SPRING MOVEMENTS OF FEMALE BLUE GROUSE: EVIDENCE FOR SOCIALLY INDUCED DELAYED BREEDING IN YEARLINGS

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ABSTRACT.—When compared to adults, yearling female Blue Grouse (*Dendragapus obscurus fuliginosus*) breed later in the season, and some may not breed at all. Movements of adults and yearlings in spring are strikingly different. Adult movements become restricted early, whereas yearlings continue to wander over large areas for a longer period. Gonadal development in yearlings begins soon after they have localized, and localization of yearlings occurs when movements of adults are restricted around nests. Aggressive calling begins when hens have localized and continues until incubation is initiated. We suggest that adults interact aggressively with yearlings, preventing them from settling until adults begin to nest. *Received 17 December 1981, accepted 11 April 1982.*

IN many species of birds, females breeding for the first time lay later than older females (Coulson 1966, Mills 1973, Crawford 1977, Pinkowski 1977, Middleton 1979, Ross 1980). Two hypotheses have been presented to explain this phenomenon. Lack (1968) proposed that first-time breeders were inexperienced at finding food and that this delayed egg formation. Wynne-Edwards (1962) attributed the delay in breeding to the inferior social position of younger birds in competition with older birds for breeding space. A third possibility is that yearlings are less sexually mature than adults; this may not be a sufficient condition to delay breeding, however. Yearling California Quail (*Lophortyx californicus*) have smaller ovaries than adults but initiate laying at the same time (Lewin 1963).

Yearling Blue Grouse lay eggs later than adults (Zwickel 1977), and some yearling females may not breed at all. Extra yearling females were available to replace residents during removal experiments (Bendell et al. 1972; Zwickel 1972, 1980), and the ovaries of some of these would not have developed in time for them to breed (Hannon and Zwickel 1979). These were termed nonbreeders. Zwickel (1972) and Hannon (1978) proposed that female Blue Grouse may compete for space on the breeding range and that delays or suppression of yearling breeding activity may occur as a result of interactions with adults and other yearlings.

The objectives of this study were to examine the following questions: (1) Do adult and yearling female Blue Grouse differ in their use of space and time of settling?; (2) Could this account for the delayed or nonbreeding reproductive status of yearlings?; and (3) What form of spacing behavior do females exhibit that could limit the number of hens that breed?

METHODS

This study was conducted on Vancouver Island in an area 15 km west of Courtenay, British Columbia. The study areas were Comox Burn (485 ha), Tsolum Main (625 ha), and a buffer area (640 ha) between the two. These are described in more detail by Zwickel (1972, 1977). Blue Grouse were censused here during all breeding seasons from 1969 to 1977 (Zwickel 1980).

We documented the movement patterns of adult and yearling females during the pre-incubation period and related these to the birds' reproductive condition and to an index of aggressiveness during the same time period. Detailed observations of movement patterns were limited to a sample of 26 radio-tagged hens, but reproductive status and an index of aggressive behavior were also monitored for other females in the population.

Movements.—We captured 16 yearling and 10 adult hens on Comox Burn and the buffer area between 4 April and 5 May 1977. Birds were individually marked with colored leg bands and fitted with radio transmitters attached on the back with a harness that encircled the neck and passed under the wings. The complete package weighed 16–22 g, approximately 2% of body weight. A hand-held antenna was used

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to locate birds to within 5 m of their positions about three times a week until incubation began.

Three classes of movement were defined: (1) the size of the area over which an animal travelled, or its home range; (2) the range length or the greatest movement during a particular time period; and (3) the maximum distance away from the nest site during a particular time period. Boundaries of home ranges were determined by the method of Harvey and Barbour (1965), as modified by Herzog and Boag (1978), and the areas of the resulting polygons were measured. Only birds for which we had more than 10 observations before the onset of laying were used in this analysis ($n = 20$). Range length was the straight line distance between the two locations that were farthest apart during 10-day periods from 1 to 40 days before the first egg was laid. Ten-day periods were chosen because the gonads of female Blue Grouse develop to egg-laying size in 9 or 10 days during rapid recrudescence (Hannon 1978). Thus, 10 days is a biologically relevant period in the reproductive cycle of Blue Grouse. Distance to nest site was the straight-line distance from nest site to the farthest of locations taken during 5-day periods from 1 to 45 days before the first egg was laid.

Stage of reproductive cycle.—The frequent surveillance of radio-tagged hens enabled us to find nests and determine when each hen had laid her first egg. All radio-tagged hens eventually settled and nested. By backdating from the date of laying the first egg, we determined whether hens had quiescent (before development) or rapidly developing ovaries by referring to a graph that plotted the development of an average follicle to egg-laying size against time (Hannon 1978). The reproductive status of nonradio-tagged hens was assessed by backdating from the date of hatch (Zwickel 1977).

Female vocalizations related to settlement.—During the breeding season some females give a cackle call that has an aggressive function (Stirling 1968, Hannon 1980). To monitor seasonal fluctuations in female aggressiveness, we played a taped cackle call at five stations situated 400 m apart on each of four transects along abandoned logging roads. The tape was played for 5 min, and the number of cackles given in response was recorded. We surveyed each transect once weekly from 6 April to 2 June, starting 1 h before sunset. The point of initiation of each transect was switched end for end each week. Cackles that we heard given spontaneously throughout the day were also counted. We compared the time of peak cackling to the period of settling of adults and yearlings.

RESULTS

MOVEMENTS

Home range.—Average home ranges of yearlings before incubation began were three times as large as those of adults [yearlings: $\bar{x} = 20.7$ ha ± 5.08 SE ($n = 12$); adults; $\bar{x} = 6.4$ ha ± 2.19 SE ($n = 8$); t-test, $P < 0.05$]. We considered a female to be settled or localized on an area if she did not move more than 400 m from the boundary of the area eventually occupied during the period from 10 days before laying (DBL) until the end of laying. Home ranges during localization were $\bar{x} = 2.3$ ha ± 0.33 SE ($n = 12$) for yearlings and $\bar{x} = 2.3$ ha ± 0.50 SE ($n = 8$) for adults.

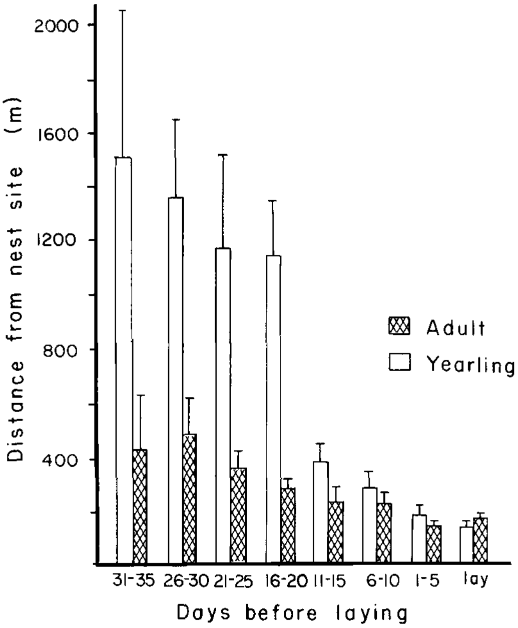

Fig. 1. Mean maximum distance (±SE) from nest site during laying and during consecutive 5-day periods before laying for adult and yearling hens.

Distance to nest site.—Yearlings were farther from their eventual nest sites than were adults up to 15 DBL, when the maximum distance to nest site dropped abruptly and was not significantly different from maximum adult distance (Mann Whitney U-test, $P < 0.05$) (Fig. 1). Adults stayed close to their potential nest sites throughout the pre-incubation period (laying and 1–35 DBL).

Range length.—Adult movements were short throughout spring, particularly during laying and in the 20 days before laying, when range length was generally less than 400 m (Fig. 2A). Yearlings moved over much longer distances than adults during all time periods except laying, but range length was reduced markedly during 1–10 DBL (Fig. 2B). Both adults and

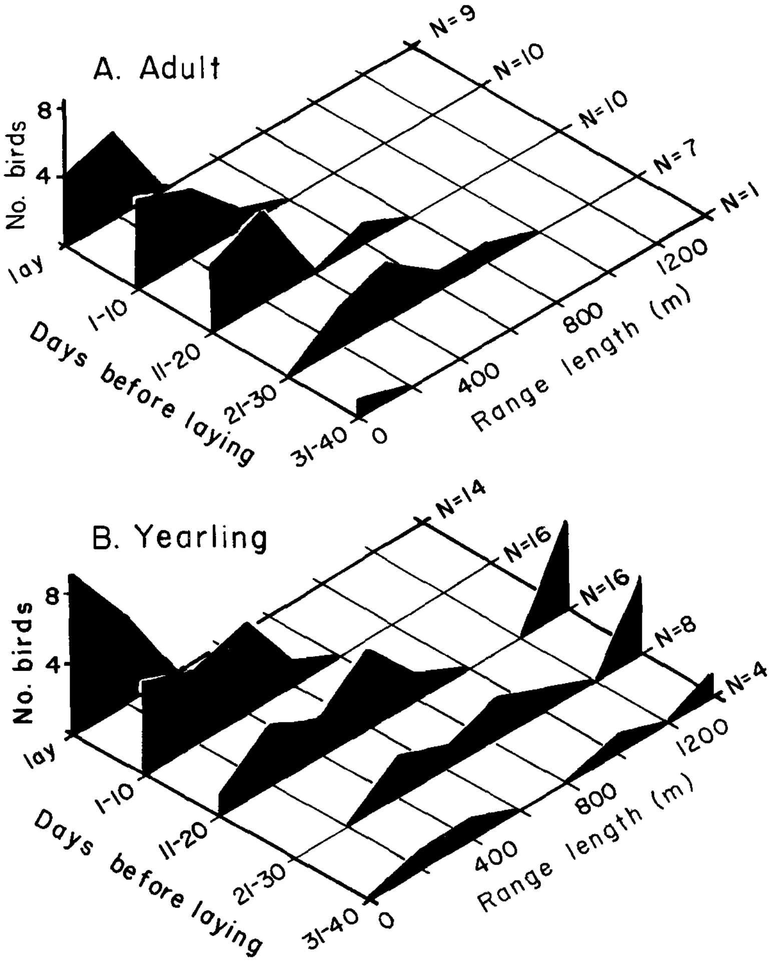

Fig. 2. Range lengths of adults (A) and yearlings (B) during laying and consecutive 10-day periods before laying (n = sample size).

yearlings had the shortest movements during laying.

We distinguished three types of yearlings based on their range of movements during 10-day periods from 1–30 DBL: adult-like, early settlers, and late settlers. All yearlings had restricted movements, similar in extent to adults, during 1–10 DBL. Two of 16 yearlings had restricted movements throughout the 30 DBL (adult-like yearlings). Three yearlings moved widely (range lengths greater than 700 m) during 21–30 DBL but had shorter movements, similar to adults, from 1–20 DBL (early settlers). Eleven of the 16 ranged widely until 1–10 DBL (late settlers). These patterns suggest that most yearlings exhibit long-distance movements when they arrive on the breeding range and do not restrict their movements until they are close to laying.

Time of Settling Related to Reproductive Status

Adults settled earlier in the season than yearlings and earlier in the ovarian cycle. Eight of the 10 adults had localized by 20 April, whereas yearlings did not begin to settle until 26 April, and most had not localized until after 6 May. The earlier yearlings localized, the earlier they laid their first egg ($r = 0.75$, $P < 0.01$). The majority of yearlings did not localize until 15 DBL, while most adults settled earlier in the

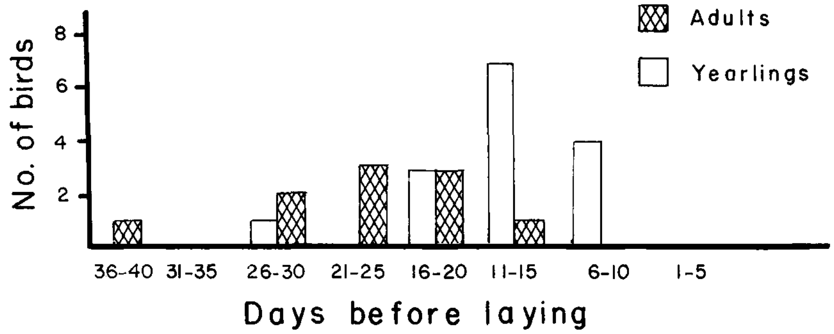

Fig. 3. Time before laying when adults and yearlings localized.

reproductive cycle (Fig. 3); some yearlings, however, settled at a similar time to that of adults. The development of an ovarian follicle proceeds at a slow rate until 9–10 days before ovulation, when development suddenly accelerates (Hannon 1978). Thus, the follicles of most yearlings began to increase in size almost immediately after the birds had settled around a nest site. Thus, for the majority of yearlings (late-settlers), initiation of laying was directly related to localization. In adults settling was not immediately followed by rapid ovarian development.

We compared the timing of yearling localization to reproductive events in adults. Yearlings did not localize until most adults had begun to lay eggs. Mean date of localization for yearlings was 7 May (±1.4 SE, n = 15), 2 days after adults began to lay eggs (5 May ± 1.6 SE, n = 32) (NS, t-test), a period when adult displacement was lowest. Thus, most yearlings did not settle until adult movement was restricted around nests.

FEMALE VOCALIZATIONS RELATED TO SETTLEMENT

An aggressive call, the cackle, is given by females during April and May (Hannon 1980). and this call may be used to advertise occupancy of an area. We compared the frequency of all cackles recorded in 1977 to the proportion of hens on Comox Burn that had localized (Fig. 4). The numbers of cackles heard increased as the number of hens that had localized increased. Peak cackling coincided with the period when most hens were localized but had not begun to incubate. The frequency of calling declined as more hens began to incubate.

DISCUSSION

The behavior of adult and yearling females in spring was clearly different. Adults localized early, and their movements were restricted. Most yearlings wandered and travelled relatively long distances over the breeding range, their localization occurred later than that of adults, and it coincided with the period when movements of adults were restricted around nests. Ovarian development in yearlings began soon after. Perhaps adults interact aggressively with yearlings, preventing them from settling. Although overtly aggressive interactions among female Blue Grouse have rarely been observed in the field, in an aviary hens attack their mirror images (Stirling 1968) and each other (Cooper 1977) during spring.

If hens rarely fight, then how do they interact? The cackle call is temporally associated with localization of birds on an area before incubation and may be a mechanism for monopolizing and defending space. The cackle seems to be an aggressive call, as it is given by females during fights in the aviary (Stirling 1968, Cooper 1977) and is directed toward other hens, and not males, in the field (Hannon 1980). The cackle may have a similar function to territorial calls given by males. Female Spruce Grouse (*Dendragapus canadensis franklinii*) replied to an aggressive call only when localized on territories (Herzog and Boag 1977). Female Blue Grouse, once settled, may advertise their presence on that area by cackling, and this serves to warn other hens to stay away. Thus females may space themselves by mutual avoidance. Once all hens have settled and have begun to incubate, cackling ceases (Fig. 4).

Previous estimates of sizes of home ranges

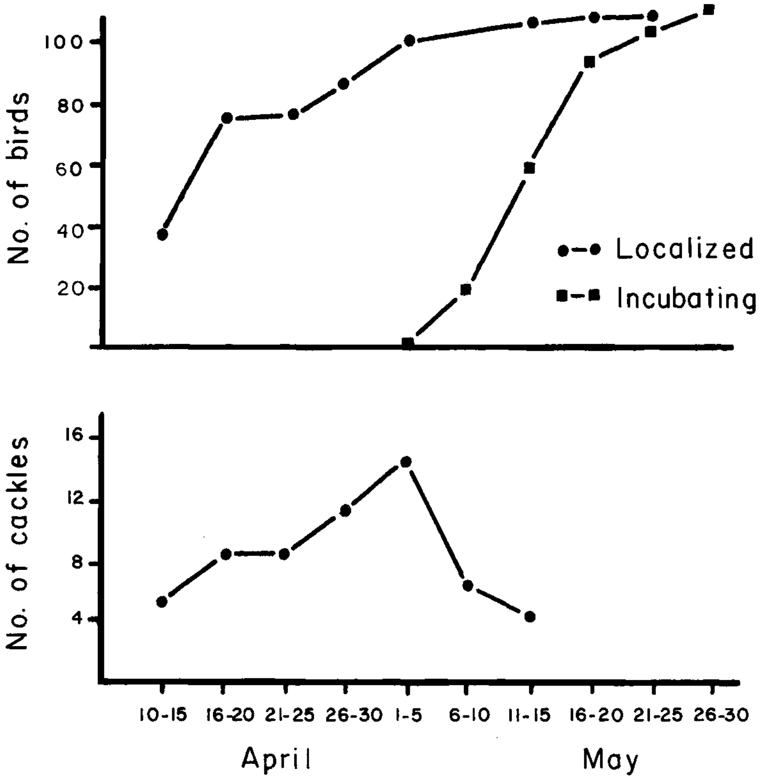

Fig. 4. Frequency of cackling on Comox Burn compared to number of hens localized and number incubating (based on the proportion of radiotagged hens that had localized extrapolated to all hens on Comox Burn).

for female Blue Grouse were either based on locations throughout the prebreeding period or did not distinguish between adult and yearling movements, and home ranges were reported to overlap extensively (Boag 1966, Bendell and Elliott 1967). Recent work on the Spruce Grouse, a species with a similar mating system to that of Blue Grouse, indicates that size of home range and degree of overlap among hens changes throughout the season, being lowest in late spring when females are territorial (Herzog and Boag 1978). Size of home range of female Ruffed Grouse (*Bonasa umbellus*) also decreases from the prelaying to the laying periods (Maxson 1978). Our study indicates that adult female Blue Grouse constrict their home ranges from 6 to 2 ha and yearlings from 20 to 2 ha from early to late spring. Whether home ranges of localized females are mutually exclusive during late spring is unknown. We need to monitor the movements of all females in a particular area to determine this. Females do appear however, to be spaced out on the breeding range (Bendell and Elliott 1967).

The density of resident females on Comox Burn has been fairly stable over time, varying from 21 to 29 females per 100 ha from 1969 to 1977 (Zwickel 1980). Yearlings account for about 30% of the breeding population. Adults arrive early on the breeding range and settle where they had resided the year before (Boag 1966, Bendell and Elliott 1967). Thus, 15–20 adults per 100 ha are likely to be present each spring. With each occupying a home range of about 6 ha, some overlap is likely, and the potential for interaction among hens is present. As movements of adult females become more restricted, some yearlings may settle (adult-like yearlings). Interactions between residents and potential recruits may prevent settling of the latter until adults restrict their home ranges before laying. More yearlings can then localize, and these early settlers prevent others from settling. Finally, when adults and adult-like yearlings begin to lay and early settlers begin to localize, a large amount of space is opened up, and some yearlings that had been moving over long distances can localize. In this study, all radio-tagged yearlings eventually settled and bred. Other studies, however, have indicated that some yearlings may not breed at all (Hannon and Zwickel 1979). These birds may have been prevented from settling on the study area by interactions with the late-settling yearlings.

Availability of food can also be an important determinant of laying date (Perrins 1970). Enhancement of food supplies can advance the date of the first egg for yearlings more than for adults in some species of passerines (Källander 1974, Smith et al. 1980). Perhaps yearlings lay later because they are denied access to space on which critical resources for egg laying are located. Although we did not test this directly, we have no evidence that yearling Blue Grouse are suffering from a shortage of food. Adults and yearlings eat the same types of foods in the same proportion during spring (King 1968), and the nesting success of yearlings is identical to that of adults (Zwickel 1975). The fact that the gonads of yearlings develop rapidly almost immediately after they localize may indicate that having a place to settle is the proximate stimulus required to bring the gonads to full maturity (King et al. 1966, Immelmann 1971, Kern 1972) and that yearlings have already accumulated reserves adequate to lay eggs. Thus, the evidence does not support Lack's hypothesis that yearlings were delayed because of inexperience at finding food.

Our data appear to support the hypothesis of Wynne-Edwards (1962) that delayed breeding in yearlings is socially induced by interactions with adults. The evidence we present is correlational, however, and a more rigorous test of the hypothesis is required. For example, another interpretation of the data could be that yearlings move long distances in order to sample the habitat before settling. What is now required is an experimental removal of adults to see whether or not yearlings can settle and breed earlier than yearlings living in an area with normal adult numbers.

The delay or inhibition of reproduction in females because of interactions with other females has been demonstrated in several other species of birds (Carrick 1963, Robel and Ballard 1974, Crawford 1977) and mammals (Christian 1971, Bujalska 1973, Dunbar and Dunbar 1977, Rood 1980). Within-sex interactions could potentially limit the number of females that breed independently of male density and behavior. Male Blue Grouse are territorial and are probably promiscuous or polygynous, because the breeding sex ratio is skewed towards females. Females briefly associate with them for copulation but usually nest off their territories and raise young without their assistance. Hence, the territorial behavior of males is unlikely to affect the settlement of females in a direct way, unless females avoid the territories of males. More data are required on the movements of males and females in relation to one another.

Redfield et al. (1978) found that females, not males, affected the survival and recruitment of young in a population of *Microtus townsendii*, indicating that the behavior of females may determine the density of both sexes. Most studies on aggression and territoriality, however, have been limited to males, making it difficult to assess the potential of female behavior in determining population density. In 1969 Brown claimed that few studies of birds had demonstrated a surplus of females (prevented from breeding by the behavior of residents) that could settle and breed if residents were removed. Several studies (e.g. Watson 1965, Holmes 1966, Watson and Jenkins 1968, Harris 1970, Young 1970, Zwickel 1972, Bendell et al. 1972, Manuwal 1974) contradict this claim. Clearly, the potential of female aggression and spacing behavior to limit the numbers of females, and perhaps males, that breed is significant and requires further study.

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