SPATIAL PATTERNS OF YEARLING MALE BLUE GROUSE AND THEIR RELATION TO RECRUITMENT INTO THE BREEDING POPULATION

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ABSTRACT.—Movements of yearling male Blue Grouse (*Dendragapus obscurus*) were monitored by radio telemetry during the springs of 1980 and 1981, on Hardwicke Island, British Columbia. The locations of the birds were clumped around territories of adult males. Most birds were associated with a few occupied territories, others settled near vacant sites that had been used as territories in previous years, and a few moved widely over the breeding range. Some territories attracted more yearlings than others. Presumed costs and benefits that may be associated with different types of spatial patterns of yearling males are discussed.
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FIRST-YEAR males of many polygynous and promiscuous species are rarely territorial (Wittenberger 1978). Rather, these birds act as a population reserve by filling in vacancies left by territorial adults that die in subsequent years. They are, thus, a necessary component of the population. Information on the mechanisms controlling the recruitment of yearling males should contribute to our understanding of how breeding densities of adult males are regulated, yet few workers have studied potential recruits in detail.

Blue Grouse are considered promiscuous (Wiley 1974). Yearling males usually do not hold territories and presumably do not breed (Bendell and Elliott 1967), even though they produce viable sperm (Hannon et al. 1979). Young adults establish territories in the same general areas they occupied as yearlings (Sopuck 1979, Jamieson and Zwickel in press). Removal studies, however, indicate that more yearling males are present on the breeding range than are necessary to replace adult males that die (Bendell et al. 1972; Zwickel 1972, 1980). Whether acquisition of a vacant site is a matter of chance or of some other factor(s) such as behavior, genetics, or size, which allows some males to gain an advantage in establishing a territory as adults, is unknown.

Zwickel (1980) suggested that spacing behavior among yearling male Blue Grouse may limit the number of 2-yr-olds that are available as recruits. If some yearlings prevent others from settling and if dispersion is the consequence of spacing, then we predict variation in spacing patterns among individuals. If yearlings are surveying potential breeding sites, they may be located near the territories of adult males, and this could give such birds an advantage in subsequently securing a vacant site.

One problem associated with studying nonterritorial birds is that they are often secretive. Radio telemetry helps alleviate this problem, because one can repeatedly learn the locations of individuals at will. In 1980 and 1981, we monitored the locations of yearling male Blue Grouse equipped with radio transmitters to try to determine how the dispersion of these birds might relate to their recruitment as adults. Yearlings did show variation in their spacing patterns, and we speculate on how these differences might affect subsequent survival and fecundity.

STUDY AREA AND METHODS

The study area was on Hardwicke Island, off the east-central coast of Vancouver Island, British Columbia, approximately 3 km northeast of the town of Sayward. A 460-ha area served as the main study site (HI-1). In 1980 only, additional information was collected from three birds on a subsidiary area (HI-2).

Both study areas were logged by clear-cutting between 1968 and 1973. 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. Douglas fir occurred mainly in plantations.

TABLE 1. Mean distances (m ± SE) of random points and locations of yearling male Blue Grouse from activity centers of the nearest territories of adult males.

Year	Study area	Random locations[a]	Yearling locations[b]
1980	HI-1	n = 150 $\bar{x}$ = 89 ± 4	n = 61 (4 birds) $\bar{x}$ = 58 ± 5
	HI-2	n = 37 $\bar{x}$ = 103 ± 7	n = 48 (3 birds) $\bar{x}$ = 83 ± 5
1981	HI-1	n = 124 $\bar{x}$ = 83 ± 4	n = 247 (12 birds) $\bar{x}$ = 65 ± 2

[a] n = number of active territories on study areas each year.
[b] Includes birds with 10 or more locations only.

Birds were found initially with the help of trained pointing dogs and captured with noosing poles (Zwickel and Bendell 1967). They were equipped with solar-powered or battery-powered transmitters by means of a harness similar to that described by Herzog (1977). Birds were caught either in late summer as juveniles, 2–3 months old, or in the following spring as yearlings, 10–11 months old. The "backpack" units weighed approximately 22 g, 2–4% of the body weight of the bird, depending on age at capture.

Movements of 10 and 14 yearling males were monitored in 1980 and 1981, respectively, from the third week in April to the third week in June. Other studies indicate this period to be most important in relation to recruitment (Sopuck 1979, Jamieson 1982). Most birds were located at least once every 2 days. Sightings of banded, non-radio-tagged yearling and adult males were available for reference to yearlings with radios as a result of concurrent studies in the area. We also censused the study area in April and May of 1982 to determine which yearlings whose movements had been monitored in 1981 had taken territories as 2-yr-olds.

"Exact" locations were determined by pacing to known reference points. "Estimated" locations were determined by triangulation from within 100 m of a bird. Both were used in analyses except for data involving distances from territories of adult males; here, only exact locations were used.

The sizes of home ranges were determined by the minimum-area method (Harvey and Barbour 1965). The entire area used by territorial males could not be accurately determined by general census procedures, because too few sightings were obtained for each male. Territorial males spend much of their time in a few specific sites, their activity centers, however (McNicholl 1978, Lewis and Zwickel 1981). We plotted the geographic center of the locations of each territorial male by the method of Hayne (1949) and used these points as an approximation of its activity center.

We use "territory" to mean the area that is occupied and defended by a male for displaying to and copulating with females (Bendell and Elliott 1967). A "territorial site" is the place where a territory is, or had been, located; it may not be occupied every year (Lewis and Zwickel 1981).

RESULTS

On average, birds with radios were located every 1.9 days (range = 1.2–4.8), and a median number of 34 (range = 8–55) locations was obtained for each one.

Distance from territories of adult males.—If yearling males are surveying potential breeding sites, then one might expect their locations to be clumped around territories of adult males. We measured the distance from each location of a yearling to the activity center of the nearest territory. We compared these to the mean distance of random points to the activity centers of nearest territories (Table 1). In both years, yearling males on the main study area (HI-1) were, on average, significantly closer to activity centers of adult males than expected from a random distribution [t-test; t = 6.0 (1980), 4.1 (1981); $P < 0.001$]. Birds outside the main area (HI-2) were also significantly closer to activity centers than expected (t-test; t = 2.4; $P < 0.01$), but individuals there were further away from activity centers than the others (ANOVA; F = 13.5; $P < 0.01$). Reasons for this difference are not known, and the birds from the HI-2 site were omitted from the following analysis.

Yearling males varied significantly in the mean distances they were found from activity centers of territorial males (range = 46–83 m) (ANOVA; F = 1.8; $P < 0.05$; n = 16). Mean distances were similar in 1980 and 1981 (ANOVA; F = 1.4; $P > 0.10$); therefore, the variation among individuals was not due to year. Although a gradient existed, there appeared to be behavioral differences between the five birds whose mean distances were furthest from activity centers (71–83 m) and those that were closer (46–65 m). Here, we must examine the individual case histories of the five that stayed farthest away. Three localized in areas with no occupied territories in the immediate vicinity but near territorial sites that had been occupied the year before. If the distances from the locations of these individuals to the previous activity centers of these sites are measured, the average distances of the three from activity centers

decrease and are within the range of the other yearlings. One yearling was highly localized and singing, and therefore should be considered territorial (Bendell and Elliott 1967). This helps explain his relatively large distance from other territorial males. Another maintained the greatest average distance from territories. He localized for only a brief period, then moved widely about the study area and had the second largest home range (32.8 ha) among all yearlings (median = 10.8 ha; range = 0.6–40.7). He disappeared mid-way through the summer and was not seen again.

A sixth yearling, which had the largest home range (40.7 ha), was located on the study area only five times and was not included in the above analysis. That bird also moved widely and was killed by a predator mid-way through the breeding period.

Association with territories of adult males.—To examine whether or not yearlings were localizing near particular territories, we had to define the distance that the location of a bird had to be from a territory for it to be considered "near." We considered a location to be in the vicinity of a territory if its distance from the activity center of the territory was less than the average distance than random points were from activity centers (Table 1). For simplicity, any location of a bird meeting this criterion was termed a "visit" (to a territory). An "association" with a territory (or territorial site) describes a bird that had a larger proportion of visits to that territory than would be expected from an equal distribution among all territories visited by that yearling.

If yearlings were attracted to territories of adult males, how many territories, on average, did they associate with during the breeding season? Of 160 territories visited by yearlings, 80% had 1–4 visits; 20% had more than 4. The median number of territories that each of 22 yearlings visited was 9 (range = 3–17), and the median number of territories with which they associated was 2 (range = 0–6). There was a positive correlation between size of home range and the number of territories visited (Spearman's Rank Correlation Test; $\rho = 0.5$; $P < 0.05$). but none between size of home range and number of associations ($\rho = 0.2$; $P > 0.10$). Although most yearlings associated with at least one territory, three associated with unoccupied territorial sites, as noted above.

Only five transmitters that had been placed on yearling males operated for more than one breeding season. Therefore, during April and May of 1981 and 1982, areas where birds had localized as yearlings were searched with dogs to determine whether or not these birds had established territories as 2-yr-olds.

The fates of only 3 of 7 (1980) and 8 of 13 (1981) yearlings that were believed to be alive at the end of the summer of each year are known. Of these, six established territories as 2-yr-olds on sites with which they had associated as yearlings; one settled on a territorial site that had not been occupied the year before, and he was killed there by a predator in early spring. A seventh was killed by a predator before we determined whether or not he was territorial. The four remaining birds were nonterritorial as 2-yr-olds, and the sites with which they had associated as yearlings were reoccupied by the previous territory holders. One had associated with two territories in 1980, both of which were reoccupied by the previous occupants in 1981. He was sighted several times as a nonterritorial 2-yr-old and, in the spring of 1982, established a territory on one of these sites when one of the previous residents failed to return. This case, plus others, suggests that some adults may not take territories unless one of the sites with which they had earlier associated becomes vacant.

Association with specific territories.—Some territories may be more attractive to yearlings than others. To examine this question, we searched a 50-ha area in early spring, 1981, and seven yearling males caught there were equipped with radios. We censused this area intensively for most of the breeding period, and only two other yearlings were sighted, each only once and both near the edge of the area. We believe all resident yearlings on this plot were radio-tagged.

First, we examined the dispersion of these birds on a day-to-day basis. To compare locations of a number of individuals found at different times of the day, we had to determine the extent to which birds were moving. A bird was located twice on the same day 50 times during the study. The median distance moved per hour was 2 m (range = 1–24). Because movement appeared to be minimal during the day, we assumed locations of individuals on any one day to be fixed points for this analysis. On any given day all yearlings were usually distributed randomly over the area (Clark and

TABLE 2. Presumed costs and benefits associated with three patterns of dispersion of yearling male Blue Grouse.

Pattern A:	Association with high-quality territories
Costs—	High competition for these sites
	—Low rate of turnover of territorial males (few vacancies)
Benefits—	Survival and fecundity rates high
Pattern B:	Association with low-quality territories
Costs—	Survival and fecundity rates low
Benefits—	Little or no competition for these sites
	—High rate of turnover of territorial males
Pattern C:	Move widely about the breeding range with no associations with territories
Costs—	High mortality rate?
	—Low probability of breeding
Benefits—	None known

Evans Nearest Neighbour Analysis; $R = 0.7$–1.5; $P > 0.10$ for 15 of 17 days). The median distance from any bird to his nearest neighbour was 210 m (range = 18–637).

The seven birds showed variation in their behavior. One moved widely over the area, and two localized near unoccupied territorial sites. Two of these were not seen as adults in 1982 (and presumed dead), and one was killed by a predator as a yearling. The other four associated with 2–4 territories, and each had 1–3 associations in common with another yearling. On 14 occasions two birds from this group were found less than 100 m apart on the same day. In 10 of these cases, they were visiting the same territory, and, in 8, they both had a common association with that territory. Two of these males took territories in 1982. The other two were nonterritorial, and one was killed by a predator in early spring.

Of the 18 territories of adult males on this area, 8 had 0, 7 had 1, 2 had 2, and 2 had 3 yearlings associating with them. Thus, some territories may attract more yearlings than others.

DISCUSSION

Yearling male Blue Grouse were found closer to territories of adults than expected, and most associated with only a few territories. Behavioral observations described elsewhere (Jamieson 1982) indicate that yearlings sometimes interact with residents of these areas. Some workers have suggested that site-specific experience may be important in subsequent attempts to establish a territory (Gullion 1967, Smith 1978, Yasukawa 1979, Vos 1983). Not all radio-tagged birds associated with occupied territories, however, as some settled near vacant sites that had been used as territories in previous years. One yearling appeared to have been territorial, but this is probably rare (Bendell and Elliott 1967).

Two birds moved widely over the study area. One was killed by a predator; the other disappeared and was presumed dead. Of 30 yearling males that Sopuck (1979) followed, 3 did not localize, and all 3 were killed by predators. Greater movement may result from not being able to settle in areas already occupied by other yearlings and may decrease survival.

One factor that may be important for successful territorial establishment by 2-yr-olds is that sites must become vacant within the home range a bird used as a yearling. Most territorial replacements in a removal experiment on Blue Grouse were by nonterritorial adults, many of which presumably would not have settled unless territorial sites were made available (Lewis and Zwickel 1980). Yearlings resighted as territorial adults in our study settled on sites with which they had previously associated. Those that did not take territories had associated with areas that were reoccupied by previous residents. Therefore, an opening may be necessary on a site with which it earlier associated before a male will become territorial, as reported for Black Grouse (*Lyrurus tetrix*) by Vos (1983).

In the portion of the study area in which we marked all resident yearlings, some birds did not associate with occupied sites, whereas others associated with the same 2 or 3 territories, perhaps resulting in competition for these sites. Yearlings will displace others, and site-related dominance may be important in determining which birds replace adult males that fail to return to their territories (Jamieson 1982).

Why do some territories attract more yearlings than others? Lewis and Zwickel (1981) found that adult males preferred certain territorial sites over others. Sites were either occupied each year (persistent) or used intermittently (transient). There were twice as many transient as persistent sites, and approximately one-half of the transient sites were vacant in any given year. Males on persistent sites survived longer and had more females near their territories during the breeding period. Furthermore, both nonterritorial adult and year-

ling males preferred persistent sites when both types were made available in a removal experiment (Lewis and Zwickel 1980). This suggests that birds can assess territorial quality.

Our study area has been censused only for 4 yr, so background data are insufficient to distinguish between persistent and transient sites. If sites do vary in quality, however, then some yearlings may compete for certain territories, especially if there are few high-quality (= persistent) sites. Considering this assumption, we have outlined some presumed costs and benefits that may be associated with three possible patterns of dispersion of yearling male Blue Grouse (Table 2).

Not all yearlings may be able to compete equally for high-quality sites, and it may be more advantageous for some birds to associate with low-quality sites. It should not be assumed, however, that all yearlings showing "Pattern A" dispersion will have a greater fitness than birds showing "Pattern B." Although the benefits of associating with a high-quality site are high once one of these territories is secured, the costs, as a yearling, may also be high. Among individuals, costs related to competition may depend on the dominance ranking of birds, while costs related to turnover rates of territorial adults on high-quality sites may depend more on chance. These points need further study.

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