

# LOCAL VARIATIONS IN THE TIME OF BREEDING OF FEMALE BLUE GROUSE

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Restricted breeding seasons are generally accepted as being evolutionary adaptations to the optimum timing of availability of food for the young (Lack 1968, Immelmann 1972). Immelmann also noted that food "may have an immediate influence on the time of egg-laying by affecting the adult bird directly." Other factors that may cause proximate variations in time of breeding are photoperiod, rainfall, temperature, local habitat, and behavioral interactions (Immelmann 1972:131-132). Clearly, time of breeding has both evolutionary and short-term implications. In fact, Lack (1968:302) argued, "the date each year at which laying takes place is as important an adaptation for breeding as any discussed in this book . . ."

From 1969 to 1975, my colleagues and I studied two local populations of Blue Grouse (*Dendragapus obscurus*) on the east-central slope of Vancouver Island, British Columbia (Zwickel and Bendell 1972, Zwickel 1972). Although these populations are only about 2 to 3 km apart and, in reality, portions of one continuous population, there have been consistent variations in the time of breeding among years, between populations, and between age classes. A documentation and interpretation of these variations is the main purpose of this paper.

## STUDY AREAS AND METHODS

The two study areas are Comox Burn (485 ha) and Tsolum Main (625 ha). They are separated by a buffer area about 2 to 3 km wide (Fig. 1) and may be described as mountain foothills.

Comox Burn has a generally east-facing aspect with average slopes of about 20° to 25°. Elevations range from about 240 to 460 m above sea level. Many small streams dissect the area, mostly draining from west to east.

Tsolum Main is somewhat higher, with elevations of about 400 to 640 m. The general aspect is east-facing but a major stream system drains through the center of the area, making a large section basin-like. The topography is less broken than at Comox Burn and the southwest boundary terminates on steep slopes of mountains to the west, which reduces afternoon insolation. Because of its generally higher elevation and local topography, Tsolum Main is usually cooler (Fig. 2), has more precipitation (Table 1), collects more snow, and holds snow longer than Comox Burn (Table 2). Comparative temperature regimes at Comox Burn and Tsolum Main are illustrated with data from April and early May 1974

because this was the only year when we gathered climatological records at both areas beginning in early April. These data are generally representative of differences between areas throughout the breeding season. I used snowpack records for 1974 for the same reason; they are representative of differences between areas in other years.

Both areas were in relatively early stages of succession (post-logging or post-burning) during studies reported here. Comox Burn was swept by wildfire in September 1961, after being block-logged between 1947 and 1961. About one-half of Tsolum Main was burned in the same wildfire, with the rest of the area logged by 1969. Both areas were replanted with douglas fir (*Pseudotsuga menziesii*) by 1969. For further detail see Zwickel and Bendell (1967, 1972).

The present analysis requires that dates of breeding be estimated. "Breeding" is used in its general sense, to refer to all events during the reproductive cycle; I use "copulation" to refer to the specific act of breeding. Dates of hatch of nests of individually banded females, as determined by back-dating from ages of chicks captured in the wild, are used as indicators of variations in time of breeding. Ages of chicks were estimated as described by Zwickel and Lance (1966) and modified by Redfield and Zwickel (1976). In each year, over 60% of the total hatch (except 1969 at Comox Burn = 59%) occurred during a two-week period. Within years, I consider these two weeks as the period of peak hatch.

Every year I operated a continuous-recording hygrothermograph near the center of each area; each was enclosed in a small weather screen at ground (grouse) level. Totalizer rain gauges (Daubenmire 1947) were used to measure weekly rainfall. General field methods are documented elsewhere (Zwickel and Bendell 1967, 1972, Zwickel 1972).

## RESULTS

### ARRIVAL ON BREEDING RANGE

Since most Blue Grouse are migratory, timing of breeding may relate to time of arrival on the breeding range. Bendell and Elliott (1967) reported that spring migration varies among years in Blue Grouse but I do not know how much variation occurs on my study areas. However, different sex-age classes do not arrive at the same time, as judged by early spring observations in 1974 and 1975.

At Tsolum Main, in 1974 and 1975, adult males arrived in late March and early April. Significant numbers of yearling males and adult females first began to appear about 15 April, and yearling females about one week later. A few observations at Comox Burn in 1974 indicate that adult males arrived at about the same time as at Tsolum Main, even

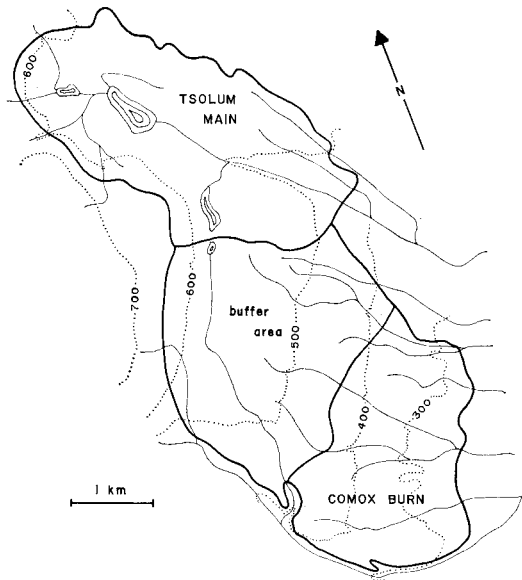


FIGURE 1. Comox Burn and Tsolum Main study areas, Vancouver Island, B.C. Elevations are in meters.

though there was much less snow than at Tsolum Main. Timing of migration may not, therefore, vary between areas, at least among adult males.

#### VARIATIONS IN TIME OF BREEDING

I used periods of peak hatch to examine variations in time of breeding among years (fig. 3). At both areas, the hatch was clearly late in 1971 and early in 1973, with most other years being "normal." At Comox Burn, 1972 may have been a late year, but data from Tsolum Main do not agree.

A likely cause for differences in timing of breeding among years is variation in spring weather, perhaps operating through food supply. Copulation begins in late April and early May. If one assumes that weather conditions on breeding range have the greatest effect on the inception of copulation, and subsequently on periods of peak hatch, then

TABLE 1. Annual spring and summer precipitation (cm) as measured at Comox Burn and Tsolum Main, 1969 to 1975.

Year	Dates sampled	Comox Burn	Tsolum Main
1969	12 May–21 August	25.08	31.02
1970	20 April–24 August	18.74	24.48
1971	26 April–28 August	26.94	30.37
1972	24 April–1 September	26.38	29.88
1973	16 April–3 September	28.58	38.05
1974	8 April–30 August	27.43	33.14
1975	22 April–19 August	20.08	22.50
Average		24.75	29.92

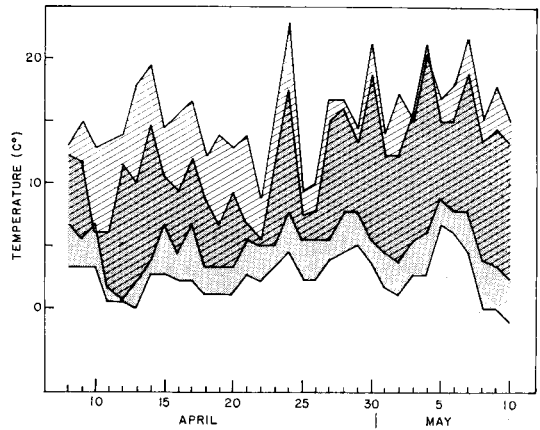


FIGURE 2. Daily maximum and minimum temperatures at Comox Burn (cross-hatched) and Tsolum Main (stippled), 8 April to 10 May 1974.

variations in April weather would seem the likely cause of variations in time of breeding among years.

My field season has begun too late in most years to use weather data from my specific study areas to examine this problem. I therefore examined mean maximum and mean minimum daily temperatures and total precipitation from the town of Comox for each April for the years 1969 to 1975 (Fig. 4); the weather station at Comox is near sea level and is about 20 km E of the study areas.

The month of April was clearly cool and wet in 1972 and warm and dry in 1973. The

TABLE 2. Snowpack at Comox Burn and Tsolum Main in spring of 1974; from field notes.

- 19 March. Comox Burn—some south-facing slopes 95% bare; up to 1 m of snow on north-facing slopes; 20–25 cm of snow on level at mid elevations.
- 22 March. Tsolum Main—60–180 cm of almost solid snow cover; most stumps buried.
- 4 April. Comox Burn—from 1% snow cover on south-facing slopes and lower areas to 90% snow cover up to 60 cm deep at upper elevations.
- 6 April. Tsolum Main—almost solid snow cover from 50 cm to over 120 cm deep in areas covered today.
- 11 April. Comox Burn—no snow.
- 13 April. Tsolum Main—from 50% snow cover, 25–40 cm deep at lower elevations, to almost solid snow cover to over 120 cm deep at upper levels.

#### TSOLUM MAIN ONLY:

- 18 April. Almost solid snow cover in most areas covered today, 40–90 cm deep.
- 25 April. From no snow on some south-facing slopes to greater than 95% coverage to over 120 cm deep.
- 30 April. Some south-facing slopes bare but snow cover in many areas, 45–75 cm deep.
- 4 May. Still 10–50% snow cover on many areas, 15–40 cm deep.

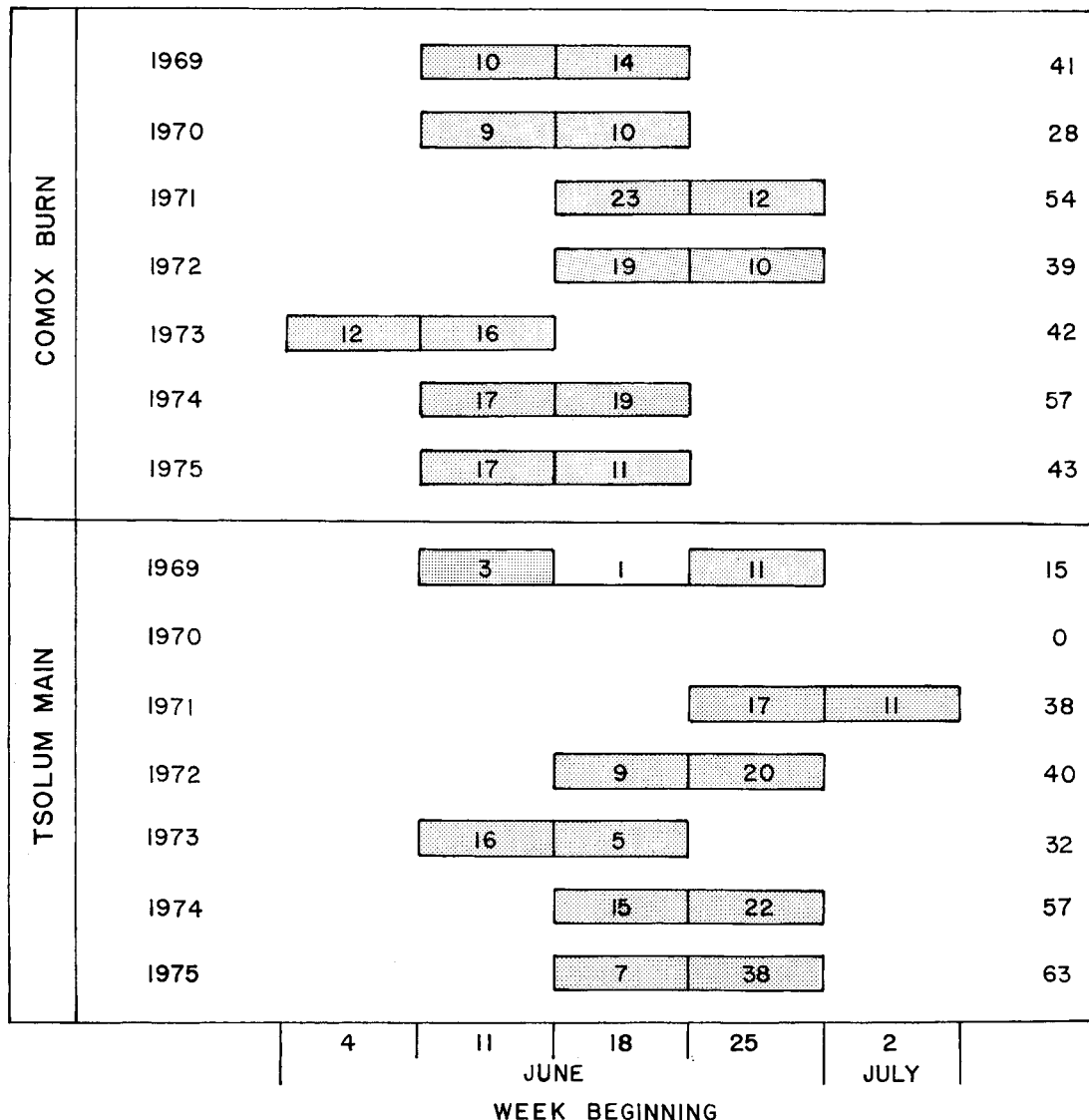


FIGURE 3. Periods of peak hatch at Comox Burn and Tsolum Main, 1969 to 1975. Weekly sample sizes are shown within the peak hatch bars; total annual sample sizes are shown in the right hand column.

early hatch in 1973 correlates nicely with the climatological data for that year, but late hatches in 1971, and possibly in 1972, are more difficult to explain. The first half of April was cool in 1971, but total precipitation for April was about average.

Interactions of climatic phenomena may be too complex to explain variations in time of breeding on the basis of standard meteorological records from a station 20 km away and several hundred meters lower in elevation. Nevertheless, there is a suggestion that a year of early hatch (1973) was warm and dry during the pre-nesting period; likewise, that a year (1972) of possibly two (1971 and 1972) retarded breeding seasons was cool and wet, with early April 1971 also cool, but not

especially wet. The picture is less clear in other years.

If there is a relationship between climate and breeding, one might expect the hatch to be later at Tsolum Main than at Comox Burn. This is true, whether considering individual years only (Fig. 3) or combined data for all years (Fig. 5). This conclusion holds for all females and when age classes are examined separately. The hatch at Tsolum Main has always been one to two weeks behind that at Comox Burn.

I can separate breeding birds into two age classes only, *adults* (> 22 months of age) and *yearlings* (ca. 11-13 months). The average hatch dates for yearlings were substantially later than for adults at both areas (Fig. 5),

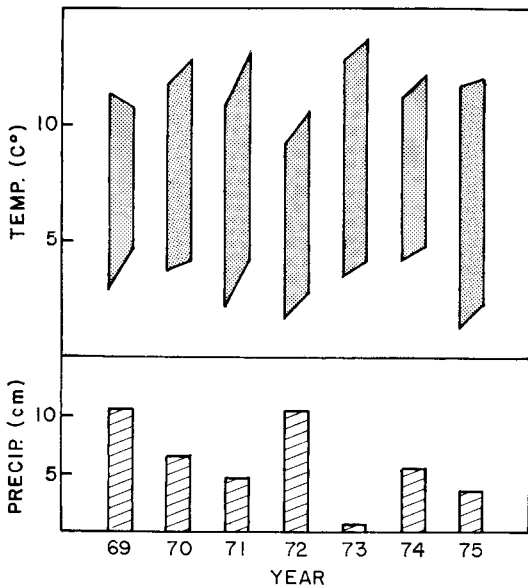


FIGURE 4. Mean daily maximum and minimum temperatures and total precipitation for April at the town of Comox, B.C., 1969 to 1975. Left sides of temperature bars = 1 to 15 April; right sides = 16 to 30 April.

and the period of hatch was longer (up to 10 weeks) for adults than for yearlings (up to 7 weeks). First hatches of adults began about one week earlier and extended about two weeks later than for yearlings.

Blue Grouse may renest (Zwicker and Lance 1965). I suspect that most, if not all, late hatches of adults were from renesting attempts. Fewer yearlings were found with late-hatched chicks than adults. These data suggest that yearlings are less likely to renest than adults.

#### ESTIMATES OF PRE-HATCH DATES

Dates of hatch represent only one breeding season event but can be used to estimate those antecedent to these dates if the required intervals of time are known. I used the following data in back-dating from hatch dates to estimate time of copulation, dates when first eggs were laid, and dates when incubation began: (1) The incubation period of Blue Grouse is 26 days (unpubl. data). This figure was used to estimate dates when incubation began. (2) Eggs of Blue Grouse are laid at an approximate rate of 1.5 days per egg (Standing 1960); first egg dates were computed by back-dating from the start of incubation, using mean clutches of 6 eggs for yearlings and 7 for adults (Zwicker 1975). (3) It is not known when copulation occurs in relation to when first eggs are laid for Blue Grouse, but Bump et al. (1947) reported that

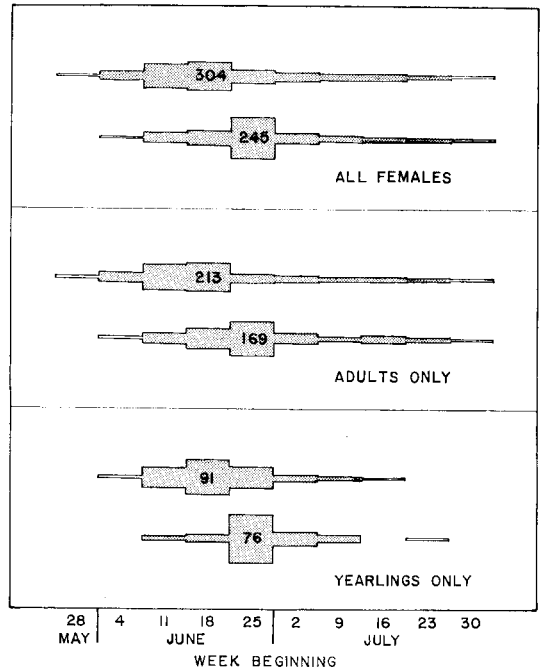


FIGURE 5. Dates of hatch, in percent per week, for all females, adult females only, and yearling females only at Comox Burn (above) and Tsolum Main (below), combined data for 1969 to 1975. Sample sizes are shown inside bars. Statistical probabilities for Comox Burn against Tsolum Main are: all females,  $\chi^2 = 12.59$ , 6 df,  $P < 0.05$ ; adults only,  $\chi^2 = 72.40$ , 7 df,  $P < 0.001$ ; yearlings only,  $\chi^2 = 42.58$ , 4 df,  $P < 0.001$ . Statistical probabilities for adult against yearling females are: at Comox Burn,  $\chi^2 = 22.06$ , 5 df,  $P < 0.001$ ; at Tsolum Main,  $\chi^2 = 13.11$ , 4 df,  $P < 0.01$ .

copulation occurs 3 to 7 days prior to laying of the first egg in Ruffed Grouse (*Bonasa umbellus*). I used 4 days as the time between copulation and the laying of the first egg to estimate dates of copulation of my birds because Bump et al. (1947:267) said that "the shorter period is most frequent."

I combined data from the four "normal" years (1969, 1970, 1974, and 1975) at Comox Burn to estimate these parameters. This analysis indicates that the peak period of copulation normally occurs in the first two weeks of May at Comox Burn (Fig. 6). Hence, most females are on the breeding range only 2 to 3 weeks prior to the time they copulate. Most nests are begun in the second and third weeks of May, and incubation most often begins in the third and fourth weeks of May. Nevertheless, copulation may occur into mid- to late June, first eggs may be laid in late June, and incubation may begin as late as early July. Most of the latter extremes almost certainly represent renesting. Copulation of yearling females occurs only after most adult females have begun to nest. Clearly, copulation in the

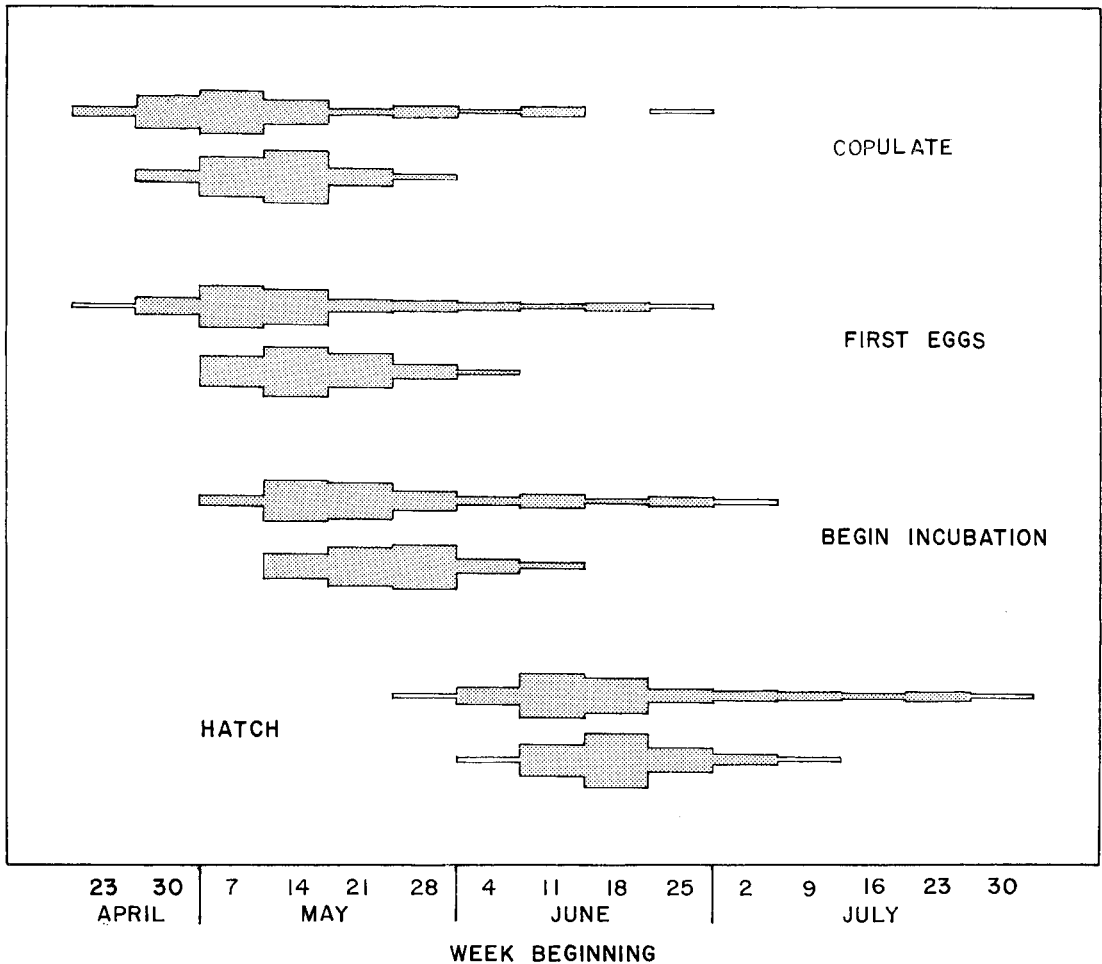


FIGURE 6. Estimated times of copulation, dates when first eggs were laid, when incubation began, and of hatch, in percent per week, for adult (above) and yearling (below) females at Comox Burn; data for 1969, 1970, 1974, and 1975 combined. n (adults) = 120, n (yearlings) = 49.

two age classes is largely temporally separated.

The estimated dates of all breeding events are based on back-dating from captured chicks; hence, they represent parameters for successful breeders only. Experimental removal studies were conducted at Tsolum Main in 1970, 1974, and 1975 (Zwickel 1972, unpubl. data). I therefore compared estimates of time of copulation and first egg dates of yearling females to ovarian weights of yearling females that were removed from Tsolum Main (Fig. 7); data from Comox Burn were adjusted backward by one week to approximate these events for Tsolum Main. Clearly, the data from back-dating and those from ovaries of collected birds are in close agreement and suggest that the back-dating is accurate. They also indicate that estimates of breeding events by back-dating from chicks of successful females do represent antecedent events in the breeding cycle of all females.

### DISCUSSION

Since the early experiments of Rowan (1926), daylength (light) has been generally accepted as the primary *Zeitgeber* that brings birds into breeding condition. If this were the only factor involved, then time of breeding should be constant among years, between areas at the same latitude, and between age classes at the same area. Numerous studies have now shown that other factors may have more immediate modifying influences on the time of breeding (Immelmann 1972). My findings certainly agree with this suggestion.

Available data are insufficient to say with certainty what caused variations in the time of breeding of Blue Grouse among years on my study areas. However, my data suggest that weather was involved in one "early" year and perhaps in one "late" year. I believe weather is the most likely potential cause of these variations but cannot identify the pre-

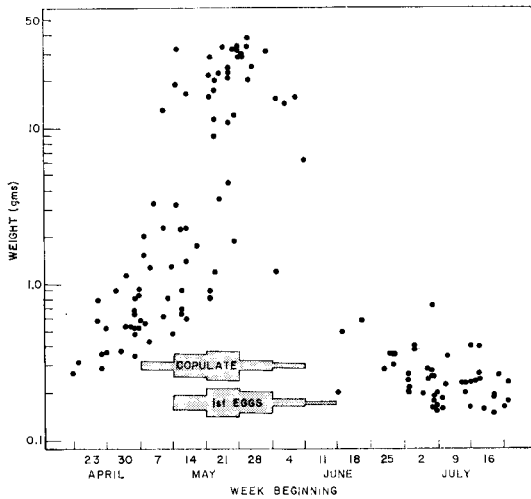


FIGURE 7. Estimated times of copulation and dates when first eggs were laid for yearling females at Tsolum Main (1969, 1970, 1974, and 1975) as compared to ovarian weights of yearling females collected at Tsolum Main in 1970, 1974, and 1975 ( $n = 132$ ).

cise climatic factors that may be involved. Interactions among variables, perhaps operating through food supply, may be causal.

The peak of hatch at Tsolum Main is about one week behind that at Comox Burn. This correlates with lower temperatures, more precipitation and a later disappearance of snow at Tsolum Main than at Comox Burn, suggesting, as with variations among years, that climatic factors are involved. This could be operating indirectly through food. Snow lies longer at Tsolum Main than at Comox Burn, and snowpack certainly retards vegetative growth. The disappearance of snow at Tsolum Main is much more than one week behind that at Comox Burn, however, so variations in snowpack alone will not explain the difference between areas. If quantity or quality of food is proximately involved in the initiation of breeding, vegetation would have to have accelerated growth or more rapid qualitative increases in nutritional values at Tsolum Main than at Comox Burn to reduce the difference in breeding times at the two areas to only about one week. An alternative explanation would be that food is not critical at this time and that the grouse can begin reproduction on quantitatively and/or qualitatively different food regimes. If selection has operated mainly at the level of hatched young (Lack 1968), then perhaps the proximate availability of food is not a critical factor determining the beginning of the breeding season.

Differences in time of breeding between yearling and adult females also have impor-

tant implications. Are these differences a result of inexperience in finding food on the part of young birds—as suggested by Lack (1954) for differences in clutch size between young and older birds—or are they related to physiological maturity or amount of time on the breeding range before copulation takes place? The latter explanation would also indicate that food might be critical. Alternatively, can adult females be suppressing yearlings until they themselves are well along in the nesting cycle? A further possibility might be that yearling females, as new recruits to the population, do not participate in breeding activities until they have established themselves on the breeding range. In this view, new recruits may not begin breeding until after “surplus” females (Bendell et al. 1972, Zwickel 1972) have been excluded, and such exclusion may result from interactions among yearlings. Unpublished experimental evidence from current studies suggests that the latter explanation cannot be ruled out. The last two possibilities both involve social behavior and have important implications to theories of population regulation.

I examined variations in the time of breeding in females only and the cycle of the female may be keyed to that of the male. Simard (1964) examined the testicular cycle of Blue Grouse on Vancouver Island. He had too few data to determine with confidence whether it varied among years, yet “fragmentary” evidence indicated there were no such variations. The proximate control of time of breeding in males might therefore be different and temporally separate from that of females; but, the effective breeding period of at least some males must span the entire receptive period of females. In a “normal” year at Comox Burn, this would cover the time from mid-April until the end of June and this does fall within the period when males show active spermatogenesis (Simard 1964), sing, and hold territory in this area. This interpretation agrees with the suggestion of King et al. (1966) for the White-crowned Sparrow (*Zonotrichia leucophrys gambelii*) that maintenance of a long period of spermatogenesis is “presumably an adaptation that allows a considerable latitude of accommodation to a female gonadal cycle that is affected more strongly than that of the male by local ecological conditions.” On the basis of available evidence, I doubt that the breeding cycle of female Blue Grouse is proximately controlled by the male. Selection appears to have acted upon females by favoring the optimum timing of production of young, which may vary with

specific local conditions, and upon males to cover the entire range of variation that may occur in females, including reneating.

## SUMMARY

Timing of breeding of female Blue Grouse was studied in two populations living about 2-3 km apart. Timing of breeding varied among years, between populations, and between adults and yearlings. Variations in time of breeding among years showed some correlation with annual differences in April weather. Breeding was about one week later on the area that was higher in elevation, cooler, wetter, had more snowpack, and held its snowpack longer in spring.

Most yearling females copulated only after most adult females were beginning to nest. The period of copulation was up to 10 weeks long in adult females but only up to 7 weeks long in yearlings. Most females were on breeding range only about 2-3 weeks prior to copulation. While there was a 3-4 week difference in timing of loss of snow between areas, there was only a one week difference in timing of breeding.

Differences in timing of breeding between age classes may relate to differences in physiological maturity, amount of time on the breeding range prior to copulation, harassment of yearlings by adults, or interactions among new recruits (yearlings) themselves.

Proximate control of the reproductive cycle of females appears most subject to local ecological conditions. The breeding period of males has likely been selected to cover the entire receptive period of females, including annual, geographical, and age-class variations.

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