUDY AREA AND METHODS

STUDY AREA

The present study was carried out largely at Metchosin, about 15 miles SW of Victoria on the southern tip of Vancouver Island, British Columbia (fig. 1).

The Metchosin study area is in a farming district. The topography is gently undulating, with the average altitude less than 30 m above sea level. On these farms there is an abundance of blackberry bushes, wild roses, and other shrubbery which provides food and cover for quail (fig. 2).

The climate on the southern end of Vancouver Island is characterized as Cool Summer Mediterranean (Chapman 1952), with about 71 cm of rain annually. Generally, temperatures are moderate, with a mean annual temperature of 50°F.

The vegetation on the southern end of Vancouver Island is in a dry subzone of the Coastal Douglas Fir zone. The dominant tree species are Garry oak (*Quercus garriana*) and Douglas fir (*Pseudotsuga menziesii*). This zone is part of the Pacific Coast

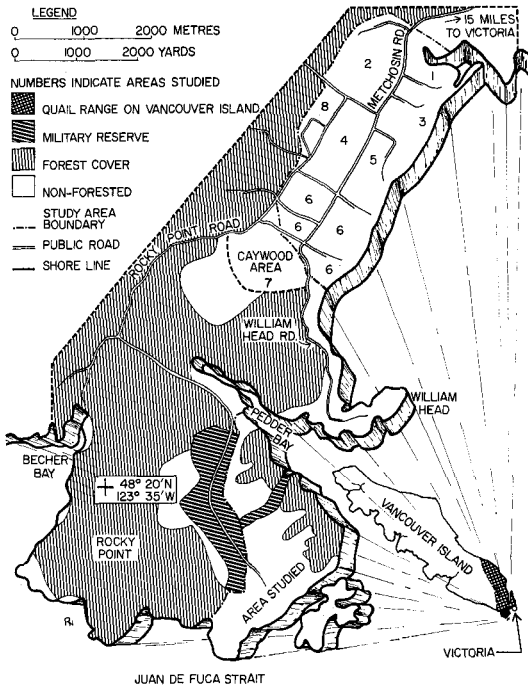


FIGURE 1. The study area, showing its position on Vancouver Island (the black spot on the southern tip) and some of the surrounding forested area. The Metchosin study area is the area containing numbers northeast of Caywood area. The numbers refer to subsections of the study area for censusing purposes.

Mesothermal Forest Region (Krajina 1965). Besides oak and fir, there are scattered patches of arbutus (*Arbutus menziesii*). Douglas fir is the dominant species a few miles north of Victoria, while Western hemlock (*Tsuga heterophylla*) is dominant on the west coast of the island. Thus the area favorable to quail is quite limited and the distribution of the quail coincides almost exactly with this xeric subzone. Only isolated groups of quail occur in favorable habitats north of this dry subzone. The numbers and persistence of quail in the area suggest that the habitat is favorable, although local extinctions have taken place on some of the Gulf Islands nearby following years with persistent snow and cold weather.

California Quail were first introduced to Vancouver Island in the 1860s (Carl and Guiguet 1957). The largest population of quail presently exists in the vicinity of Victoria. However, a few quail persist in favorable habitats approximately 161 km NW of Victoria.

DEMOGRAPHIC METHODS

Complete censuses were obtained each autumn from 1969 to 1972. A house-to-house canvass was made to determine if quail were present on each farm and a complete count was attempted of each covey located. The canvass probably missed some isolated groups, hence an intensive effort was made to find coveys in the few large uninhabited areas.

Each September (1969 to 1972) the age and sex composition of much of the population was determined by direct observation. Not all coveys could be examined, however, and the data from the study area were augmented by sex and age ratios taken

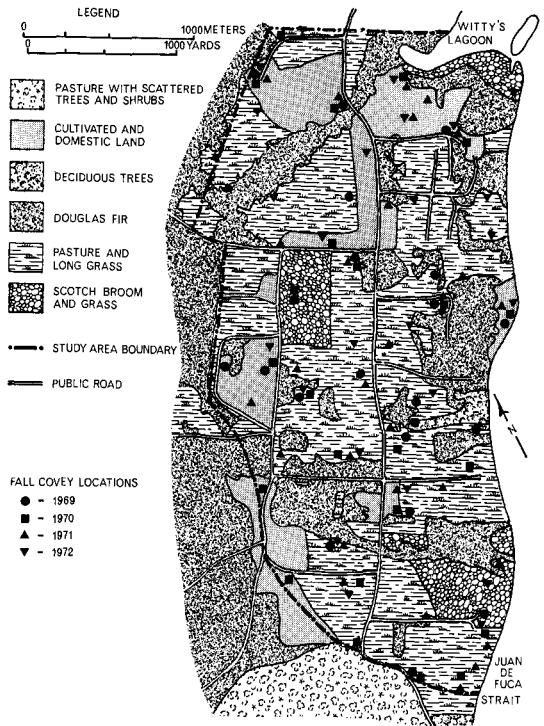


FIGURE 2. The Metchosin study area showing vegetation cover and land use. The locations of all coveys found during the fall censuses are shown.

from the Greater Victoria area. It is likely that the ratios from these two areas were similar, since the two areas are only 24 km apart.

During the winters of 1968-69, 1969-70, and 1970-71, weekly counts were made of some coveys. These counts were used to estimate the sequence and extent of mortality.

Wild chicks (less than 7 days old) were captured in 1970 and 1971 and hand reared. Also in 1970, eggs were collected and hatched in a small incubator. Feather and wing lengths and body weights were recorded from these captive chicks in both years. One brood hatched in captivity was measured daily to obtain an accurate set of growth curves. In 1970 and 1971, wild chicks were captured and aged on the basis of the growth curves from the captive birds in order to establish hatching curves. When broods were encountered but no chicks captured, the age of the brood was estimated based on a rough estimate comparison of characteristics with those of hand-reared chicks.

BEHAVIOR METHODS

In April of 1970, 1971, and 1972, we placed wild-caught males together to compare aggressiveness of yearlings (8-12 months old) vs. adults (over 19 months old). Two cocks and a hen were placed together in a cage (18 in x 18 in x 24 in) and it was noted which cock established dominance. In every pairing, the accompanying hen came from a different covey than either of the two cocks. Each trial consisted of a 15-min period during which the number of agonistic acts of each cock was recorded, the cock with the greater total of aggressive acts being the winner. Only if the scores of the two cocks were considerably different did we decide on a winner.

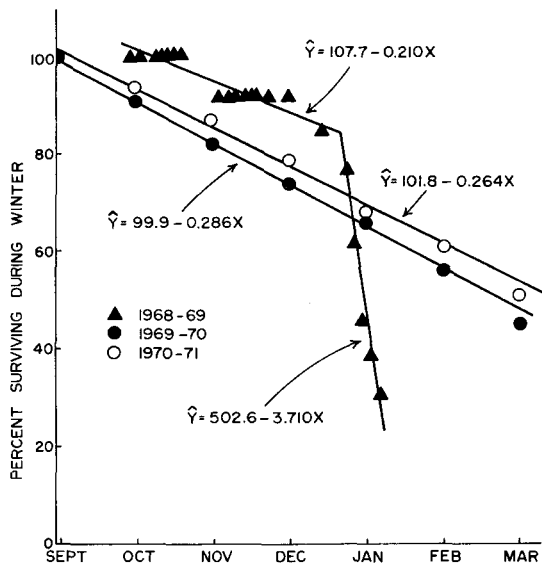


FIGURE 3. Winter mortality for the years 1968-69 to 1970-71. The lines are regression lines. The winter 1968-69 has two lines due to much higher mortality during January than for the rest of the year.

The agonistic criteria recorded to decide on the winner between males were:

1. Pecks—One bird would peck the other or pull at a feather.
2. Rushes—One bird would suddenly run toward the other. This usually ended either in a peck or by the aggressor stopping short.
3. Frontal Display—A stance in which the chest is pushed forward and the head held high and slightly forward. This is sometimes accompanied by the sneeze call (Williams 1969). The wings are held pressed tightly to the body.
4. Jump upwards—Helped by a flap of the wings; often ends with a peck.
5. Intention movement—The start only of a rush or peck.

The matched pairs of cocks were of similar weight and were usually from different coveys, one member of each pair being adult and the other a yearling. No bird had more than two paired encounters during one day.

In 1970, the only quail tested were those caught during the spring of 1970. In 1971, in addition to wild birds captured that spring, several hand-reared quail were tested which had been captured as chicks the previous summer. This latter group permitted a comparison in aggression of the same birds both as chicks and as adults (see following).

Aggressive behavior of captive chicks. Chicks were captured in June and held in cages 2 ft × 2 ft × 1 ft. Most of the chicks were about one day old when captured, thus minimizing maternal influence on behavior. Each cage contained the chicks from one brood. Each day a 5 × 7 in mirror was put into each cage and the total pecks at it by the brood were noted during a 5-min period. The tests continued until the chicks were 5 or 6 weeks old.

During the summers of 1970 and 1971, behavioral observations were recorded on free-ranging quail in the study area. Six behavioral attributes were recorded as being possibly relevant to measuring ag-

TABLE 1. September density statistics from the Metchosin study area.

	1969	1970	1971	1972	Means and totals
Total coveys	21	26	34	28	27
Total quail	305	411	407	362	1485
Quail per sq. mile	161	216	214	191	195 ^a
Mean covey size ^b	14.5	15.8	12.3	12.9	13.9
C. V. (covey size)	0.37	0.42	0.61	0.40	0.456 ^a

^a A weighted mean.

^b Obtained by dividing total quail by total coveys.

gressiveness: (1) whether or not the birds hid while being disturbed; (2) whether or not the birds flushed; (3) flushing distance—the distance of the birds from the observer when (if) they flushed; (4) the distance flown if they flushed; (5) whether or not they flushed to the nearest available cover; and (6) the general type of habitat in which they landed if they flushed.

We also recorded 10 environmental factors that we thought might possibly influence these above behavioral attributes: (1) the year; (2) the bird's position—on the ground vs. on some structure; (3) the number of birds present—few or many; (4) the vegetation type—open or dense; (5) time of day; (6) temperature; (7) degree of cloud cover; (8) wind direction; (9) wind speed; and (10) date.

POPULATION CHARACTERISTICS

POPULATION STATUS

The quail population was likely reduced in the fall of 1969 due to the cold winter of 1968-69 (fig. 3). The annual Christmas bird count in 1969 indicated 172 quail, compared with 582 in 1968. The mean annual Christmas bird count, 1958-70, was 341.5 and ranged from 151 to 584. The number of runs (i.e., increasing or decreasing trends) was 10, which was one more than the expected value of 9. Thus the population changes appear to be compensatory in that runs occur more often than at random. The small ranges of these counts suggest that the population may have been fairly stable for these 14 years. The number of quail found during these counts was not correlated with any of seven different annual weather statistics: June-July rainfall, total annual snow, June-July wet days, April-May temperature, number of Dec.-Mar. freezing days, Dec.-Mar. precipitation, and June-July temperature. There was also no significant correlation between these weather data and the population trend (increase or decrease relative to the previous year).

During our study, the population in the study area in the fall increased from 1969 to 1970 (305-411 birds, table 1), remained the same in 1971 (407 birds), and decreased in September 1972 to 362 birds.

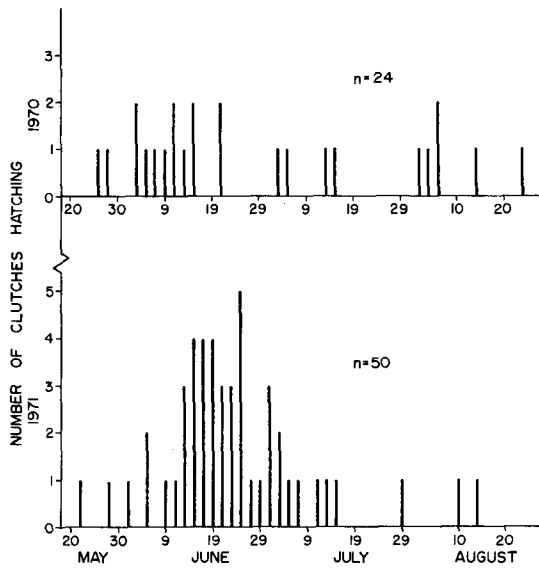


FIGURE 4. Hatching curves for 1970 and 1971. Points on the X axis are pairs of adjacent days which are lumped for ease of graphic portrayal.

MORTALITY

Winter mortality for 1969-70 was calculated at 62% and for 1970-71 was 55% (table 2). The slopes of the survivorship lines for 1969-70 and 1970-71 were not significantly different, but both differed from the slope of the line for the latter half of the 1968-69 winter (fig. 3). This latter period was of cold weather, with a daily mean temperature of 23°F for the two weeks of heaviest mortality and a total snowfall in January of 73.4 cm, with 18 days of January having snow on the ground.

In order to estimate summer mortality of adults, it was necessary to estimate the total quail alive in April. The April population was estimated by subtracting the number of quail estimated to have died in winter (based on fig. 3) from the total quail counted the previous September (table 1). The calculated

TABLE 2. Calculated summer and winter mortality rates.

	1969-70	1970-71
Mortality September to February ^a	44%	39%
Estimated mortality from September to April ^b	62%	55%
Estimated spring population ^c	116	185
Estimated mortality April to September ^d	33%	36%

^a Based on regression lines of figure 4.
^b Sample calculations for 1969-70: (7/5)(44) = 62 (i.e., extrapolation factor times observed mortality).
^c Adults in April calculated: (100 - 62)/100 (305) = 116 (i.e., % surviving the winter times fall population).
^d Adults in September = 18.9 (% adults) × 411 (total population) = 78; (116 - 78)/116 = 33%; where 116 is the estimated spring population.

summer mortality was 33% in 1970 and 36% in 1971 (table 2).

ANNUAL REPRODUCTIVE CYCLE

Nesting began about the beginning of April and continued throughout the summer, with only a small fraction of the quail nesting at any particular time (fig. 4). Peak hatching occurred in 1970 and 1971 about the second week of June; there was apparently little difference between these years in the date of hatching (fig. 4).

Nesting success may have differed between these two years. The percentage of pairs with chicks in July 1970 was 86% (n = 14), whereas in July 1971 only 36% of pairs had young (n = 59, binomial probability of no difference < 0.05) The high percentage of pairs with chicks in July 1970 indicates that the nesting success may have been nearly 100% that year.

Recruitment also varied between years (table 3). The most favorable young : adult ratio was in 1970: 81.1 : 18.9 or 4.27 young/adult. The lowest ratio was in 1971: 70.9 : 29.1 or 2.45 young/adult (table 3).

TABLE 3. September age and sex ratios from the Metchosin study area and greater Victoria.

	1969	1970	1971	1972	Means and totals
Percent adults	20.2	18.9	29.1	23.8	23.0
Percent juveniles	79.8	81.1	70.9	76.2	77.0
95% conf. limits (adults) ^a	14.9-26.8	13.7-25.0	22.9-35.9	18.6-30.2	20.4-25.7
Sample size	203	336	282	291	1112
Percent males	51.4	54.6	58.9	53.4	55.1
Percent females	48.6	45.4	41.1	46.6	44.9
95% conf. limits (♀)	34.2-63.1	38.4-53.9	34.2-48.3	39.5-53.8	41.4-48.4
Sample size	66	360	204	227	857

^a Confidence limits obtained from tables for confidence limits for percentages in Rohlf and Sokal (1969).

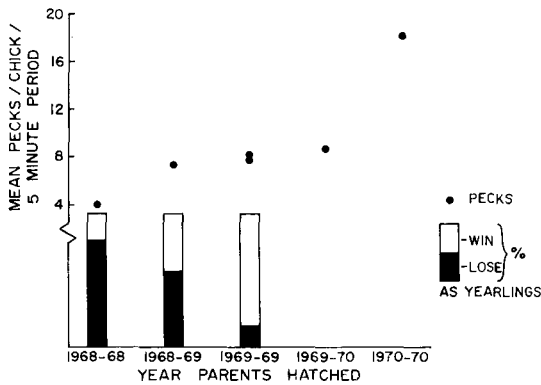


FIGURE 5. Chick aggression plotted against the years in which the parents were hatched. Since observations were made in two summers (1970 and 1971), the chicks with two yearling parents in 1970 and chicks with two adult parents in 1971 both had parents hatched in 1969, hence the two dots above 1969-69. Also shown is the percent win and lose of the yearlings captured as chicks in 1970 and tested using nine cock pairings in 1971. These birds are also classified with respect to the age of their parents.

BEHAVIORAL CHARACTERISTICS

BEHAVIOR OF CAPTIVE ADULTS

The results of the dominance tests between yearlings and adults suggest that the yearlings usually dominated the adults in 1970 and 1971 (table 4). In 1972, adults usually dominated yearlings. Since the birds were matched according to weight, any weight differences between dominant and subordinate birds would have been partially masked. However, if weight was important in determining dominance, any behavioral differences due to weight should have been consistent in the data. In 1970 and 1971 the dominant birds weighed less than the subordinates, whereas in 1972 the subordinates weighed less (table 4). A 2×2 chi-square test done on the frequencies of birds classified with respect to dominant-subordinate vs. light-heavy yielded a χ^2 value of 2.94 ($0.05 < P < 0.10$). Thus it appeared that dominance behavior was not simply a matter of age or weight but varied between annual cohorts. Further, a comparison of all the weight data indicated no significant difference between years ($P < 0.747$).

BEHAVIOR OF CAPTIVE CHICKS

In the mirror tests of chick pecking behavior in 1970 and 1971, those chicks whose parents were both yearling (YY) pecked the mirror most while chicks with two adult parents (AA) pecked least (fig. 5). Chicks with yearling parents pecked the mirror significantly more in 1971 than any other group in either year ($P < 0.05$). Chicks with adult

TABLE 4. Establishment of dominance by pairing two captive cocks with a hen in spring.

	1970	1971	1972
Number of times:			
Yearling wins	23	8	7
Adult wins	11	0	13
No win occurred	22	32	21
Mean agonistic acts per 15 min period ^a			
Yearling	24.6	35.3	8.7
Adult	7.2	1.3	14.6
Total number of birds paired			
	27	24	22
Mean weight of (g):			
Dominant birds	165	171	183
Subordinate birds	170	173	179
Sample size	68	16	40
Yearlings	167	175	179
Adults	175	175	186
Sample size	27	24	22
Probability of no difference between:			
Age of winner and loser	< 0.05	< 0.01	< 0.14
Weight of winner and loser	> 0.15	> 0.25	> 0.20

^a Based only on pairs in which a win was recorded.

parents pecked the mirror significantly less ($P < 0.05$) in 1970 than any other group in either year (fig. 5).

The chicks in the summer of 1970 were kept in an outdoor aviary over the winter and retested using cock pairings in the spring of 1971, as well as with mirrors. These yearlings with YY parents pecked the mirror an average of 41.2 times (± 9.79) per test period, those with YA parents pecked 27.7 times (± 4.98), and those with AA parents pecked 15.7 times (± 4.45). This was the same rank order that had been displayed when these same birds were chicks. Also yearlings from YY parents most often dominated over yearlings of the other two parental types in cock pairings (fig. 5). Yearlings with AA parents pecked less than the other two groups and were least often dominant while yearlings with YA parents were intermediate (fig. 5). These results were consistent with the pattern observed in mirror tests when these same birds had been tested with the mirror as chicks (fig. 5).

BEHAVIOR OF FREE-RANGING WILD BIRDS

In the initial multivariate analysis of environmental factors, year, location, number of birds, and vegetation type were used as independent variables. The other six factors measured were used as covariates. However, cloud cover and wind direction were corre-

TABLE 5. Field observations multivariate analysis of variance (MANOVA program) probabilities and strengths of effect

Factor	Dependent variables											
	Hide		Flush		Flushing distance		Distance fly		Where land		Fl. nearest cover	
	p	η^2 ^a	p	η^2	p	η^2	p	η^2	p	η^2	p	η^2
Year (Y)	0.001	6.86	0.052	1.41	0.004	2.95	0.215	0.53	0.180	0.95	0.006	3.72
Bird location (L)	0.527	0.15	0.328	0.36	0.963	0.00	0.001	3.85	0.383	0.40	0.012	3.13
No. of birds (N)	0.851	0.01	0.004	3.07	0.174	0.66	0.471	0.18	0.592	0.15	0.142	1.05
Vegetation type (V)	0.212	0.58	0.670	0.07	0.962	0.00	0.118	0.84	0.479	0.27	0.520	0.20
Y × V	0.046	1.48	0.030	1.75	0.197	0.60	0.027	1.69	0.815	0.03	0.497	0.22
L × N	0.936	0.00	0.042	1.53	0.537	0.14	0.232	0.49	0.881	0.01	0.863	0.02
Y × L	0.863	0.01	0.029	1.77	0.646	0.00	0.155	0.70	0.837	0.02	0.777	0.04
Error df	241		241		264		264		183		183	

^a η^2 is given as a percentage and is the strength of effect measure found by dividing the SS ($\times 100$) of the factor by the total SS. It is the correlation between the given pair of dependent and independent variables (Hays 1963).

All main effects and interactions had one df.

Only significant interactions are shown (i.e., interactions significant on at least one dependent variable). Probabilities indicate the probability of no factor effect.

lated with the independent variable year, invalidating their use as covariates. Also, day was correlated with bird location. None of the remaining three covariates apparently had much effect on the six behavioral attributes (flushing distance, distance fly, hide, flush, where land, and flush nearest cover), though, as all the associated probabilities were well above 0.05.

Of the independent variables, the year had more influence on the behavior than any other single factor measured (table 5). The birds seen in 1970 hid more and flushed less than in 1971 (tables 5 and 6). Those birds in 1970 who did flush flew more often to trees or bushes than to the ground, whereas in 1971 birds flew more often to the ground. Also in 1970, the birds flushed beyond the nearest cover more than in 1971 (tables 5 and 6). Suggestive, but not significant, was the indication that the birds in 1970 flushed closer to the observer and flew farther than in 1971 (tables 5 and 6). Thus it appeared that birds in 1970 were more wary than those in 1971.

TABLE 6. Comparison of the effects of year on four behavioral attributes in the field study on wild birds. The two attributes not included were not significant. The numbers are means.

Attribute	Year	
	1970	1971
Hide ^a	51	18
Flush ^a	81	90
Flushing distance from observer (yards)	11.7	16.6
Flush nearest cover ^a	41	68

^a In percentages—the complementary percent is found by subtracting from 100, e.g., percent which did not hide in 1970 was 100 - 51 = 49%.

Bird location (ground or tree) significantly affected the distance flown and the propensity to flush to the nearest cover. Birds who flushed from trees flew farther than those on the ground and flushed past the nearest cover more often (table 5). This latter point, however, is mainly a matter of semantics as birds in trees are, by definition, at the nearest cover. The number of birds present significantly affected only whether or not they flushed. Large groups flushed more often than small groups. The vegetation type did not affect any of the behavioral attributes (table 5).

There were three significant interactions in the field observations, all of which were two-way interactions (table 5). The year \times vegetation interaction was significant for both flush and distance fly. The location \times numbers was significant for flush, but this is easily explained on the basis that groups with very young chicks would always be seen on the ground and they would never flush. Year \times location was significant only for flush.

DISCUSSION

POPULATION DYNAMICS

The quail population around Victoria has apparently been fairly stable for several years, although at the beginning of the study the density was probably below the average level. However, the population increased rapidly in 1970, remained stable in 1971, and decreased in 1972.

The fall juvenile : adult ratios reflected the observed increase between years, while the adult winter and summer mortality appeared to remain relatively constant. Thus the population trends during this study appear to be largely a result of differential recruitment of chicks rather than compensatory mortality of

adults at any time during the year. Furthermore, the recruitment of chicks was inversely correlated with the spring density. Summer recruitment appeared to be the only factor that varied enough to account for most of the changes in numbers which were recorded (with the exception of the winter of 1968-69).

The mechanism responsible for this differential summer recruitment may result partly from differences in nesting success as well as possible differences in chick mortality. Calculations shown in table 7 suggest that a large part of the differences in fall juvenile : adult ratios may have been due to differences in nesting success. Thus, if the assumptions of these calculations are correct, chick production per brood was 47% more in 1971 than in 1970. There are two basic assumptions: (1) adult mortality of pairs with broods is the same as for pairs without broods; (2) little re-nesting occurred in August. If adult mortality of pairs with broods was greater than that of broodless pairs, then the summer adult loss should have been greater in 1970 than in 1971. This would tend to inflate the figures of chick production for 1970. Thus, the chick production in 1970 may have been even lower than calculated. However, the assumption of no re-nesting in August is almost surely false, and this would produce a bias in the other direction; that is, the number of broods in the fall would be underestimated by the above calculations if much re-nesting took place in August in 1971. Thus, the chick production per brood was probably overestimated in 1971. Another factor that makes this overestimation probable is that the peak hatching occurred a little over a week later in 1971 than in 1970. Also, the fact that the average age of the broods was greater in 1970 than in 1971 probably means that 1970 broods would have been easier to see in July than would 1971 broods. These biases are a strong indication that the number of broods hatched in July 1971 was underestimated, and hence chick production was overestimated. Also, the sample size in 1970 was quite small.

Only differences in nesting success were inferred from this study as no estimates of chick mortality were obtained. It is possible that differences in successful pairs between 1970 and 1971 were not due to nesting success but that the complete loss of broods was much higher in 1971 than in 1970. If this were the case, differential mortality would be almost solely responsible for the lower survivorship in 1971. We were not able to separate the effects of nesting success and chick mortality in arriving at the recruitment figures.

TABLE 7. Calculations for a comparison of summer chick production for the years 1970 and 1971.

	1970	1971
Fall adults	78	118
Estimated fall pairs	35	49
% pairs with broods in July	86	36
Pairs with broods in July	30.1	17.6
Estimated chicks per adult	$\frac{30.1X}{78} = 0.39X$	$\frac{17.6X}{118} = 0.15X$
Estimated ratio of 1970 to 1971		$\frac{0.39X}{0.15X} = 2.59$
Observed ratio of 1970 to 1971		$\frac{4.29}{2.44} = 1.76^a$
Estimated/observed		$\frac{2.59}{1.76} = 1.47$
Percent that estimated is more than observed		47

^a Obtained by dividing the percent yearlings by percent adults.

BEHAVIORAL DIFFERENCES

We observed several kinds of behavior, some of which are probably agonistic and others are probably not. As we do not know of a thorough study of the behavior of the California Quail, we must refer to the behavior of closely related species that have been studied in detail.

Stokes (1967) considered pecks, attacks, chases, frontal displays, and bill fighting to be aggressive in Bobwhites (*Colinus virginianus*) while such acts as turning away, the absence of motion, walking or running away, nudging beneath the rival, taking flight, and giving the avoidance trill are submissive or avoidance behavior. We saw most of these acts in California Quail and interpreted them likewise. Similar behavior has been recorded as being agonistic in the Chukar (*Alectoris graeca*) (Stokes 1963) and the Hungarian Partridge (*Perdix perdix*) (Jenkins 1961).

Phylogenetically, the California Quail is most closely related to the Gambel Quail (*Lophortyx gambelii*). Most of the calls of Gambel Quail (described by Ellis and Stokes 1966) are nearly the same as those of California Quail (described by Sumner 1935 and Williams 1969). Ellis and Stokes (1966) elicited fighting behavior in Gambel Quail by introducing a hen into a pen of sexually deprived males. This is essentially how we attempted to measure aggressiveness of two cocks. In addition, all of the acts that we

recorded as being aggressive in the paired-cock encounters have been described, with a few slight modifications, as being aggressive in Gambel Quail. Thus we feel it reasonable to consider that we were measuring aggression in the cock pairings.

In the paired-cock encounters, yearlings were significantly more aggressive than adults in 1970 and 1971, while adults were more aggressive than yearlings in 1972.

The birds hatched in 1970 seemed the most aggressive. As yearlings in 1971, they usually dominated adults hatched in 1969. As adults, the 1970 cohort dominated the yearlings hatched in 1971 (table 4).

The interpretation of chick behavior is less clear, but not without precedent. Theberge (1971) counted pecks at a mirror to measure aggression in ptarmigan chicks. He later used the same technique on some of these same birds as adults and found that the results were similar, although not identical. Our results show the same trend, the birds exhibiting similar pecking behavior both as chicks and later as yearlings. In addition, yearlings tested using a mirror and also using the method of cock pairings yielded similar indices of aggression. These findings support the interpretation of chicks pecking a mirror as a measure of aggression.

If pecking a mirror does represent aggression, then we found some evidence of differences between coveys in the amount of aggression displayed by the chicks. Chicks with AA parents in 1970 pecked significantly less than chicks of other parent combinations in 1970 or any groups in 1971. Also, chicks from YY parents in 1971 pecked significantly more than all other groups. These results suggest that there are intrinsic differences in behavior of coveys from parents of different generations because the chicks were captured while very young and were presumably exposed to negligible maternal influence before capture.

In our field study, the birds were shown to behave differently in 1971 than 1970. The 1970 birds hid more, flushed less, and flushed to trees more often than the birds in 1971. These findings might be interpreted as indicating that the 1970 birds were generally more nervous and less ready to remain in the vicinity of possible danger than the birds in 1971. This nervousness might be conceived as being negatively related to aggressiveness. If this interpretation is valid, then the 1971 birds were generally less nervous and perhaps more aggressive than the 1970 birds in the field. With a 70–80% rate of turnover

annually, most of the birds in any one year would be of one age class; most of the birds in 1970 would have been hatched in 1969. Thus the field data suggest that the young of 1969 were less aggressive than the young of 1970. This agrees well with the results of the behavioral experiments, which show the same trend.

SOCIAL BEHAVIOR AND POPULATION REGULATION

In general, the 1970 cohort was more aggressive than the 1969 or 1971 cohorts in paired encounters. Furthermore, chicks hatched by the 1970 cohort in 1971 were more aggressive than chicks hatched by the birds of 1968 and 1969 cohorts in 1970 and 1971. In 1971, when the population was dominated by the 1970 cohort, wild birds appeared less secretive than in 1970 when the population was composed primarily of the 1969 cohort. Also in 1971, these less secretive birds provided fewer recruits than in any other year and the population declined in 1972. Conversely, the less aggressive cohorts in 1968 and 1969 produced more chicks in 1969 and 1970, the population increased in 1970 and remained the same in 1971.

We tested our birds in paired encounters free from density effects. Also, the chicks we tested could not have been influenced directly by density interactions. This sequence leads us to suggest that density interactions and physiological stress were not causes of inversivity in this study, but that density considerations, behavior, and survival of young all may have depended, in part, on the prepairing quality of the stock. The intrinsic quality of the stock might vary in response to the magnitude of natural selection. The winter of 1968–69 was severe and many birds died. This selection may have "improved the quality" of the stock, resulting in many non-aggressive birds that produced viable young in 1969 and 1970 causing population increase.

These findings are more in agreement with Chitty's (1967) views on population regulation, which involve genetic changes in the quality of the stock, than with the views of Christian and Davis (1964). The latter feel that the regulation of numbers can be explained solely on a phenotypic basis in which physiological stress results from social interactions at high densities.

A crucial experiment that would predict different outcomes between the rival hypotheses of Christian and Davis vs. Chitty might be to remove birds of a specific quality from a population. For example, removal of birds

of "high quality" (e.g., birds of high weights, or nonaggressive, or more secretive) from a population would, according to the stress theory, be expected to result in high survival of young and inversivity because of the lowered density; however, from the Chitty view, there would be no improvement in survival of young and inversivity compared to a control population.

SUMMARY

California Quail were studied from 1969 to 1972 on the southern end of Vancouver Island, near Victoria, B.C., in an attempt to test the null hypothesis that there are no intrinsic differences in the behavior of birds between cohorts that might relate to the regulation of numbers. Hatching curves, fall sex and age ratios, fall censuses, and winter mortality gave measurements of the population. In addition, behavioral data were gathered which might relate to aggression. Chicks from several coveys and three parentages were compared during the summer by observing pecks at a mirror. Mature cocks were subjected to paired encounters in the spring to establish dominance relationships and this dominance was related to aggressiveness of cohorts. Several behavioral attributes that may relate to aggression were recorded in field studies. Population change was apparently a function of differential recruitment of young between years, the summer rate of gain being inversely proportional to the spring density. Behavioral differences were found between cohorts in the adults in both the pairing experiments and in the field studies and both studies appeared to indicate the same trend. We hypothesize that social behavior based on intrinsic differences between cohorts plays some part in these differences in annual recruitment.

LITERATURE CITED

- BENNETT, R. 1951. Some aspects of Missouri quail and quail hunting 1938-1948. Mo. Conserv. Comm. Tech. Bull. 2.
- BERGERUD, A. T. 1970. Population dynamics of the willow ptarmigan *Lagopus lagopus alleni* L. in Newfoundland 1955-1965. *Oikos* 21:299-325.
- CARL, G. C., AND C. J. GUIGUET. 1957. Alien animals in British Columbia. Br. Col. Prov. Mus. Nat. Hist. and Anthropol. Handb. No. 14. The Queen's Printer, Victoria.
- CHAPMAN, J. D. 1952. The climate of British Columbia. Trans. Fifth Br. Col. Nat. Res. Conf., ed. D. B. Turner.
- CHITTY, D. 1960. Population processes in the vole and their relevance to general theory. *Can. J. Zool.* 38:99-113.
- CHITTY, D. 1967. The natural selection of self-regulatory behavior in animal populations. *Proc. Ecol. Soc. Aust.* 2:51-78.
- CHRISTIAN, J. J., AND D. E. DAVIS. 1964. Endocrines, behavior and population. *Science* 146:1550-1560.
- ELLIS, G. R., AND A. W. STOKES. 1966. Vocalizations and behavior in captive Gambel Quail. *Condor* 68:72-80.
- EMLEN, J. T., JR. 1940. Sex and age ratios in survival of the California quail. *J. Wildl. Manage.* 4(1):92-99.
- ERRINGTON, P. L. 1945. Some contributions of a fifteen-year local study of the northern bobwhite to a knowledge of population phenomena. *Ecol. Monogr.* 15(1):1-34.
- HAYS, W. L. 1963. *Statistics for Psychologists*. Holt, Rinehart, & Winston, New York.
- HICKEY, J. J. 1955. Some American population research on gallinaceous birds, p. 326-396. *In* A. Wolfson [ed.], *Recent studies in avian biology*. Univ. Illinois Press, Urbana.
- JENKINS, D. 1961. Social behaviour in the partridge *Perdix perdix*. *Ibis* 103:155-188.
- JENKINS, D., A. WATSON, AND G. R. MILLER. 1963. Population studies on red grouse, *Lagopus lagopus scoticus* (Lath.) in northeast Scotland. *J. Anim. Ecol.* 32:317-376.
- KABAT, C., AND D. R. THOMPSON. 1963. Wisconsin quail 1834-1962. Population dynamics and habitat management. Wisconsin Cons. Dept., Tech. Bull. 30, Madison, Wisc. 136 pp.
- KRAJINA, V. J. 1965. Biogeoclimatic zones and biogeocoenoses of British Columbia, p. 1-17. *In* V. J. Krajina [ed.] *Ecology of Western North America*. Dept. of Botany, Univ. of B.C.
- McMILLAN, I. I. 1964. Annual population changes in California quail. *J. Wildl. Manage.* 28:702-711.
- MOSSOP, D. H. 1971. A relation between aggressive behavior and population dynamics in blue grouse. MSc Diss. Dept. of Zoology, Univ. of B.C., Vancouver, B.C.
- RAITT, R. J., AND R. E. GENELLY. 1964. Dynamics of a population of California quail. *J. Wildl. Manage.* 28:127-141.
- ROHLF, F. J., AND R. R. SOKAL. 1969. *Statistical tables*. W. H. Freeman Co., San Francisco.
- STOKES, A. W. 1963. Agonistic and sexual behavior in the Chukar partridge. *Anim. Behav.* 11:121-134.
- STOKES, A. W. 1967. Behavior of the bobwhite, *Colinus virginianus*. *Auk* 84:1-33.
- SUMNER, E. L., JR. 1935. A life history study of the California quail, with recommendations for its conservation and management. *California Fish and Game* 21(3-4):167-256, 277-342.
- THEBERGE, J. 1971. Population fluctuation and changes in the quality of rock ptarmigan in Alaska. PhD Diss. Univ. of B.C., Vancouver, B.C.
- WATSON, A. 1965. A population study of ptarmigan (*Lagopus mutus*) in Scotland. *J. Anim. Ecol.* 34:135-172.
- WILLIAMS, H. H. 1969. Vocal behavior of adult California quail. *Auk* 86:631-659.

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