NESTING PARAMETERS OF BLUE GROUSE AND THEIR RELEVANCE TO POPULATIONS

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Animal populations ebb or flow in relation to the balance between natality and mortality. A fundamental problem is whether mortality is fixed and natality dependent, or vice versa (von Haartman 1971). For instance, Wynne-Edwards (1962) argued that either side of the population equation may vary. Yapp (1970) suggested that mortality is more or less constant and that natality varies and Lack (1954, 1966), von Haartman (1971), and others, indicated that variations in mortality are most important in the regulation of numbers. Clearly, there is a need to document rates of natality and mortality in natural populations, especially where they can be related to the state of the populations. I will consider clutch size, fertility and hatchability of eggs, and nesting success of Blue Grouse (*Dendragapus obscurus*). All concern the natality side of the above controversy.

Several colleagues and I have conducted intensive population studies of Blue Grouse almost continuously from 1962–1973 in an area near Courtenay, British Columbia, on Vancouver Island. We found 151 nests of Blue Grouse, of which 136 were used in the present analyses. Estimates of some reproductive parameters have been reported for Blue Grouse on Vancouver Island (Bendell 1955a, Bendell and Elliott 1967, Zwickel and Bendell 1967, 1972, Redfield 1972), but generally were based on smaller samples.

During the period 1962–1973 breeding populations have shown both stability and change. From 1962–1965, breeding densities were stable at a relatively low level (Zwickel and Bendell 1967, unpubl. data). From 1969–1971 breeding densities increased steadily (Zwickel 1972) and have now stabilized at about the 1971 level, approximately 40% higher than in the period 1962–1965. These factors allow a comparison of reproductive parameters between a low density, stable breeding population and a higher density, increasing population.

STUDY AREA

The study area is approximately 15 km northwest of Courtenay in a region intermediate between the Douglas fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) bioclimatic zones (Krajina 1959). For descriptions of this area see Zwickel and Bendell (1967, 1972), Redfield et al. (1970), and Zwickel (1972).

Information for 1962–1965 is from Comox Burn, Wolf Lake, and immediate surroundings (Zwickel and Bendell 1967), an area of about 1200 ha. Data for 1969–1973 are from Comox Burn, Tsolum Main, and immediate surroundings (Zwickel 1972), a region of about 2000 ha. There is no indication of any variations in parameters to be discussed here between Comox Burn, Wolf Lake, or Tsolum Main.

METHODS AND DEFINITIONS

Field methods are discussed in some detail elsewhere (Zwickel and Bendell 1967, 1972, Zwickel 1972). In brief, study areas were searched almost daily throughout each nesting season with trained pointing dogs. Practically all nests found were located by dogs. From 1962–1964, many eggs were taken from nests for aviary studies. Except where noted, aviary data are not included here.

Most nests used in these analyses were active when found. Exceptions are two cases in which hens with broods of very young chicks were found near newly hatched nests and three cases in which nests that appeared undisturbed were found by dogs (which indicates recent scent) but for which females were never seen.

Except where noted, the Mann-Whitney U-test was used for statistical evaluations of clutch size. Chi-square 2×2 contingency tests, or G-tests (Sokal and Rohlf 1969) where expected values were less than 5, were used for other statistical analyses. Data were considered significantly different if $P < 0.05$.

Clutch size refers to completed clutches only; clutches were considered complete if incubation was underway, or in a very few cases, almost certainly underway. *Fertility* is used in relation to individual eggs, not the population, as it is sometimes applied (Wynne-Edwards 1962). Figures for fertility were based on hatched eggs plus an examination of unhatched eggs that were known to have undergone incubation. Unhatched eggs were examined for the presence of embryos and in some cases very young embryos may have been missed. Estimates of fertility are therefore minimal. *Hatchability* refers to the inherent ability of individual eggs to hatch, not to clutches of eggs or nests. Except where noted, data on hatchability are from hens that were successful in completing the nesting cycle in the wild. *Gross hatchability* includes both fertile and infertile eggs. *Nesting success* describes the fate of nests in the wild (i.e., females were either successful or not successful in completing the nesting cycle). These data include all nests, whether the clutch was complete or not, except those from which we took all eggs for our aviary. If at least one egg hatched, a nest was classi-

TABLE 1. Mean clutch sizes and range in size of clutches of all females, by year.

Year	No. of clutches	No. of eggs	Mean (±SE)	Range
1962	13	73	5.62 ± .31	4–7
1963	5	32	6.40 ± .75	4–8
1964	11	80	7.27 ± .43	5–9
1965	1	5	—	—
Total, 1962–1965	30	190	6.33 ± .27	4–9
1969	12	69	5.75 ± .49	3–9
1970	10	69	6.90 ± .38	4–8
1971	27	173	6.41 ± .21	4–9
1972	16	104	6.50 ± .40	4–8
1973	23	147	6.39 ± .25	5–8
Total, 1969–1973	88	562	6.39 ± .14	3–9
Grand total	118	752	6.37 ± .13	3–9

fied as successful. Hatching success refers to the number, or proportion, of living young hatched in the wild (i.e., to Wynne-Edwards' [1962] fertility at the population level).

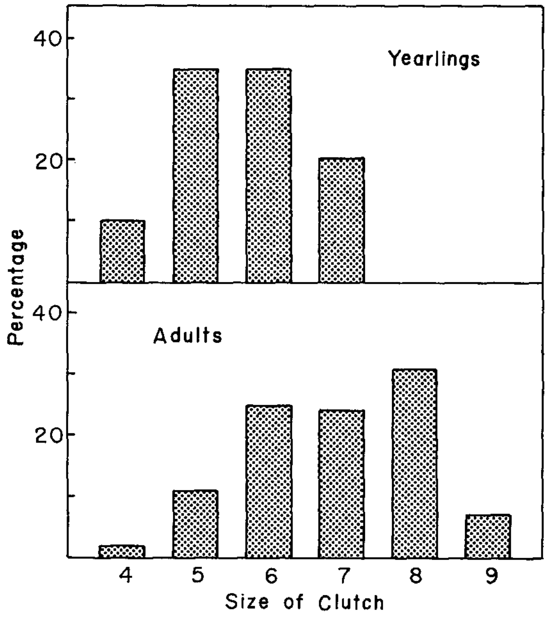

FIGURE 1. Frequency distribution of clutches of yearling (n = 20) and adult (n = 55) females. Data from 1962–1965 and 1969–1973 are combined.

RESULTS

CLUTCH SIZE

Age of the female—as to yearling (*ca* 11–13 months of age) or adult (> 23 months of age) —was known for 75 females for whom clutch size was determined. Clutch size was not significantly different between 1962–1965 and 1969–1973 for yearling or adult females so I combined these data (fig. 1). Clutch size of yearlings ($n = 20$, $\bar{x} = 5.65 \pm .21$SE, range = 4–7) was significantly less than that of adults ($n = 55$, $\bar{x} = 6.93 \pm .16$SE, range = 4–9). Clearly, adults had larger clutches and a greater range in size of clutch than yearlings.

Date of hatch was determined for the nests of 46 females whose ages were known. A distinct break in the distribution of clutch sizes was evident at about 30 June for adults (only one clutch of a yearling hatched after 30 June). Therefore, I compared clutch size of adults for the period up to and including 30 June ($n = 33$, $\bar{x} = 7.30 \pm .18$SE) to that after this date ($n = 13$, $\bar{x} = 6.00 \pm .36$SE). Clutch size was significantly different for the two periods. Since Blue Grouse renest (Zwickel and Lance 1965), most clutches hatching after 30 June likely represented attempts at renesting. If so, clutches are smaller for renesting attempts than in first nests.

Data on clutch sizes in different years are presented in table 1. Excluding data from 1965 because of the small sample, clutch sizes from each year were compared to those of every other year. In 28 such comparisons there were 4 significant differences; clutch size in 1962 and 1969 was significantly lower than in 1964 and 1970. Thus, although clutch size is relatively constant from year to year, it may vary significantly.

Theoretically, variations in clutch size among years could be related to variations in the age structure of the breeding population or amount of renesting. The proportion of yearling females in the population did not vary significantly among any of the years 1962, 1964, 1969, or 1970. Observed variations in clutch size cannot, therefore, be related to age structure. Samples are too small to examine for annual differences in the amount of renesting.

If breeding populations respond to variations in reproductive parameters, recruitment

TABLE 2. Percentage yearling females among breeding age females at Comox Burn as related to clutch size in the previous year.

Year	Clutch size	Percent yearling females in following year
1962	5.62	41
1963	6.40	33
1969	5.75	38
1970	6.90	51
1971	6.41	38
1972	6.50	32

TABLE 3. Fertility and hatchability of eggs of yearling and adult females in the wild. Data from 1962–1965 and 1969–1973 combined.

	Age of female	
	Yearling	Adult
Fertility		
No. of clutches	16	39
No. of eggs	88	234
No. fertile	87	230
Percent fertile	98.9	98.3
Hatchability		
No. of clutches	15	36
No. of eggs	78	216
No. hatched	77	204
Percent hatched	98.7	94.4

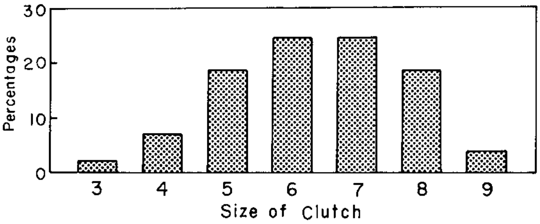

FIGURE 2. Frequency distribution of clutches of all females (n = 118). Data from 1962–1965 and 1969–1973 are combined.

in one year could be related to size of clutch in the previous year. I examined this possibility by comparing the proportion of yearlings among breeding age females in one year to clutch size the previous year (table 2); this analysis assumes a constant mortality rate among adults, which has been shown for birds in this area (Zwickel and Bendell 1972). The regression coefficient for these data was not significant ($t = 0.137$, $P > .20$), suggesting no relationship between clutch size and subsequent breeding density.

I combined all data within each of the periods 1962–1965 and 1969–1973 (table 1). Breeding densities were stable at a relatively low level, and increasing and relatively high, respectively. The proportion of clutches from yearlings and adults was approximately the same in each sample. There was no significant difference in size of clutch between the two periods. The combined mean of 6.37 (table 1) seems the best general estimate of clutch size of Blue Grouse for the Courtenay region. A frequency distribution of all clutch sizes combined is shown in figure 2.

FERTILITY

Data on fertility of eggs of known-aged females were combined for the periods 1962–1965 and 1969–1973 because of very small samples during the earlier period (table 3). There was no significant difference in the proportion of fertile eggs from yearling or adult females.

Fertility values were compared among the years 1969–1973 (table 4). In 10 such comparisons, there were 2 significant differences. Both involved 1971, with fertility in that year lower than in 1972 and 1973. More than one infertile egg was found in a single clutch in only two cases. Both (one with four infertile eggs out of seven, and one with two infertile eggs out of seven) occurred in 1971 and account in large part for the lower indicated fertility in that year. Indicated differences may result from chance variation and I conclude that fertility was high and constant among years.

TABLE 4. Fertility and hatchability of eggs of all females by year (1969–1973) and for the two periods (1962–1965 and 1969–1973). Hatchability is based only on eggs from nests of hens that were successful in completing the nesting cycle.

	1969	1970	1971	1972[a]	1973	1962–1965	1969–1973
Fertility							
No. of clutches	9	5	26	10	25	8	75
No. of eggs	43	22	146	53	125	34	389
No. of fertile eggs	42	22	138	53	125	33	380
Percent fertile	97.7	100	94.5	100	100	97.1	97.7
Hatchability							
No. of clutches	8	2	22	9	18	7	59
No. of eggs	41	10	142	54	103	29	350
No. hatched	39	10	132	51	102	26	334
Percent hatched	95.1	100	93.0	94.4	99.0	89.7	95.4
No. of fertile eggs	40	10	135	54	103	28	342
Percent of fertile eggs hatched	97.5	100	97.7	94.4	99.0	92.9	97.6

[a] Two eggs were not useable for the analysis of fertility in 1972.

TABLE 5. Fertility and hatchability of eggs of known-aged females and of all females (includes some eggs for which age of female was not known) in the aviary (1962–1964).[a]

	Yearling	Adults	All females
Fertility			
No. of clutches	6	18	29
No. of eggs	32	94	146
No. fertile	29	91	132
Percent fertile	90.1	96.8	90.4
Hatchability			
No. of clutches	6	9	15
No. of eggs	32	53	85
No. hatched	25	43	68
Percent hatched	78.1	81.1	80.8
No. of fertile eggs	29	47	76
Percent of fertile eggs hatched	86.2	91.4	89.5

[a] No data for hatchability are included for 1964 because of incubator problems in that year (Zwickel and Bendell 1967).

Data for fertility of eggs for 1962–1965 are compared to those for 1969–1973 in table 4. Fertility was not significantly different in these periods. Of all eggs left in the wild, 97.6% (413/423) were fertile.

HATCHABILITY

Data for hatchability of eggs of known-aged females were combined for the periods 1962–1965 and 1969–1973 (table 3). There was no difference in the hatchability of eggs of yearlings or adults.

Gross hatchability among years was examined for 1969–1973 only (table 4). In 10 paired comparisons there was one significant difference, hatchability in 1971 being lower than in 1973. The relatively low hatchability in 1971 seems related to the low indicated fertility in that year for there were no significant differences in hatchability of fertile eggs among years. I conclude that hatchability was high and constant among years.

Hatchability of eggs left in the wild in 1962–1965 is compared to that for 1969–1973 in table 4. Neither gross hatchability nor hatchability of fertile eggs only was significantly different for the two periods; hatchability was high and similar in 1962–1965 and 1969–1973. Gross hatchability for all years combined was 95.0% (360/379) and that for all fertile eggs was 97.3% (360/370).

FERTILITY AND HATCHABILITY IN AVIARY

Data from eggs that were taken from the wild and handled in our aviary (1962–1964) were analyzed separately from those left in the wild because of possible treatment effects (table 5). I found no significant differences in the fertility or hatchability of eggs of yearling or adult females. These data agree with, and confirm, the conclusion from eggs left in the wild.

TABLE 6. Nesting success of yearling and adult females. Data from 1962–1965 ($n = 10$) and 1969–1973 ($n = 52$) combined.

Age of female	No. of nests	No. hatched	No. to predators	No. deserted	Percent hatched
Yearling	16	14	0	2	87.5
Adult	46	39	5	2	84.8

To examine for treatment effects in our aviary, I compared fertility and hatchability of eggs in the aviary to those for all eggs left in the wild. Fertility, gross hatchability, and hatchability of fertile eggs only were all significantly less in eggs handled in the aviary.

I did not attempt to analyze fertility and hatchability among years in the aviary or in the wild for the period 1962–1965 because of the relatively small samples involved. However, indications are that fertility and hatchability were constant among years during that period (Zwickel and Bendell 1967), thus agreeing with data from 1969–1973.

NESTING SUCCESS

Nesting success of all known-aged females is summarized in table 6. There was no significant difference in the success of yearling and adult females.

Too few nests were left intact in the wild in 1962–1965 and 1970 to examine nesting success among these years. Therefore, among year statistical comparisons involve data for 1969 and 1971–1973 only (table 7). In six possible comparisons, nesting success was significantly different between 1971 and 1972 only. This difference seems to result mainly from a very high rate of nest predation in 1972. There was no obvious reason for such a high rate of nest

TABLE 7. Nesting success of all females by year (1969–1973) and for the periods 1962–1965 and 1969–1973.

Year	No. of nests	No. hatched	No. to predators	No. deserted	Percent hatched
1969	16	10	2	4	62.5
1970	4	2	2	0	50.0
1971	30	22	5	3	73.3
1972	22	9	10	3	40.9
1973	29	16	7	6	55.1
1962–1965	21	10	6	5	47.6
1969–1973	101	59	26	16	58.4
Total	122	69	32	21	56.6

TABLE 8. Frequency distribution of "successful" and "unsuccessful" nests in relation to size of clutch.[a]

	Size of clutch							
	3	4	5	6	7	8	9	Total
No. successful	2	1	14	17	16	12	4	66
No. unsuccessful	0	4	6	7	10	9	1	37
Total	2	5	20	24	26	21	5	103

[a] Only nests in which clutches were complete were used in this analysis.

predation in that year and perhaps this result was due to chance. Generally, nesting success was relatively constant from year to year.

Data on nesting success of all females for the 1962–1965 and 1969–1973 periods of study are presented in table 7. There was no significant difference in the proportion of nests hatching in the two periods.

Overall, 57% of all nests in the wild hatched successfully, with 26% destroyed by predators, and 17% deserted. Hence, of unsuccessful nests, 60% were lost to predation and 40% deserted. Of 16 desertions in the period 1969–1973, 10 were by females that were still laying. Our activities likely caused a high proportion of these desertions as 8 out of 10 of the females were not seen after the first contact. In only 5 of the 16 desertions was incubation underway, and in 3 of these cases clutch size was decreasing. Here, desertion was likely caused by a small predator taking individual eggs. Our activities may have also increased predation rates on nests. Hence, 57% is a minimum estimate of nesting success.

Clutch size is variable and possibly some sizes may be most successful, which over the long term would result in selection for the more successful size(s). I examined the frequency distribution of successful and unsuccessful nests in relation to size of clutch (table 8) with the G-test. There was no significant difference, suggesting that clutches of all sizes had an equal probability of hatching.

HATCHING SUCCESS

Based on data presented above, of every 1000 eggs laid, approximately 566 (56.6%) would be expected in nests in which females completed the nesting cycle. Of these, approximately 552 (97.6%) would be fertile, with approximately 538 (97.3%) of the fertile eggs hatching. Hence, for every 1000 eggs laid, approximately 54% would hatch. Since percentages for nesting success and fertility are minimal, this seems a conservative estimate of hatching success.

DISCUSSION

In birds, any reproductive parameters associated with nesting may affect recruitment. Those studied here are of interest in terms of both the biology of Blue Grouse and in relation to current population theory.

NESTING PARAMETERS AND THE BIOLOGY OF BLUE GROUSE

Size of clutch varies with age of female in various species of birds (Lack 1954, Cody 1971, von Haartman 1971). Of the four reproductive parameters I considered, only clutch size differed significantly between yearling and adult female Blue Grouse. Redfield (1972) also reported a difference in mean size of clutch of yearling and adult female Blue Grouse, but probably because of small samples, did not find a statistically significant difference. Bendell and Elliott (1967) reported no statistical difference in the size of clutches of yearlings and adults and I suspect their result was also related to small samples. From my more complete data, I conclude that, on average, adults have larger clutches than yearlings.

Lack (1954) argued that differences in clutch size between young and older birds are related to experience in finding food rather than to differences in physiological maturity between the two age classes. If experience were involved, this argument might also apply to nesting success. Experience in finding food, and its resultant effects on reproductive capacities, might also affect hatchability and fertility of eggs. In none of these parameters was there a difference between age classes of Blue Grouse. Therefore, the smaller clutches of yearlings are likely related to physiological maturity. This conclusion is based in part on the fact that yearling females are lighter than adults (Bendell 1955b, Zwickel et al. 1966, Boag 1965, Redfield 1973). Also, while yearlings may not be able to renest (Zwickel and Lance 1965, unpublished data), adults can.

Johnsgard (1973) summarized data on nesting success for Blue Grouse and other tetraonids. He showed a nesting success of 75% for Blue Grouse as derived from earlier studies on Vancouver Island (Bendell 1955a). This figure is substantially higher than reported here. The difference probably results from the fact that figures presented by Johnsgard were from 36 nests of which only 6 were active when found. Data from inactive nests may not be representative for an analysis of nesting success, because inactive nests with all eggs removed (by far the most common type of nest predation) are rarely found. Thus, figures on nesting success presented by Johnsgard may be too high.

Johnsgard's summary of hatchability (gross) of several tetraonids shows a range of 84 to 98%. The gross hatchability of 95% for Blue Grouse in the Courtenay region is near the upper range of hatchability figures of the different tetraonids. Johnsgard's summary of nesting success of different tetraonids shows a range of 40 to 80%; the minimum nesting success of 57% for Blue Grouse in the Courtenay region lies in about the middle of this range of values.

Clutches of eggs used in this analysis almost certainly include some from renesting attempts. Hence, a 57% nesting success does not equate to success of the population. For example, Errrington and Hamerstrom (1937) pointed out that although only 59% of all Ring-necked Pheasant (*Phasianus colchicus*) clutches in one area hatched, because of renesting some 70 to 80% of all females were successful at bringing off broods. Blue Grouse do renest but the extent to which they do so is not known. Clearly, the proportion of females bringing off broods exceeds 57%.

My data indicate that a minimum of 54% of all eggs laid can be expected to hatch and this percentage is probably applicable to other populations of Blue Grouse on Vancouver Island. This conclusion is based on the observation that clutch sizes and nesting success reported for Blue Grouse on other areas of Vancouver Island are generally very similar to those reported here (Bendell 1955a, Bendell and Elliott 1967, Redfield 1972).

NESTING PARAMETERS AND POPULATIONS

All nesting parameters reported here except hatchability showed some significant deviations among years. Are these deviations related to subsequent performance of the populations? This possibility exists for clutch size for the maximum difference of 1.65 eggs between low and high means represents over 20% of the maximum annual mean. However, there was no significant relationship between clutch size and subsequent recruitment of yearlings into the population. Thus, variations in clutch size among years must have been overridden by other factors.

Fertility was high and relatively constant among years. The magnitude of variation among years (85–100%) leaves little room for causing significant variations in population density. Hatchability was also high and constant among years. Neither annual variations in fertility nor hatchability appears to be an important potential contributor to population change.

Annual variations in nesting success are more difficult to evaluate because of smaller samples and the lack of comparable data for the early years of study. Generally, nesting success was relatively constant among years and appears to have had little effect on subsequent breeding density. However, larger sample sizes are needed to evaluate this parameter more critically.

Some of the problems associated with sample sizes among years can be avoided by comparing nesting parameters between 1962–1965, a period of relatively low and stable population, and 1969–1973, a period of generally increasing and higher density population. There were no significant differences in any of the parameters examined between these two periods. These results support conclusions above which indicate no relationships between any of the parameters examined and subsequent performance of the breeding population. Hence, none of these parameters appears to be involved in the process of population regulation. I see no evidence in data presented here for correlations between nesting parameters and density of the subsequent breeding population, as reported for Red Grouse, *Lagopus lagopus* (Jenkins et al. 1963, Watson and Moss 1972), and Rock Ptarmigan, *Lagopus mutus* (Watson 1965, Weeden and Theberge 1972). Perhaps the lack of agreement among studies results from the ptarmigan being so-called "cyclic" species.

In summary, data presented here do not support the contention that variations in reproductive parameters associated with natality are necessary to bring about changes in the breeding density of Blue Grouse. This conclusion is in agreement with the generalization of Lack (1954, 1966), von Haartman (1970) and others about the relationship between natality and subsequent populations.

AVIARY DATA

Aviary programs cannot exactly duplicate conditions in nature. Data presented here indicate that the fertility and hatchability of eggs in our aviary were significantly less than in the wild. Despite this finding, the fertility and hatchability of eggs handled by us were generally comparable to those found in other aviary studies with both domestic and wild galliforms (Zwickel and Bendell 1967). Hence, few or no artificial programs may be realizing the full reproductive potential of galliforms as expressed in the wild.

SUMMARY

Data on clutch size, fertility and hatchability of eggs, and nesting success were obtained from 136 nests of Blue Grouse during 9 years of studies on Vancouver Island, British Columbia. Only clutch size differed significantly between yearling and adult females, with yearlings having the smallest clutches. This difference between age classes is likely related to physiological maturity of the two groups of females.

Clutch size varied among years but these variations showed no relation to subsequent breeding density. Fertility of eggs was high in all years (95–100%) but did show some significant differences among years. Hatchability of fertile eggs was high (97.3%) and constant among years. Nesting success showed one significant difference among years but this had no apparent effect on subsequent breeding density. Overall, the parameters measured were relatively constant among years and deviations that did occur bore no relationship to breeding density in the following year.

None of the four variables examined were significantly different between a period of relatively low and stable population density and a period of increasing and higher population density. Hence, no variations were necessary in any of the parameters examined to bring about population change.

Fertility, gross hatchability, and hatchability of fertile eggs only were all lower in an aviary than in eggs left in the wild. Nevertheless, fertility and hatchability were comparable to those reported for aviary studies of other species of galliforms, both domestic and wild.

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