

BEHAVIOR OF YEARLING MALE BLUE GROUSE AND ITS RELATION TO DELAYED BREEDING

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In species of grouse with dispersed territories, first-year males rarely occupy territories and presumably do not breed (Wiley 1974, Wittenberger 1978). For example, yearling male Blue Grouse (*Dendragapus obscurus*), Ruffed Grouse (*Bonasa umbellus*), and Spruce Grouse (*D. canadensis franklinii*) usually do not defend territories (Bendell and Elliott 1967, Gullion 1967, Herzog and Boag 1978).

Wiley (1974, 1981) and Wittenberger (1978) have proposed separate hypotheses to explain delayed breeding in male grouse. Wittenberger's (1978) sexual selection hypothesis emphasizes inability of yearling males to compete with adults for territories, while Wiley's (1974, 1981) sexual bimaturism hypothesis invokes selection of delayed maturation for males as a consequence of increased early survival and later fecundity.

There have been few detailed studies describing the behavior of yearling male grouse. Important questions about their behavior in regards to the above hypotheses are: (1) do territorial adults actively prevent yearlings from occupying territories and mating with females; and (2) what behavior might enhance early survival and later fecundity? The objectives of this paper are to describe the behavior of yearling male Blue Grouse and to discuss these behaviors in relation to predictions derived from present theories on delayed breeding in grouse.

STUDY AREA AND METHODS

The study area was on Hardwicke Island, off the central-east coast of Vancouver Island, British Columbia. A 460-ha area clear-cut by logging between 1969 and 1973 served as the main study site. Vegetative structure ranged from "very open" (Bendell and Elliott 1967), consisting primarily of burned or unburned slash, mixed grasses, fireweed (*Epilobium angustifolium*), salal (*Gaultheria shallon*), and red huckleberry (*Vaccinium parvifolium*), to "open," consisting mainly of western hemlock (*Tsuga heterophylla*) and Douglas-fir (*Pseudotsuga menziesii*) 3-7 m in height.

Trained pointing dogs were used to find birds, which were then captured with a noose pole (Zwickel and Bendell 1967). Selected birds were fitted with either a solar-powered or battery-powered transmitter (Herzog 1979). Birds were captured either in late summer as 2-3 month-old juveniles, or in the following spring as 10-11 month-old yearlings. The transmitter weighed from 2 to 4% of the body weight of the bird and did not appear to affect their behavior.

Observations were conducted in 1980 and 1981 from 14 April, when yearlings first arrived on their summer range, to 22 June. Aggression and spacing behavior are most evident among Blue Grouse during this interval (Jamieson 1983). Observational sessions for individual

birds lasted for at least 1 h and were conducted from after sunrise to darkness. Since I attempted to locate all radio tagged birds during the day as part of the work for other aspects of this study, doing both dawn and dusk observations would not have been feasible. Birds were observed with the aid of binoculars at a mean distance of 20 m (range = 10–80 m), using vegetation as a natural blind. Recording of behavior commenced when the bird appeared undisturbed. Activity was classified as either stationary or moving. A bird was considered to be moving if his position changed more than 1 m in less than 1 min. An interaction was defined as any incident where the behavior of a bird changed in response to the presence of a nearby conspecific. Males were considered territorial if they were highly localized and singing.

RESULTS

Time budget and diurnal activity patterns.—Twenty-four yearling males were watched during 63 and 58 observational sessions in 1980 and 1981, respectively, for a total of 126 h. A median of four sessions (range = 1–14) was conducted on each yearling.

Yearlings were stationary for 74% of the observed time during which they were either inactive (56%) or feeding (18%). Moving occurred 26% of the time and included three activities: feeding (15%), interacting (6%), and walking (5%). At first sighting, birds were in the open, away from vegetative cover, only 30 of the 171 times (18%) that they were located. Individuals located twice in the same day ($N = 50$) had moved a median distance of 2 m per h (range = 1–24 m).

Percentage of time that yearlings were active (including moving and feeding) ranged from 28% at the 2-h interval around midday to 50% during the 2-h interval before sunset. At dusk, yearlings moved about in the open and sometimes ran 5–15 m in short bursts, or flew short distances of 10–30 m. Twenty-three of the 29 interactions (79%) recorded occurred within 1 h of sunset. In summary, yearlings remained in or near cover and moved very little during the daytime; activity increased at dusk. Yearlings spent approximately one-third of the observed time feeding.

Territorial behavior.—Only one yearling behaved as if on a territory. This bird had stayed in a 0.6-ha area and was heard singing during most of the day for 6 consecutive days. His home range was considerably smaller than that of other yearlings (median = 10.8 ha, range = 0.6–40.7 ha), but similar to that of territorial males (Lewis 1984). In one instance, this male chased away another yearling from his territory. I noted seven other instances of singing by yearlings, two by the same bird; five of these occurred at dusk.

Intraspecific interactions.—Yearling males were observed to encounter territorial males on 25 occasions and each resulted in an agonistic interaction. Adult males that detected yearlings on or near their territories immediately ran or flew toward the yearling and assumed a threat posture

(Jamieson 1984). Yearlings invariably assumed a neutral posture during encounters with territorial males. On 10 occasions they remained in this position for 10–30 sec before flying from the area. In 14 other cases an adult rushed at a yearling and displaced him. I saw only one physical attack in which a territorial male rushed at a yearling and pecked his back, removing several feathers.

In most instances I could not determine what initiated interactions between yearlings and territorial males. However, on at least eight occasions, yearlings made direct movements of 20–250 m towards specific territories where resident males were singing. The movements of the yearlings were conspicuous and once they approached the territories they were chased by the adults in all instances. In all of these cases the yearlings occurred frequently near these particular adults and their territories during the breeding period (Jamieson and Zwickel 1983).

Three yearlings localized near sites that were not occupied by territorial males but which had been occupied the year before. There was no evidence of these males behaving in a territorial manner. One of these birds was resighted the next breeding season and had established a territory where he had localized as a yearling.

Five instances of yearling males interacting with both females and territorial males were observed. In these cases yearlings flew approximately 40–100 m toward females that were calling on or near territories of adult males. They were met immediately by the resident males who courted the females only after they had chased away the yearlings.

Eleven cases in which yearling males interacted with lone females were noted. These interactions were initiated usually in one of two ways; males either walked or flew toward females that had been calling ($N = 5$), or they encountered them while moving about ($N = 5$). In one other case a female flew into an area and a yearling responded by flying to where she had landed. On two occasions yearlings did not respond to females that were nearby; both occurred relatively late in the breeding period (4 and 6 June).

Upon approaching a female, yearlings assumed a full or partial display posture and exhibited “head bobbing” (Stirling and Bendell 1970), but did not drag their wings or “whoop” (Stirling and Bendell 1970) as territorial males do during courtship. On three occasions yearlings showed what appeared to be “displacement” behavior by suddenly moving away from the female and pecking at nearby bushes. Yearlings were not observed attempting to mount females as after 1–5 min of displaying they slowly returned to a neutral posture and began feeding. In cases where the responses of the female were monitored, the birds appeared disinterested and either remained still ($N = 3$) or fed ($N = 4$). In contrast to yearling males, territorial adult males showed the full range of courtship

responses and attempted frequently to mount females even relatively late in the breeding period when hens were with broods.

DISCUSSION

In promiscuous species of grouse in which territorial males are dispersed, territories presumably allow males to attract, court, and mate with females without interference from other adult males (Bendell and Elliott 1967). Males that localize and perform advertisement behaviors are considered territorial. In my study only 1 of 24 yearling males appeared to be territorial. Instead, yearlings had relatively large home ranges that may encompass several territories of adult males (Jamieson and Zwickel 1983). Also, first-year males are secretive during the daytime and rarely sing. What factors prevent yearlings from occupying territories, thus reducing their chances of breeding? Although testes of yearlings are lighter in weight, develop later, and regress sooner than adults, yearlings produce viable sperm (Hannon et al. 1979) and many will occupy territories and sing if territorial adults are removed (Bendell et al. 1972; Zwickel 1972, 1980). Testes of replacement yearlings are similar in size to those of nonterritorial yearlings (Simard 1964, Zwickel 1980). Therefore, gonadal immaturity does not appear to be sufficient to explain the absence of territorial behavior in yearlings.

Wittenberger (1978) proposed that breeding is delayed in some species of grouse because first-year males cannot compete effectively for territorial sites with older, more experienced adults. My data confirm that adult males can displace yearlings and prevent them from courting females that are on territories of adult males. However, adult male Blue Grouse establish territories 2 weeks before yearling males arrive on the breeding range (F. C. Zwickel, pers. comm.). Therefore, effectively, there is no competition between yearling and adult males for sites. While there may be competition among yearling and older, nonterritorial males for high quality territorial sites when they become available (Jamieson and Zwickel 1983), every year some low quality sites remain vacant on the breeding range (Lewis and Zwickel 1981). A few first-year males localize near these vacant sites, but do not exhibit territorial behavior until their second year. Therefore, inability to compete with adult males is not necessarily a factor in explaining why some yearling males do not behave territorially.

My observations show that yearling male Blue Grouse are sedentary in the daytime, usually feeding in or near vegetative cover. They are most active for short periods at dusk, presumably when potential predators, such as diurnal raptors, are inactive. High activity of yearling males occurs probably at dawn as well (Bendell 1955). In addition, yearlings rarely sing. Although similar data on the time and energy budgets of territorial males

are not available, these males can be heard singing at any time of day and usually from a few specific sites within their territories (Bendell and Elliott 1967, McNicholl 1978). These sites are mainly on open, elevated areas. If territorial behavior increases conspicuousness and vulnerability to predators, as suggested by Wiley (1974), then young, inexperienced birds might have higher mortality rates if they were territorial. Wiley (1974, 1981) argued under the sexual bimaturism hypothesis that yearling males that defer reproduction could be at an advantage if early survival is enhanced. Survival could be increased if time and energy spent in reproductive activities, such as territorial advertisement and maintenance, could instead be allocated to feeding and hiding from predators. Although mortality rates of nonterritorial yearling male Blue Grouse are relatively low (Bendell and Elliott 1967, Lewis and Zwickel 1982), this hypothesis can only be tested by removing territorial adults and then comparing survival rates of replacement yearlings to those of nonterritorial birds. Why do some yearlings take territories if adults are removed? A void of adult males would create an unnatural situation in which the contact rate with receptive females would probably increase as well as allow yearlings to occupy high quality territorial sites.

Some yearling male Blue Grouse associate with a few territories occupied by adult males (Jamieson and Zwickel 1983) and appear to initiate interactions with territorial males on these sites. Similarly, yearling male Spruce Grouse seemed to be attracted to sites of advertising males and some made flights of unknown motivation onto territories where they were immediately displaced by the resident male (Nugent 1979). Territories of Blue Grouse differ in quality as males on some sites have higher survival and better chances to breed than males on other sites (Lewis and Zwickel 1981). Males that do not occupy territories as yearlings, but instead localize near high quality sites, may increase their chances of securing one of these sites once they become available (Jamieson and Zwickel 1983). This agrees with Wiley's (1974, 1981) suggestion that deferment of reproductive activity may result in increased fecundity at a later age.

Finally, I wanted to know if adult males could inhibit yearlings from attempting to mate with females. Wiley (1981) remarks that even when an optimal life history pattern involves a deferment of reproductive activities at early ages, an individual should not pass up opportunities to breed if risk and effort are low. Adult Blue Grouse displaced yearlings that had intruded onto territories to court females, but yearlings also displayed to females encountered away from territories of adult males. Yet, in these cases, they did not express the full range of courtship responses shown by territorial males. Furthermore, they did not attempt to

copulate and, in some cases, quickly became disinterested in the females. There may be several proximate factors affecting the mating behavior of yearlings. These factors include: (1) the full range of courtship behaviors may not have been developed or learned (see Kruijt and Hogan 1967: 234); (2) females may have to show receptive postures before yearlings become motivated to elicit mating responses; or (3) a territory must be acquired before yearlings show mating behaviors similar to adults. In removal experiments, replacement yearlings sang, occupied territories, and presumably bred (Bendell et al. 1972; Zwickel 1972, 1980). However, no observational data were published on their mating behavior.

Inability of yearling male Blue Grouse to compete for territories with adult males does not explain why some yearlings do not behave territorially on unoccupied sites. Sedentary or secretive behavior of yearlings coupled with associating with high quality territorial sites could conceivably enhance early survival and later fecundity as proposed by Wiley (1974, 1981), but this has yet to be tested. Failure of yearlings to attempt to copulate with females suggests that more emphasis is needed on proximate causes and development of mating behaviors in order to derive a better understanding of the phenomenon of delayed breeding.

SUMMARY

Yearling male Blue Grouse (*Dendragapus obscurus*) were inactive during the day and were usually in or near vegetative cover; overt activity increased at dusk. Adult males displaced yearling intruders from their territories. However, some yearling males appeared to initiate agonistic interactions with territorial males. Other yearlings localized near unoccupied territorial sites but did not behave territorially. Yearlings displayed to, and courted, females away from territories of adult males but did not show the full range of courtship behaviors given by territorial males, and made no attempt to copulate. Results partially support predictions on behavior of yearling males derived from the sexual bimaturism hypothesis to explain why first-year males of most promiscuous species of grouse delay breeding.

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