BEHAVIOUR AS A CONTROLLING FACTOR IN THE POPULATION DYNAMICS OF CALIFORNIA QUAIL

by

HUGH JOHN BARCLAY

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Supervisor: Dr. A. T. Bergerud

ABSTRACT

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 differences in the behaviour of birds between cohorts which might relate to the regulation of numbers. Demographic data were gathered which consisted of hatching curves, fall sex and age ratios, fall censuses, and winter mortality. In addition, behavioural 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 with a hen present in the spring to establish dominance relationships and this dominance was related to aggressiveness of cohorts. In addition wild birds were studied in the field and several behavioural attributes were recorded which may relate to aggression. 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. Behavioural 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. It is hypothesized that social behaviour based on intrinsic differences between cohorts plays some part in these differences in annual recruitment.

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TABLE OF CONTENTS

POPULATION CHARACTERISTICS (cont.)

LIST OF TABLES

LIST OF FIGURES

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INTRODUCTION

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 inversity (Errington, 1945); that is, the rate of summer gain is inversely proportional to the spring density of adults. Inversity appears to be a function of survival of the young between years rather than due to annual changes in fecundity (Hickey, 1955).

I studied the demography and behaviour of California Quail (*Lophortyx californicus* Shaw) on Southern Vancouver Island from 1969 to 1972. The purpose of the study was (1) to describe the demographic parameters of the population, (2) to determine if inversity occurred, and (3) to determine, if possible, the underlying mechanisms that could cause changes in survivorship between years.

The specific null hypothesis that I tried to refute was that there was no intrinsic difference in the behaviour 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 behaviour of adults varies between cohorts and/or in space, and was correlated with survival (Watson, 1965; Jenkins, Watson & Miller, 1963; Bergerud, 1970; Theberge, 1971; Mossop, 1971). Other workers who have documented the occurrence of inversity in the Phasianidae have either not discussed possible underlying factors (McMillan, 1964; Bennitt, 1951) or have postulated that inversity results from phenotypic social stress between pairs in spring (Kabat & Thompson, 1963). No one has yet 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 which involve social behaviour. 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-behavioural mechanism in which selection occurs for socially intolerant individuals at high density, resulting in the density decreasing to a point where this selection no longer operates.

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% annually (Sumner, 1935; Emlen, 1940; Raitt & Genelly, 1964). In addition quail can be trapped and are sedentary which facilitates censusing. Conversely, a disadvantage is that they are socially tolerant. Coveys with 30 birds are common. The birds are least tolerant in the spring when they form pairs. This period thus may be important if regulation is accomplished through social behaviour. I investigated the aggressive behaviour 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 behaviour, as any differences in behaviour between coveys would probably result from genetic differences.

California quail were first introduced to Vancouver Island in the 1860's (Carl & Guiguet, 1957) and have been reintroduced several times since then. The largest population of quail presently exists in the vicinity of Victoria on the southern tip of Vancouver Island. However a few quail persist in favourable habitats as far north as Parksville, approximately 100 miles northwest of Victoria.

DESCRIPTION OF THE STUDY AREA

The present study was carried out largely at Metchosin, about 15 miles southwest of Victoria on the southern tip of Vancouver Island, B.C. The Metchosin study area measured about one by two miles (Fig. 1). Rocky Point, which is south of Metchosin, (see also Fig. 1) was included only for fall censuses. Christmas Hill, in a semirural part of Victoria, was a small area densely populated by quail and which was used to augment age and sex ratios in the fall and to obtain average weights in spring. All three areas are in the same general vegetation zone and are quite similar floristically.

The Metchosin study area is in a farming district; most of the farms are small, averaging about two acres. The topography is gently undulating with the average altitude less than 100 feet above sea level. On these farms 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 28 inches 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 menzesii*). This zone is part of the Pacific Coast Mesothermal Forest Region (Krajina, 1965). Besides Oak and Fir there are scattered patches of Arbutus (*Arbutus menzesii*). 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 favourable 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 favourable habitats north of this dry subzone. The numbers and persistence of quail in the area suggest that the habitat is favourable, although local extinctions have taken place on some of the Gulf Islands nearby following years with persistent snow and cold weather.

DEMOGRAPHIC METHODS

Density and Population Structure

Complete censuses were obtained each autumn 1969 to 1972 (Table 1). I found that most of the people living in the study area were aware of whether quail were present on their farms. 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 house to house canvass probably missed some isolated groups, hence an intensive effort was made to find quail in the few large uninhabited areas, such as the Metchosin golf course.

Each September (1969 to 1972) the age and sex composition of much of the population was determined (Table 2). Not all coveys could be examined, however, and the data from the study area was augmented by sex and age ratios taken from the Greater Victoria area. It is likely that the ratios from these two areas were similar, since the two areas are only 15 miles distant.

In other quail populations that have been studied there was a surplus of males in the spring population (Sumner, 1935; Emlen, 1940). Cocks that don't find a mate give a call termed a "cow call" in spring. Males in these studies continued to cow call until June or until they found a mate. To get an estimate of the spring population I counted the number of cow callers in my study area in the late spring of 1970 and 1971. I made an intensive search for pairs in a smaller area adjacent to the study area (see section 7, Fig. 1), and then used the number of calling cocks in this section to estimate the total quail in the study area (the other seven sections). This count was made during a two week period in mid May.

Winter Mortality

During the winters of 1969-70 and 1970-71 weekly counts were made of several coveys in the Greater Victoria region to estimate the sequence and extent of mortality (Fig. 4). Again, it is likely that mortality in this region was similar to that of the study area. The counts were complicated by the amalgamation of coveys as well as the difficulty of obtaining weekly counts. Sometimes the number of birds in a covey appeared to increase between successive weekends. Unless this increase was large and permanent it was assumed that an incorrect count had been made the previous week, in which case the previous week's data were adjusted.

Feather Measurements of Chicks

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. The other broods captured during the first week of life were measured only once weekly in an attempt to detect any differences in growth rates between broods.

In 1970 and 1971 wild chicks were captured and aged on the basis of the growth curves (to be published separately) 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.

Capture of Adult Birds

Some adults were captured with baited traps from February to May 1970-1972 to determine spring weights (Table 8) and for tag and release studies. Successive weights on some birds were obtained by repeat captures. Some birds captured March to May (mostly 1971) were tagged with coloured plastic leg bands and released to obtain information on home range and possible territoriality. These birds were observed until June when pairs had started nesting.

Yearlings and adults were distinguished in these samples by the appearance of the primary coverts which are mottled in yearlings and plain brown in adults (Sumner, 1935).

BEHAVIOUR METHODS

Aggressive Behaviour of Captive Adults and Yearlings

In April of 1970-72 I placed captive males together to determine the relative aggressiveness of yearlings (8 to 12 months old) to adults (over 19 months old). Two cocks and a hen were placed together in a cage (18 in. by 18 in. by 24 in.) and it was noted which cock established dominance (Table 4). In every pairing the accompanying hen came from a different covey than either of the two cocks and thus would likely be unfamiliar to both cocks.

The tests were conducted in an area free from outside disturbance. I observed the birds by means of a hidden video camera. Each trial consisted of a 15 minute 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. 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 towards 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 cocks were matched according to three criteria; these were, in decreasing order of priority: (1) that one cock be yearling and the other be adult, (2) that if possible the cocks be of similar weight,

(3) that the cocks be from different coveys. It was not possible to conduct all possible pairings between yearlings and adults, so the order of the pairings was arranged so that at any one time each adult had been paired with about the same number of yearlings and each yearling with about the same number of adults. In addition it was arranged that no bird had more than two paired encounters during one day.

In 1970 the quail that were tested were captured from January to April. Many of these birds lost weight in captivity and were not in good condition when the experiment was conducted in late April. In 1971 and 1972 the birds that were tested were only captured in late March and early April and these birds lost little weight prior to the experiment in April.

In 1970 the cocks were housed individually and the hens were kept either individually or in small groups. The birds were housed in cages approximately 18 inches cubed. They were isolated visually so the males did not see each other or the hens until the experiment. I felt that this period of isolation was probably long enough for cocks from the same covey to once again show agonistic behaviour; in chickens this only requires a few weeks (Guhl, 1953). I decided in 1971 and 1972 to keep all the birds together in an outdoor aviary since the birds in 1970 had damaged themselves in the small cages. I hoped that the dominance hierarchy that would be established in the aviary would not negate measuring aggressiveness later by cock pairings. The experiments were done during the second half of April. At this time the males appeared to be in breeding condition and hence probably more likely to interact in the presence of a hen.

In 1970 the only quail tested were those caught during the spring of 1970. In 1971 in addition to those 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.

Aggressive Behaviour of Captive Chicks

Chicks were captured in June and held in cages 2x2x1 feet. Most of the chicks were about one day old when captured, thus minimizing maternal influence on behaviour. Each cage contained the chicks from one brood. Each day a 5" by 7" mirror was put into each cage and the total pecks at it by the brood was noted during five minute periods. The tests continued until the chicks were 5 or 6 weeks old. I sat about six feet from the cages on most occasions. In addition, to test the birds' reaction to the observer, I made some observations while sitting one foot from the cages. In some of the observation periods both a mirror and a glass window were present and the pecks on each counted. It was thought that pecks received by a glass window would result from nonaggressive acts, as most of the light was coming from the outside thus minimizing reflections from the glass, and would be a useful comparison with the pecks received by an image in a mirror (Table 6).

Behaviour of Wild Birds

During the summers of 1970 and 1971 behavioural observations were recorded on quail in the study area. Six behavioural attributes were recorded as being possibly relevant to measuring aggressiveness: (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.

Ten environmental factors were also recorded which I thought might possibly influence these above behavioural attributes: (1) the year, (2) the bird's position - on the ground vs up 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 (Table 9).

ANNUAL REPRODUCTIVE CYCLE

Pairing

The onset of pairing, based on the initiation of cow calling, appeared to vary from year to year. In 1970 the first cow call was heard on March 27, in 1971 on April 18, and in 1972 on March 18. In California Genelly (1955) reported pairs about the first of March.

Covey breakup was apparently a gradual process since intact coveys were observed as late as April 7. However it was evident that pairing was in progress since pairs would occasionally temporarily leave the covey. Emlen (1939) reported that covey breakup was only partly complete by early April in California.

There was a surplus of cocks each spring, since some males continued to cow call each year until June. The presence of surplus males plus the lack of observations of lone females suggest that there were few if any unpaired hens in the population.

Hatching

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. 3). Mr. S. Blackburn found two nests in early April 1969 near Victoria, and I saw broods in early May of 1971 and 1972. Peak hatching occurred in 1970 and 1971 about the second week of June, and there was apparently little difference between these years in the date of hatching (Fig. 3). Hatching dropped off rapidly after the peak in June. Probably many quail that were unsuccessful in their first nesting attempted renesting. These renesting attempts would explain the broods hatched after the middle of July (Fig. 3).

Home Range and Territoriality

Summer movements of pairs were quite localized and restricted, especially after hatching occurred. Even before nesting, though, the birds were so habitual that a fairly definite daily routine became established. The total home range of coveys appeared to seldom exceed 4 or 5 acres, and was possibly often much less.

Genelly (op. cit.) felt that the regular spacing of cow callers implied territoriality. I secured no data on the spacing of cow callers, however many pairs without young were seen together after pairing in May and June. Groups of two pairs were seen 27 times, groups of three pairs were seen 10 times, groups of four pairs were seen 3 times and one group of five pairs was seen. In 17 cases the birds were all within 10 feet or less of each other. After broods were hatched I observed two sets of broods in which the home ranges overlapped. The encounters between each pair of broods suggested that the broods simply avoided each other and did not defend any particular area.

POPULATION CHARACTERISTICS

Population Status

The quail population may have been reduced in numbers in the fall of 1969 due to the cold winter of 1968-69 (Fig. 4). A count made by the Victoria Natural History Society at Christmas in 1969 indicated 172 quail, compared with 582 in 1968. The mean annual count, 1958 to 1970, was 341.5 and ranged from 151 to 584. The number of runs (ie. increasing or decreasing trends) was 10, which was one more than the expected value of 9 (Fig. 5). 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 (Table 12.). There was also no significant correlation between these weather data and the population trend (increase or decrease relative to the previous year) of the quail (see also Table 12.).

I estimate that the quail population in the study area increased from 116 to 411 birds (an increase of 254%) from April to September 1970. Approximately 38 adults died and were augmented by 333 chicks (4.27 per adult in September). In 1971 the population only increased 120% between April and September (185 to 407 birds). Adult mortality was estimated at 36% (67 birds) from April to September, while during this period recruits numbered 289 (2.45 young per adult in September). In 1972 the September age ratio was 3.20 (calculated from percentages in Table 2).

These limited data support the idea of inversity (Fig. 6). There was a lower spring density of adults in 1970 than in 1971 (Fig. 6,

Table 3), a lower summer mortality rate in 1970, and also more young recruited until September in 1970 than in 1971. That is, the rate of gain in recruits was inversely proportional to the adult spring density in these two years.

Reproduction

Only three nests with complete clutches were found during the study. The number of eggs in the clutches were 18, 18, and 16. In addition, two nests found prior to the study had 15 and 17 eggs. Sumner (1935) reported an average clutch of 14 eggs for birds in California.

Nesting success may have varied between years. The percentage of pairs with chicks in July 1970 was 86% ($n = 14$) whereas in July 1971 only 36% of pairs had young ($n = 59$) ($p < 0.05$). The high percentage of pairs with chicks in July 1970 indicates that the nesting success may have been nearly 100% that year. This is also suggested by the high juvenile-adult ratio in the fall of 1970. The apparently lower rate of nesting success in 1971 was also partly substantiated by a low fall juvenile-adult ratio that year (Table 2).

Winter Mortality

During the winters of 1969-70 and 1970-71 six and seven coveys respectively were observed weekly from September 20 to March 20 to estimate winter mortality. In addition mortality data were available for one covey observed in the winter of 1968-69. Since covey breakup may commence as early as late February, the estimation of mortality was based only on counts made before Feb. 22. Since the mortality curves for 1969-70 and 1970-71 were nearly linear, a linear extrapolation was made to estimate winter mortality up until April 20 (Fig. 4). Winter mortality for 1969-70 was calculated at 62% and for 1970-71 was 55% (Table 3). The estimated mortality for the restricted period between October 15, 1968 and December, and then for the period January to February, 1969 totaled 69%. The slopes of the regression 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. 4). 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 28.9 inches with 18 days of January having snow on the ground.

Summer Mortality

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. 4) from the total quail counted the previous September (Table 1). An alternative but probably less precise method of estimating April numbers was to estimate the percentage of calling cocks in the population, then count the total number of calling cocks and multiply by the "quail per calling cock" ratio to get the total April population. The summer mortality was then estimated by subtracting the number of adults in the following fall population (Table 1) from the calculated spring population. The calculated summer mortality by method one for 1970 and 1971 were 33% and 36% (Table 3), and by method two were 28% and 21%. These estimates suggest that a bias may be present, as those calculated on the basis of winter mortality are both higher than those estimated by calling cocks. This might be due to differences in spatial patterns of calling cocks and the rest of the population. If unmated cocks were attracted to the high density of quail in section 7 (where the percentage of cow callers in the population was estimated) then the percent of calling cocks would have been overestimated. The summer mortality would thus also have been underestimated. More probable, however, is that the differences in the estimates are a result of sampling error due to the very small percentage of unmated cocks in the population. The two sets of estimates show opposite mortality trends (33% to 36% as opposed to 28% to 21%) from 1970 to 1971 which suggests sampling error in addition to any bias which may have been present.

Movement

One hundred and ten birds were tagged with plastic leg tags and released at Christmas Hill (Victoria) in 1970. Thirty birds were resighted in June and early July at distances of 0 to 0.6 miles from their earlier locations. The mean distance between captures in February was 0.071 ± 0.007 miles ($n = 67$) while the mean distance travelled after covey breakup (March to July) was 0.254 ± 0.040 miles ($n = 30$). These data agree with those of Sumner (1935) who reported that movement of quail increased during and just after the period of covey breakup in the spring.

BEHAVIOURAL CHARACTERISTICS

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 be partially masked. However, if weight was important in determining dominance, any behavioural differences due to weight should be consistant 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 x 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 behaviour 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 (Table 8).

Captive Chicks

In the mirror tests of chick pecking behaviour in 1970 and 1971 those chicks whose parents were both yearling pecked the mirror most while chicks with two adult parents pecked least (Fig. 7.). Chicks with yearling parents pecked the mirror significantly more in 1971 than any other group in either year. Chicks with adult parents pecked the mirror significantly less in 1970 than any other group in either year (Fig. 7.). The intensity of chick pecking was tested for significance between years, parental types, coveys and days using a nested analysis of variance. Years, parental types and covey effects were not significant, while days and some of the interactions were significant (Table 5). Unfortunately the power of this test favours the within (days) factor at the expense of the between groups factors (years, parental types and coveys) (Kirk, 1968, p. 247)

A statistical analysis of chick pecking behaviour compared between covey, distance of observer (6 ft. vs 1 ft) during testing, and between pecks received by a window or a mirror indicated that distance and window-mirror effects were not significant (Table 6). There was a difference in the intensity of pecking between coveys ($p<0.006$) which contrasts with the results shown in Table 5 in which no difference was detected. In the analysis of Table 6, however, the covey effect is overestimated as the distance and mirror-window factors are correlated and the error term is mixed due to multiple measurements and lack of identification of individual birds. All three two way interactions were highly significant (Table 6). The coveys by mirror-window interaction indicated that some coveys pecked the mirror more than the window, while other coveys pecked the window more than the mirror. The covey by distance interaction indicated that coveys pecking only a few times when observed from a distance of 6 feet pecked more times when observed from close up and vice versa (Table 7). The distance by mirror-window interaction suggests that when observations were made from 6 feet most of the pecking was at the mirror, while the window received most of the pecks when the observations were made from one foot (Table 7).

The chicks of 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 retesting using mirrors. 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 which 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. 8). Yearlings with AA parents pecked less than the other two groups and were least often dominant while yearlings with YA parents were intermediate (Fig. 8). These results were consistent with the pattern observed in mirror tests when these same birds had been tested with the mirror as chicks (Fig. 7). There were only six cocks in this experiment and sometimes dominance could not be determined from the pairings (Fig. 8).

Regressions done on growth rates of the first post natal set of primary feather showed no significant differences between coveys and there were no discernable trends with regard to either parentage of the broods or any other brood characteristic.

Field Studies

The field observations on behaviour were analyzed using a multivariate analysis of variance program (MANOVA) run on the University of Victoria IBM 360/44 computer. In the initial analysis of the environmental variables, year, location, number of birds, and vegetation type were used as independent variables. The other six factors measured were used as covariates (see page 12). However, cloud cover and wind direction were correlated 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 behavioural 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 behaviour than any other single factor measured. The birds seen in 1970 hid more and flushed less than in 1971. Those birds in 1970 that 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 (Table 10). Suggestive, but not significant, was the indication that the birds in 1970 flushed closer to the observer and flew farther than in 1971 (Table 10). Thus it appeared that birds in 1970 were more wary than those in 1971.

Bird location (ground or tree) significantly affected the distance flown and the propensity to flush to the nearest cover. Birds which flushed from trees flew farther than those on the ground, and flushed past the nearest cover more often (Table 9). 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 behavioural attributes (Table 9).

There were three significant interactions in the field observations, all of which were two way interactions (Table 9). The year by vegetation interaction was significant for both flush and distance fly. The location by 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 by location was significant only for flush.

Of the dependent variables only flushing distance and distance fly showed any convincing positive correlation (0.414), although flush nearest cover and where land were also significantly correlated (r = 0.230). Distance fly and flush nearest cover showed a negative correlation (-0.456), which is understandable as flight to the nearest cover would generally imply a short distance flown (Table 11).

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. Since quail have an annual turnover rate of about 70% the density would be expected to return to normal fairly quickly. My results indicate that this probably occurred in two years, as the annual census during the third fall (1971) was the same as that of the second fall (1970). 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. This agrees with Ricker (1954) and with Bennitt (1951) who pointed out that this was the usual condition. Further the recruitment of chicks was inversely correlated with the spring density (Fig. 6). Summer recruitment appeared to be the only factor observed which 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, however, may be partly a result of differences in nesting success as well as possible differences in chick mortality. Calculations shown in Table 13 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 renesting 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 renesting in August is almost sure to be 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 renesting took place in August in 1971. Thus the chick production per brood was probably overestimated in 1971. Another factor which makes this overestimation probable is that the peak hatching occurred a little over a week later in 1971 than in 1970. This would indicate that the proportion of total broods to have hatched by the end of July would be lower in 1971 than in 1970. Also, the fact that the average age of the broods was greater in 1970 than in 1971 would probably mean that 1970 broods would be 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. Errington (1945) was not able to discern the mechanism for inversity, and thus included any compensatory mechanism occurring during the summer. Hickey (1955) reported that differential chick mortality is largely responsible for inversity, and that differential adult fertility was not a factor. Kabat and Thompson (1963), however, found that adult mortality was inversely correlated with spring density. 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. My own data suggest that adult mortality was directly related to spring density (Table 3), but the difference between years was small. I was not able to separate the effects of nesting success and chick mortality in arriving at the recruitment figures. Thus if one considers inversity to be associated only with compensatory mortality of chicks, I cannot detect whether or not inversity occurred.

Behavioural Differences

The behaviour which I recorded consisted of several types, some of which are probably agonistic and some are probably not. Since a thorough study of the behaviour of the California quail has not been done, I must refer to the behaviour of closely related species which have been thoroughly studied.

Stokes considers pecks, attacks, chases, frontal displays and bill fighting to be aggressive in Bobwhites (Stokes, 1967), 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 behaviour. Most of these acts were also seen in California quail and were similarly interpreted. Similar acts have been recorded as being agonistic in the Chukar (Stokes, 1963) and the

Hungarian Partridge (Jenkins, 1961).

Phylogenetically the closest species to the California quail is the Gambel quail (*Lophortyx gambelii*). Most of the calls of Gambel quail (as described by Ellis and Stokes (1966)) are nearly the same as those of California quail (as described by Sumner, 1935, and Williams, 1969). Ellis and Stokes (op. cit.) elicited fighting behaviour in Gambel quail by introducing a hen into a pen of sexually deprived males. This is essentially how I attempted to measure aggressiveness of two cocks. In addition, all of the acts which I recorded as being aggressive in the paired cock encounters are also described, with a few slight modifications, as being aggressive in Gambel quail. Thus I feel that there is reason to consider that I was measuring aggression in the cock pairings and that my interpretation of various acts of the adults as being agonistic is supported.

In the paired cock encounters yearlings were significantly more aggressive than adults in 1970 and 1971 while adults were more aggressive (not significantly) than yearlings in 1972. Thus the aggressiveness of adults in spring differed in different cohorts.

The interpretation of chick behaviour is less clear, but not without precedent. Theberge (1971) used the technique of counting 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. My own results show the same trend, with the birds exhibiting similar pecking behaviour both as chicks and later as yearlings. I did not identify individual chicks, however, so a bird by bird comparison was not possible. In addition, yearlings tested using a mirror and also using the method of cock pairings yielded similar indices of aggression. These findings lend credence to the interpretation of chicks pecking a mirror as a measure of aggression.

Finally, the experiment in which the observer sat at different distances from the chicks during observation suggests that different qualities are being measured at different observer distances since a reversal of behaviour occurred. Chicks which pecked the mirror many times when observed from six feet pecked few times when observed from one foot, and vice versa. Also most of the pecking shifted from the mirror to the window when the observer moved closer. I believe that when the observer sits close to the chicks the pecking represents an attempt to escape, whereas when the observer sits farther away and is less conspicuous the pecking may represent aggression at the sight of their own image.

If pecking a mirror does represent aggression, then I found some evidence of differences between coveys in the amount of aggression displayed by the chicks. A general trend relating to the age of parents was evident in the complete analysis (Table 5). 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 behaviour of different coveys, as the chicks were captured while very young and were presumably exposed to negligible maternal influence before capture. These differences might be genetic.

In the field study the birds were shown to behave differently in 1971 from 1970. The 1970 birds hid more, flushed less, 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% 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 behavioural experiments which show the same trend. A general statement could then be made combining the results of both studies to the effect that the aggression displayed by the quail increased from 1969 to 1971, then levelled off or perhaps even decreased slightly from 1971 to 1972.

Social Behaviour and Population Regulation

There are many possible ways in which regulation could occur. Lack (1954) feels that food is of prime importance in the regulation of birds. Andrewartha and Birch distinguish between an absolute and a relative shortage of food. On the basis of the types of plants used for food by quail I found no shortage of food in the absolute sense at any time during the study. Judging from the quantities of food available throughout the year I would suggest that even a relative shortage could not account for the regulation of quail populations. I never found or trapped any quail which were obviously malnourished. Weather has often been cited as being important in determining animal numbers (Andrewartha and Birch, 1954). Since the numbers of quail did not correlate with any of seven weather statistics over a 14 year period, I feel that weather probably plays a part in limiting the numbers of quail during periods of extreme weather conditions. On several occasions I have heard of dead quail being found after the temperature dropped to well below freezing for several days.

Quail have been reported to be cyclic in only one study so far. Williams (1963) in New Zealand reported a four year cycle for quail. In the case of cyclic populations one would expect fewer runs than random in a runs test, both in the sense of runs across the median and in the sense of changes of direction or trends. During the 14 years for which data are available there were ten different trends (nine changes of direction). This is one more than the expected value of 9 trends, although 12 would be necessary to be significantly different from random. Cole (1951, 1954) has suggested that cycles could result from populations which undergo random perturbations but which are serially correlated due to historical influences (such as past population size) which affect present and future numbers. In this case one would expect a smoothing of population trends and fewer changes of direction than for random numbers. In fact, the expected number of changes of direction is one half times two less than the number of years under observation (equals ½(14-2) = 6; see Appendix, p.58, for the derivation of this). This might be expected to be the case here, as the size of the breeding population of many animals in spring is correlated with the population size the previous fall, the food supply from one year to another would probably be correlated, and even the weather might show serial correlation. However, population changes in this study appear to be compensatory as the number of changes of direction is greater than either for random numbers or for Cole's running sums.

Genetic polymorphisms which may influence population trends would depend on both the rate of turnover and the selective coefficient for their oscillatory frequency. The high turnover rate of quail would seem to make it possible to allow selection to proceed fast enough to permit a greater number of rums than random. If such polymorphisms were able to act in a nearly perfect density dependent manner, then any departure from the mean density would almost immediately be corrected for. On the other hand delayed density dependence as postulated by Milne (1957) would produce time lags which would be expected to produce either cycles or oscillatory instability (Hutchinson, 1948; Cunningham, 1954).

Social behaviour has often been observed to vary with population density in vertebrates and has sometimes been singled out as a causal factor in population regulation. Stokes (1954) found that hatching success in pheasants on Pelee Is. was low when the birds were at high density, and that this was largely due to nest abandonment. This study may not be representative of North American galliforms, however, as animals on isolated islands cannot disperse, and pheasants are unique among galliforms in dropping eggs before nesting. Kabat and Thompson (1963) found that summer adult mortality in bobwhite quail was directly correlated with spring density and may have been associated with breeding season stress. Myers and Krebs (1971) found that dispersal was important in regulating the numbers of microtines, and that dispersal was different for voles of different transferrin genotypes.

California quail have not been found to be territorial, at least not in the sense of defending a given area against all other males, so this factor must be ruled out as a possible means of regulation. The period of dispersal of birds in the spring would offer a possible mechanism for regulation. Birds which dispersed into unfavourable habitat could suffer greater chick loss than those in favourable habitats.

The results of the present study suggest that the quail population increased in both numbers and aggressiveness from 1969 to 1971 and then decreased from 1971 to 1972. The numbers stayed the same from 1970 to 1971 while the level of aggressiveness continued to increase. Thus if one assumes a causal relationship, density would appear to be the cause of the increase in aggressiveness. However increased aggression might also cause a drop in numbers. The density dependence (if it exists) between numbers and aggression appears to be almost perfect, and thus consistent with the hypotheses of both Christian and Chitty. Wynne-Edwards' hypothesis involves differential fertility with social behaviour playing a part in determining fertility. There is little evidence of any group behaviour such as epideictic displays which might accomplish this type of regulation.

The major finding of this study was that different cohorts of adult quail behave differently during aggressive encounters. A comparison with demographic trends suggests that these differences may be important in the regulation of the numbers of quail on Vancouver Island.

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APPENDIX

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

Table 2. 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

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[a] Confidence limits obtained from tables for confidence limits for percentages in Rohlf and Sokal's Statistical Tables (1969)

Table 3. 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 Fig. 4

[b] Sample calculations for 1969-70: (7/5)(44) = 62 (ie. extrapolation factor times observed mortality)

[c] Adults in April calculated: $\frac{100 - 62}{100}$ (305) = 116 (ie. % surviving the winter times fall population)

[d] Adults in September = 18.9 (%adults) x 411 (total population) = 78; $\frac{116 - 78}{116}$ = 33%, where 116 is the estimated spring population

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(gms):			
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 difference between:			
Age of winner and loser	<0.05	<0.01	<0.14
Weight of winner and loser	>0.15	>0.25	>0.20

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[a] Based only on pairs in which a win was recorded

Table 5. Analysis of Variance of chick pecking behaviour in summer 1970 and 1971 using a repeated measures design in which many measurements were taken on the same birds.

Source of Variation	DF	MS	F	P
Between coveys	9	8.90	0.64	>0.50
Years	1	7.77	0.56	>0.40
Parental type	2	8.13	0.58	>0.50
Years by parental type	2	0.08	0.01	>0.75
Coveys within groups	4	13.97		
Within coveys	200	0.54	2.16	<0.001
Time (days)	20	1.15	4.60	<0.001
Years by time	20	0.60	2.40	<0.01
Time by parental type	40	0.20	0.80	>0.75
Years by time by parental type	40	1.13	2.25	<0.01
Time by coveys within groups	80	0.25		

Table 6. Three way Analysis of Variance showing effects of covey, observer distance and target object on the pecking behaviour of chicks in the summer of 1971.

Source of Variation	df	MS	F	P
Coveys (1 to 4)	3	69.75	4.59	0.006
Distance (1 ft. vs 6 ft.)	1	6.05	0.40	0.530
Target object (mirror vs window)	1	14.45	0.95	0.333
Coveys by distance	3	83.22	5.48	0.002
Coveys by target object	3	83.08	5.47	0.002
Distance by target object	1	470.45	30.96	0.001
Coveys by distance by target object	3	9.48	0.62	0.602
Error	64			

Table 7. Summary table of an Analysis of Variance showing interactions between (a.) distance of observer from chicks, (b.) object pecked, and (c.) covey. Numbers are mean pecks per chick in each category.

Covey	Observer Distance					
	One Foot			Six Feet		
	Mirror	Window	Sub totals	Mirror	Window	Sub totals
1	4.8	5.2	10.0	14.6	3.8	18.4
2	4.4	13.6	18.0	6.0	3.8	9.8
3	3.2	7.6	10.8	2.2	1.0	3.2
4	5.8	7.8	13.6	12.6	4.0	16.6
Totals	18.2	34.4	52.4	35.4	12.6	48.0

Table 8. Analysis of Variance of spring quail weights showing effects of age, sex, and the year weighed. Three years are included: 1970-1972.

Source	df	SS	MS	F	P
Age	1	555.1	555.1	5.352	0.023
Sex	1	1.6	1.6	0.016	0.900
Year	2	60.8	30.4	0.293	0.747
Age x Sex	1	0.5	0.5	0.005	0.945
Age x Year	2	25.0	12.5	0.121	0.887
Sex x Year	2	6.4	3.2	0.031	0.969
Age x Sex x Year	2	289.1	144.6	1.394	0.253
Error	91	9437.6	103.7		

Table 9. 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[1]	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 x 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 x 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 x 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	

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[1] η^2 is given as a percentage and is the strength of effect measure found by dividing the SS(x 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 (ie. interactions significant on at least one d.v.).

Table 10. Comparison of the effects of year on four behavioural 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. eg. percent which did not hide in 1970 was 100 - 51 = 49%.

Table 11. Correlations of the behavioural attributes in the field study obtained from the Multivariate analysis of Variance.

Attributes	Hide	Flush	Where land	Flush Dist	Dist Fly	Flush Nearest Cover
Hide	1					
Flush	-0.136	1				
Where land	0.117	0.000	1			
Flushing distance	-0.027	-0.008	0.034	1		
Distance fly	0.006	0.027	-0.129	0.414*	1	
Flush nearest cover	-0.010	0.115	0.230*	-0.077	-0.456*	1

* $P < 0.05$

Table 12. Correlation coefficients between quail numbers and annual trend with seven weather indices. Quail numbers were obtained from Christmas bird counts. There are 14 years of data in each correlation.

	Weather Index						
	June - July Rainfall	Total annual snow	June - July wet days	April-May temp.	Dec-Mar freezing days	Dec - March precip.	June-July temp.
Numbers of quail	-0.09	0.04	-0.01	-0.49	0.25	0.18	-0.28
Annual population trend	0.02	-0.12	-0.07	-0.22	-0.24	0.15	0.12

Table 13. 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.

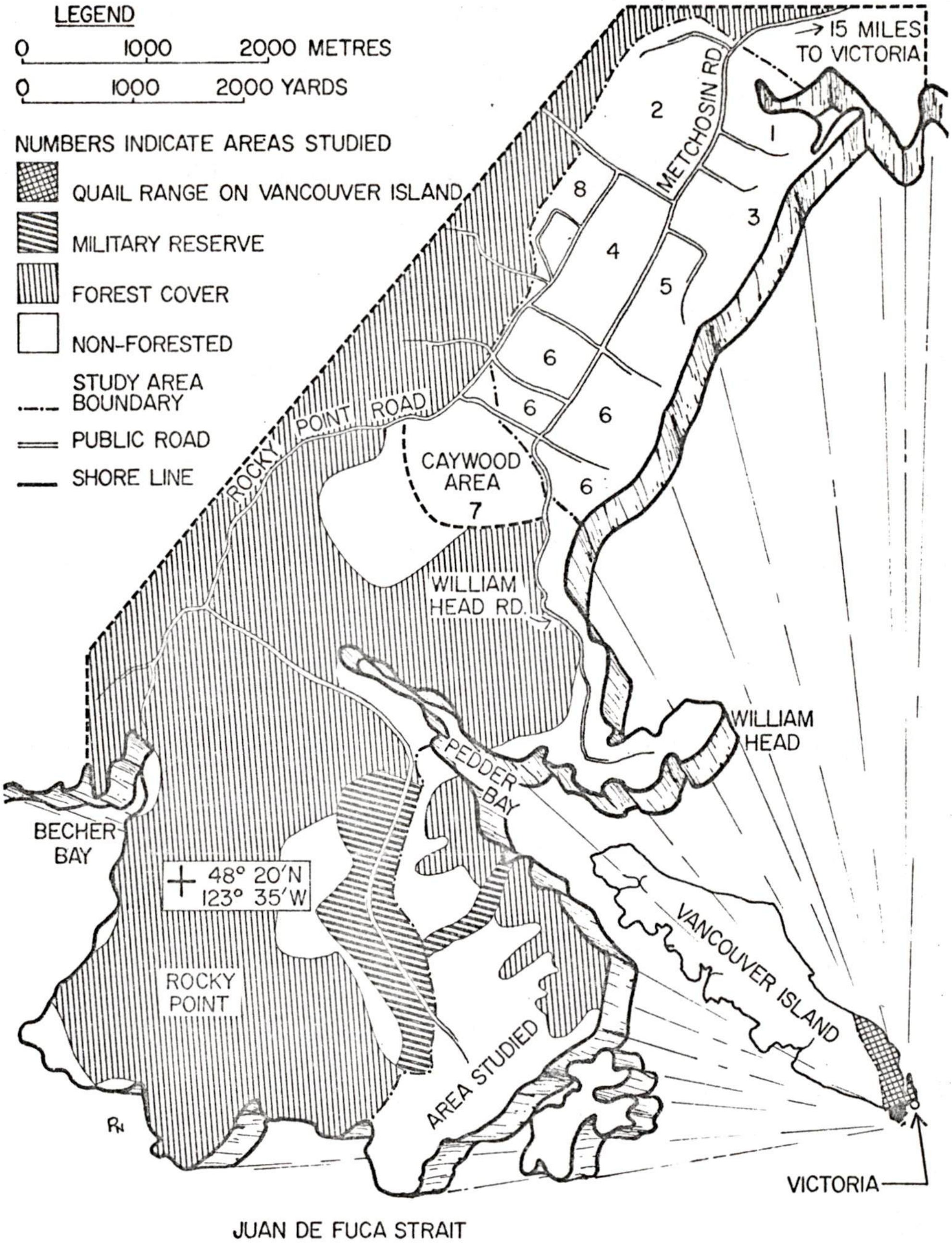

Fig. 1. The study area, showing its position on Vancouver Island (the black spot on the southern tip) and some of the surrounding forested area. The Metchosin study area is the area containing numbers northeast of Caywood area. The numbers refer to subsections of the study area for censusing purposes.

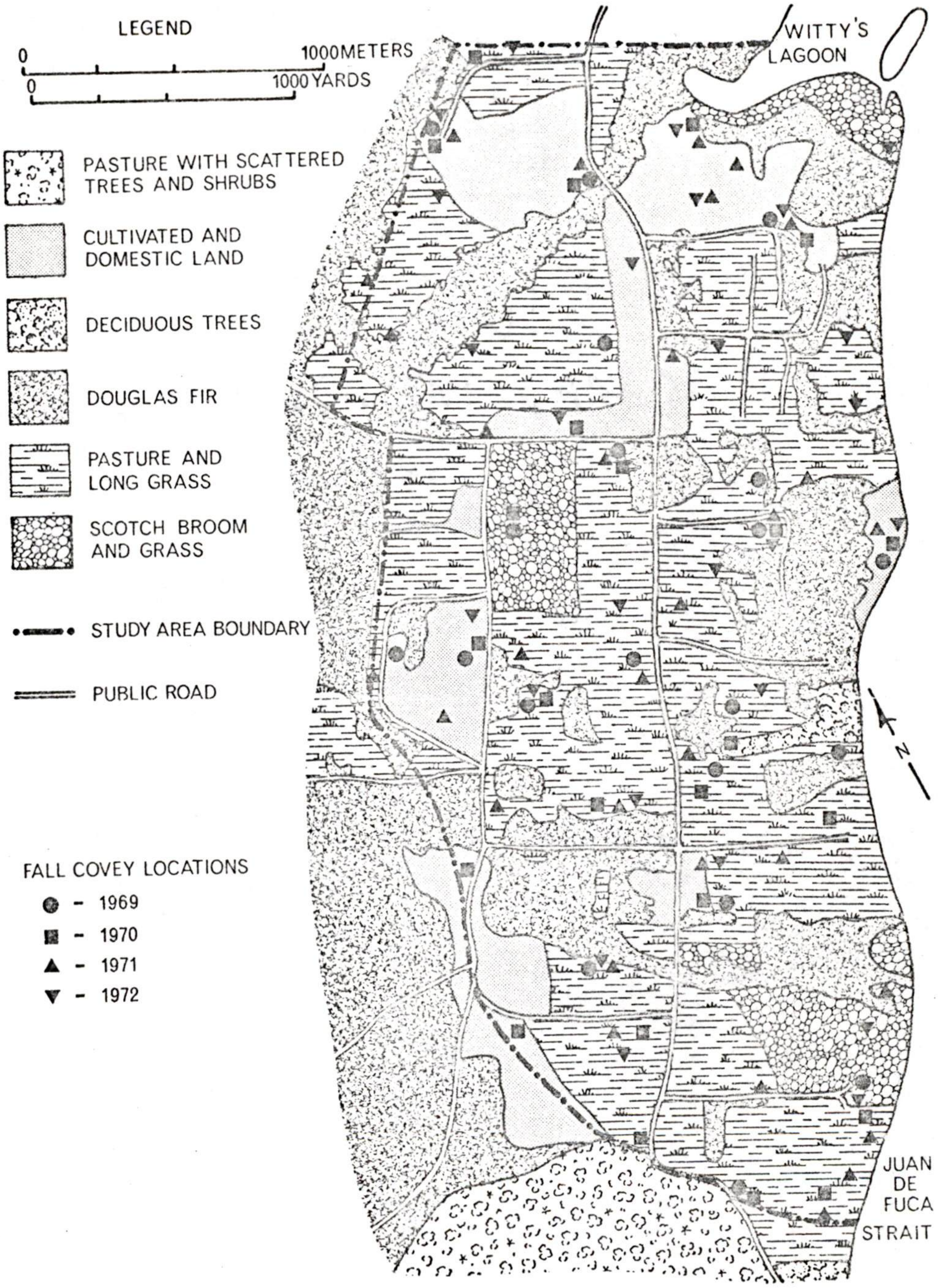

Fig. 2. The Metchosin study area showing vegetation cover and land use. The locations of all coveys found during the fall censuses are shown.

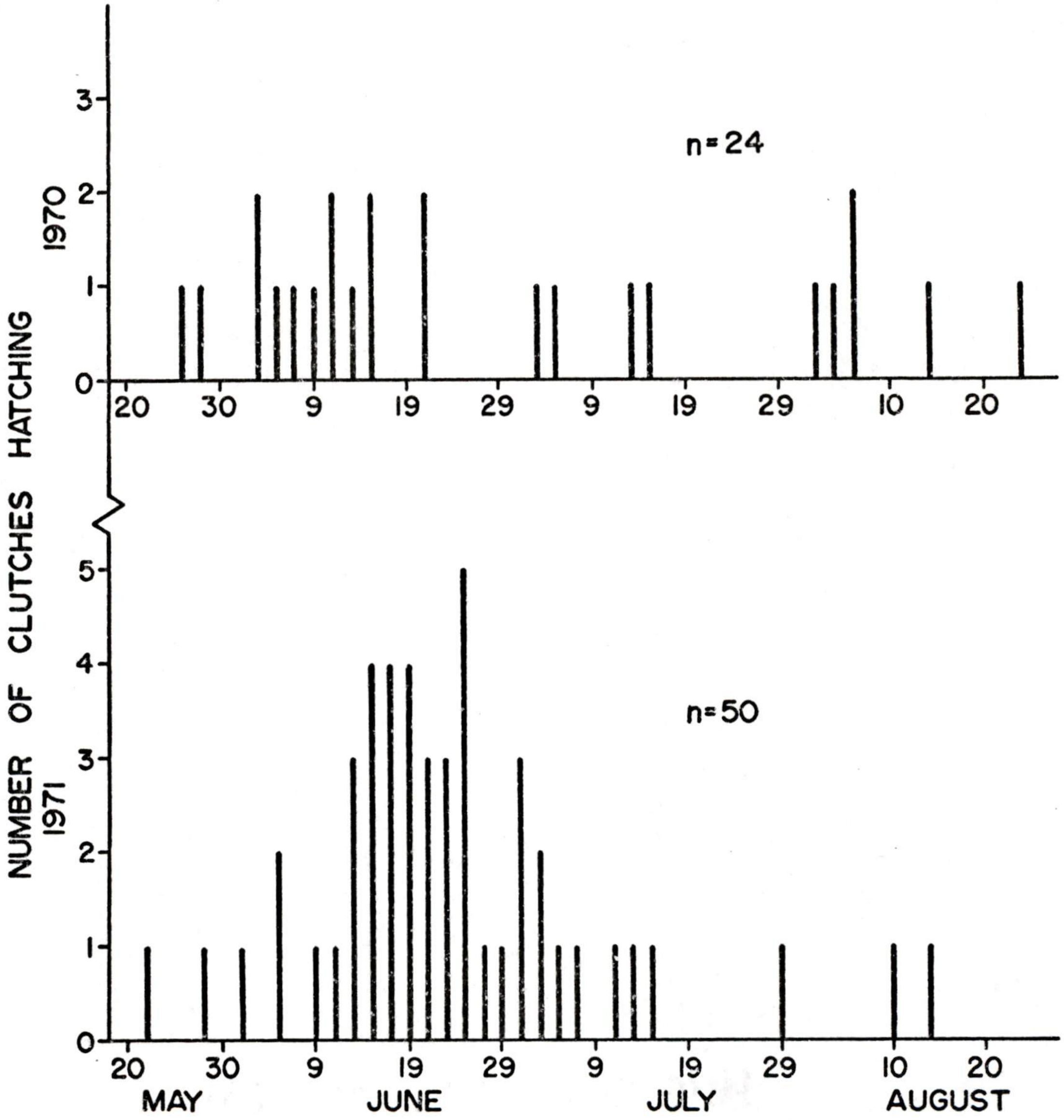

Fig. 3. Hatching curves for 1970 and 1971. Points on the X axis are pairs of adjacent days which are lumped for ease of graphic portrayal.

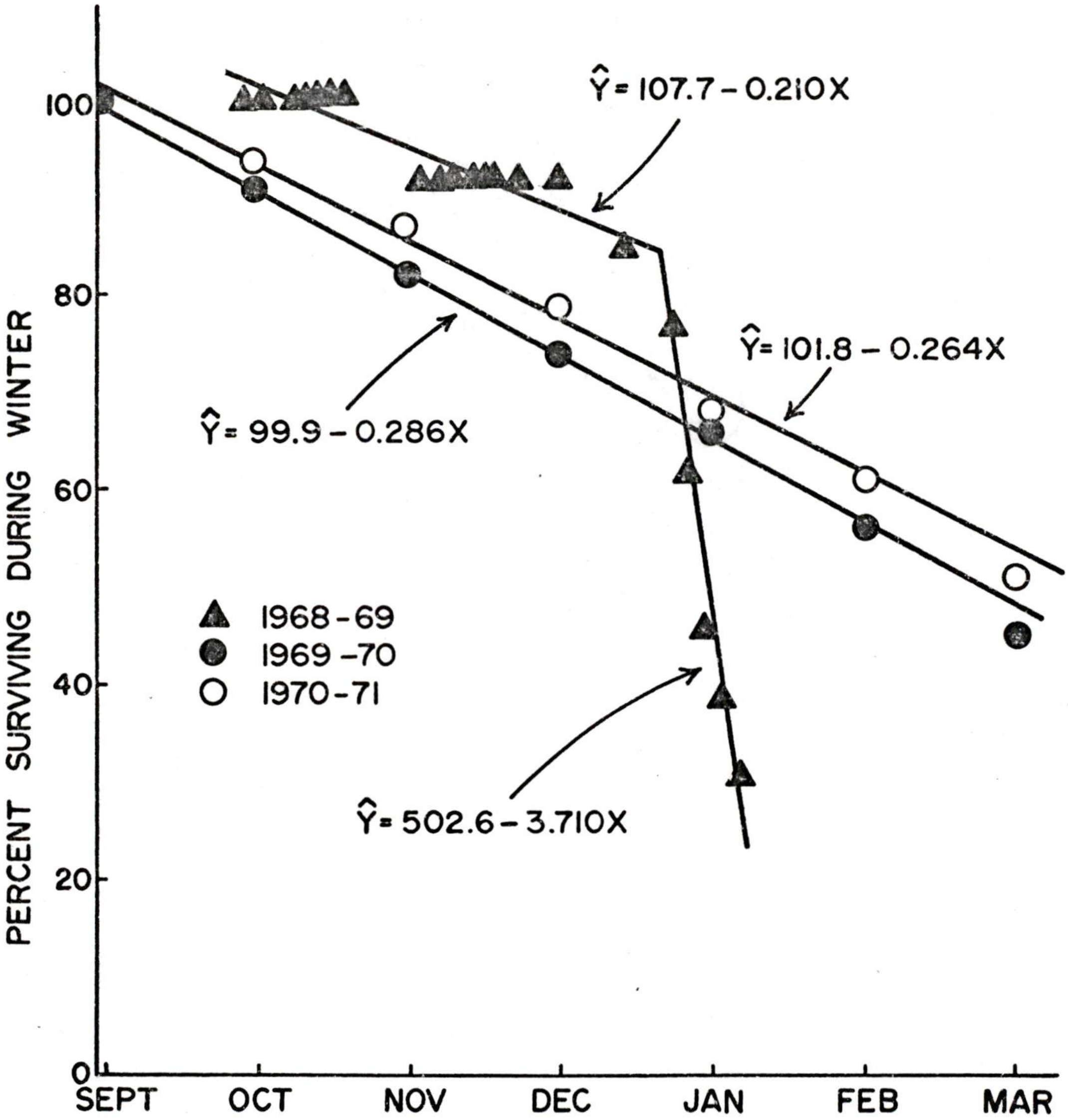

Fig. 4. Winter mortality for the years 1968-69 to 1970-71. The lines are regression lines. The winter 1968-69 has two lines due to much higher mortality during January than for the rest of the year.

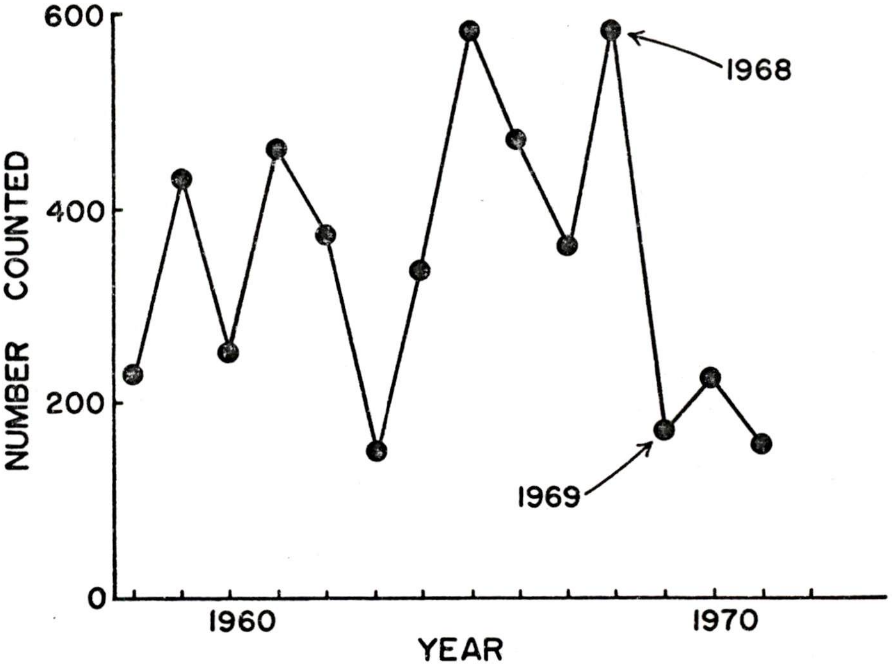

Fig. 5. The numbers of quail counted from 1958 to 1971 by the Victoria Natural History Society during the annual bird counts at Christmas.

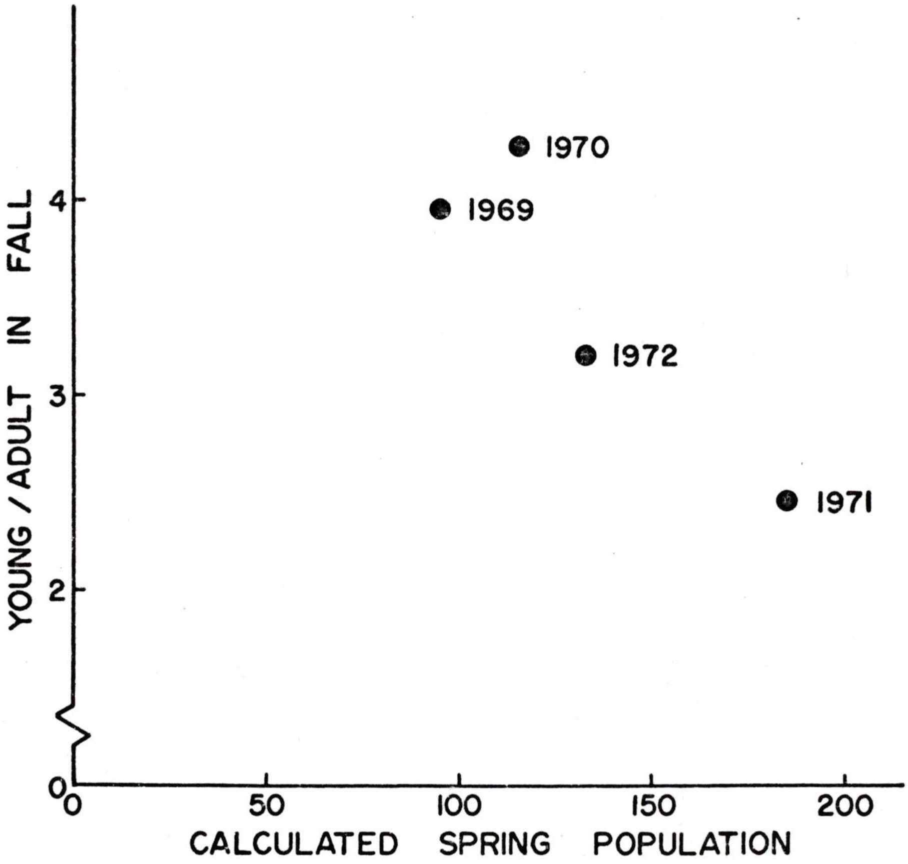

Fig. 6. The young-adult ratios plotted against the calculated spring population showing a negative relationship.

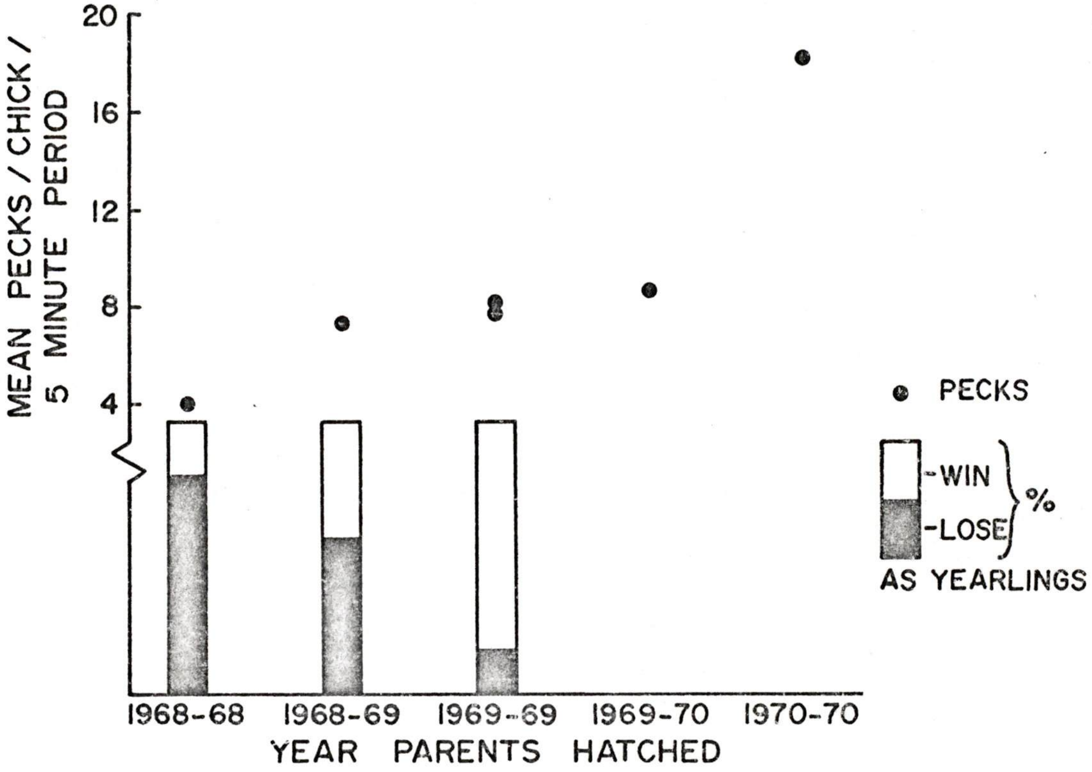

Fig. 7. Chick aggression plotted against the years in which the parents were hatched. Since observations were made in two summers (1970 and 1971), the chicks with two yearling parents in 1970 and chicks with two adult parents in 1971 both had parents hatched in 1969, hence the two dots above 1969-69. Also shown is the percent win and lose of the yearlings captured as chicks in 1970 and tested using cock pairings in 1971. These birds are also classified with respect to the age of their parents.

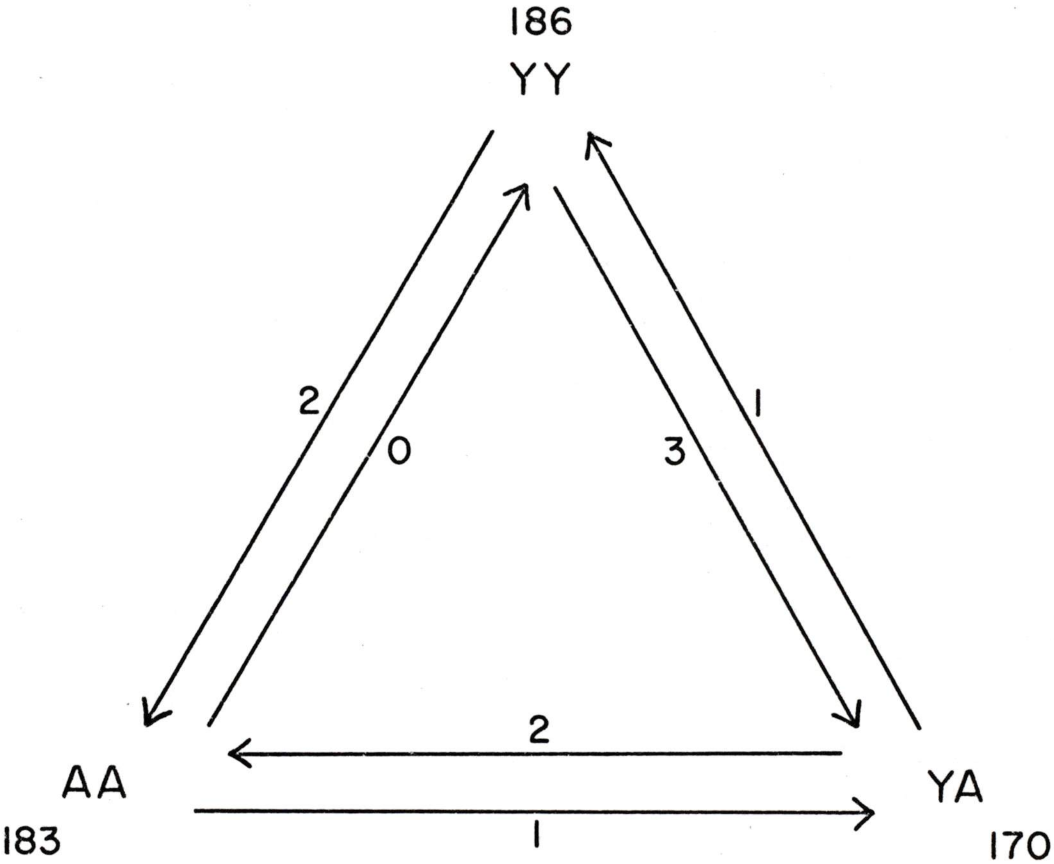

Fig. 8. Dominance established in paired encounters in the spring of 1971 by the cocks held over the winter from the summer of 1970 when they were captured as chicks. The foot of the arrow indicates the parentage of the dominant cock. The numbers on the arrows are the number of wins in each category. The numbers beside the parentages are the average weights of the birds.

Expectation of the number of trends obtained by Lamont Cole's numbers

If X is a random variable which is uniformly distributed over the interval 0 to 1, and Y is a random variable which consists of the sum of two consecutive values of X, then the following argument will demonstrate that the number of trends expected over several values of Y will be less than the number expected from a simple list of random numbers.

$Y_i = X_i + X_{i-1}$

$P(Y_{i+1} > Y_i) = P((X_i + X_{i+1}) > (X_i + X_{i-1}))$

$= P(X_{i+1} > X_{i-1}) = \frac{1}{2}$

Similarly $P(Y_{i-1} > Y_i) = P(X_i < X_{i-2}) = \frac{1}{2}$

The unconditional probability of a change of direction, then, is

$P((Y_i < Y_{i+1}) \text{ and } (Y_i < Y_{i-1})) + P((Y_i > Y_{i+1}) \text{ and } (Y_i > Y_{i-1}))$

The first term in the above can be rewritten as

$P((X_{i+1} > X_{i-1}) \text{ and } (X_i < X_{i-2})) = P(X_{i+1} > X_{i-1}) \cdot P(X_i < X_{i-2})$ as the X's are independent, and this equals $\frac{1}{2} \cdot \frac{1}{2} = \frac{1}{4}$

The second term in the above can be similarly treated and also equals $\frac{1}{4}$

Then $\frac{1}{4} + \frac{1}{4} = \frac{1}{2}$ so the probability of a change of direction between any two numbers is $\frac{1}{2}$. This is less than the probability of a change of direction for a sequence of random numbers, which in the limiting case is 2/3. If, for running sums, the probability of a change is $\frac{1}{2}$, then the expected time until a change occurs is $1/\frac{1}{2} = 2$ (Parzen, 1960). Thus the expected time for two changes to occur is 4 successive numbers. For animals with one reproductive period per year, this means that the expected period of the oscillations over a long sequence of sums is 4 years. The effect of a finite sequence is to decrease the number of oscillations observed as the first two observations cannot determine peaks, and hence the average oscillatory period is slightly increased (Cole, 1954).

Surname: BARCLAY Given Names: HUGH JOHN

Place of Birth: PORT ALICE, B.C. Date of Birth: SEPTEMBER 13, 1941

Educational Institutions Attended, with Dates of Entering and Leaving:

VICTORIA COLLEGE, VICTORIA, B.C.	1959 to 1961
UNIVERSITY OF B. C., VANCOUVER, B.C.	1961 to 1964
UNIVERSITY OF VICTORIA, VICTORIA, B.C.	1968 to 1973
	to

Degrees, Diplomas, Etc., Awarded, with Dates and Names of Institutions:

B.Sc.	1964	UNIVERSITY OF B. C., VANCOUVER, B.C.

Honors and Awards:

University of Victoria Scholarship, 1971/72

University of Victoria Scholarship, 1972/73

Publications:

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