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# DIFFERENTIAL USE OF TERRITORIAL SITES BY MALE BLUE GROUSE

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ABSTRACT.—We examined the pattern of use of territorial sites occupied by male Blue Grouse on a 485-ha area over a 10-year period, 1969 to 1978. Some sites were occupied continuously while others were used only intermittently; these were called "persistent" and "transient" sites, respectively. Approximately one-half of the transient sites were vacant in any given year. Males on persistent sites survived significantly longer and had significantly more females near their territories during the breeding season than those on transient sites. Thus, males on persistent sites may have better opportunities for breeding than males on transient sites. These results help to explain why yearling males delay breeding, despite being physiologically able to do so, and they also provide new insights into how breeding densities of males are regulated.

Emlen and Oring (1977) have suggested that with species in which males are territorial for the purpose of acquiring mates, territorial quality can be a factor in determining how many mates are obtained. This may be true even if females do not use the territories other than to come to them to breed. Male Blue Grouse (*Dendragapus obscurus*) are territorial and territories serve primarily as areas where they can display and breed without interference from other males (Bendell and Elliott 1967). Females come to territories only to copulate and, consequently, it is possible for males to breed a number of times in any given year. Males that are able to do this will potentially produce more offspring, and hence have greater reproductive success than those that breed less often. Reproductive output may also be increased in those individuals that live a long time. If a male's chances of surviving and attracting females can be affected by the quality of the territory that is occupied, then it can be hypothesized that sites of highest quality should be preferentially selected for territories.

Gullion (1967) and Boag (1976) reported that some sites used for territories by male Ruffed Grouse (*Bonasa umbellus*) were occupied more frequently than others, and Boag suggested that frequency of occupancy reflects the quality of such sites for territories. Territorial sites used by male Blue Grouse also differ in frequency of use; however, this observation was based on only four years of data (Bendell and Elliott 1966). Here we examine this phenomenon in this species in more detail using data collected from one area over 10 consecutive years. In addition, we compare sites used continuously to those used less frequently, with respect to the survival of males and the numbers of females that were seen near them during the breeding season. Lastly, we relate the results to life-history parameters, such as delayed breeding by yearling males and the importance of territorial behavior in regulating breeding densities of males.

## STUDY AREA

Our analysis is based on data collected between 1969 and 1978 on Comox Burn, a 485-ha area on the east slope of Vancouver Island, British Columbia, approximately 14 km west of Courtenay. This area is in a region intermediate between the Douglas-fir (*Pseudotsuga menziesii*) and western hemlock (*Tsuga heterophylla*) biogeoclimatic zones (Krajina 1965).

Comox Burn was clearcut between 1947 and 1961, and in September 1961 the entire area was burned by wildfire. Replanting with Douglas-fir was virtually complete by 1964. In 1969 the area consisted entirely of either "open" (Bendell and Elliott 1967) or "very open" stages of vegetation density. By 1977 some portions had become "dense" or "very dense," but most of the area was still "open" (Fig. 1). Zwickel and Bendell (1967, 1972) and Zwickel (1977) described the study area in detail.

## METHODS

We studied Blue Grouse each year from April to late August or early September. Most territorial males were located by their hooting (singing) or with the aid of pointing dogs. Attempts were made to capture and color-band all unmarked birds. Approximately 80% of the territorial males were banded within each year. By mid-May each year most territorial males had been located and individually identified, if banded.

Locations of all banded territorial males and un-

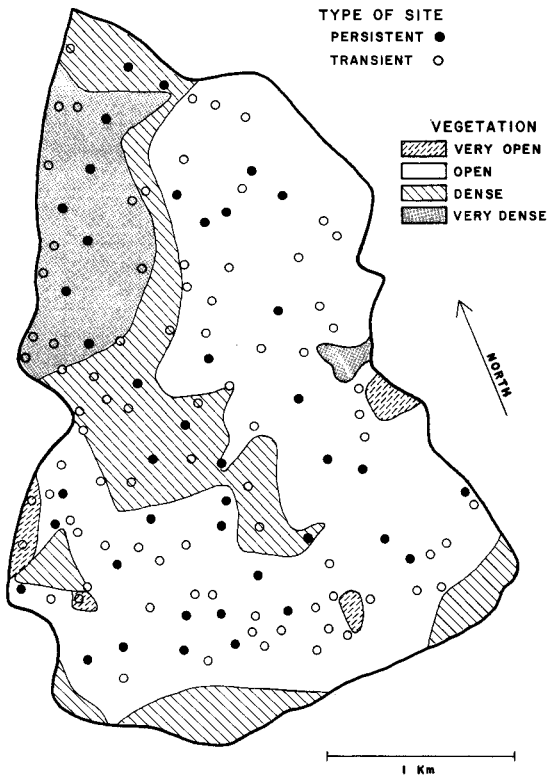


FIGURE 1. Vegetative structure (after Bendell and Elliott 1967) in 1977 and location of activity centers of persistent and transient sites on Comox Burn.

banded and unidentified males found hooting were plotted on maps for each year. All singing males were considered to be on territories, since hooting signifies occupancy of a territory (Bendell and Elliott 1967, McNicholl 1978).

We use "territory" to mean an area that is occupied, and presumably defended, by an individual male for displaying to and copulating with females (Bendell and Elliott 1967). The "activity center" includes the area within the territory where the resident most frequently hoots. A "territorial site" is the place where a territory may be located; it may not be occupied every year. Although territorial boundaries may change slightly from year to year, and with different occupants, the location of the activity center generally remains the same.

## RESULTS

### FREQUENCY OF USE

As with Ruffed Grouse (Gullion 1967, Boag 1976), some areas were used for territories every year, others only intermittently. Seven territorial sites were used for one year, 12 for two years, 9 for three years, 12 for four years, 13 for five years, 11 for six years, 11 for seven years, 7 for eight years, 11 for nine years, and 30 for ten years. Those used every year generally had a succession of males occupying them; only one male present in 1969 was still alive in 1978. A site was termed "persistent" if it was occupied for at least 9 of the 10 years of study. Those used for eight years or less were called "transient." Though "persistent" implies use in every year, we included sites occupied for 9 of the 10 years in this category because of the possibility that a site was mistakenly recorded as vacant in one year (e.g., a male may have occupied the site but died before we detected it). Boag (1976) classified sites used in more than 50% of the years as perennial (similar to our persistent sites) but we adopted the more stringent criterion.

TABLE 1. Number of persistent and transient territorial sites occupied by male Blue Grouse on Comox Burn, 1969–1978.

| Year | Type of site | | Total |
|---|---|---|---|
| | Persistent | Transient | |
| 1969 | 37 | 32 | 69 |
| 1970 | 39 | 31 | 70 |
| 1971 | 40 | 42 | 82 |
| 1972 | 41 | 41 | 82 |
| 1973 | 41 | 42 | 83 |
| 1974 | 41 | 37 | 78 |
| 1975 | 41 | 32 | 73 |
| 1976 | 38 | 34 | 72 |
| 1977 | 41 | 44 | 85 |
| 1978 | 40 | 36 | 76 |
| Total | 399 | 371 | 770 |

From 1969 to 1978 there were 41 persistent and 82 transient sites on Comox Burn (Fig. 1); numbers of territorial males per year varied from 68 to 85. In some years individual males occupied areas normally used by two different birds, but this was uncommon (12 instances). Thirty-eight transient sites had periods of use separated by intervals when they were vacant. The number of transient sites used each year ranged from 31 to 44 while the number of persistent sites occupied per year was less variable (Table 1).

### SURVIVAL

We compared mean survival of males occupying the two types of site because survival may reflect the quality of those sites. Only banded males were used to estimate survival, and males occupying territories in one year but not sighted in subsequent years were assumed to have died. Males that shifted territories during the study (N = 14) were not included in these estimates, nor were newly banded males on territories that had an unbanded occupant in the previous year (N = 16). We excluded the latter

TABLE 2. Survival of male Blue Grouse occupying persistent and transient territorial sites on Comox Burn, 1969–1978.

| Survival (years) | No. males from Persistent sites | No. males from Transient sites |
|---|---|---|
| 1 | 12 | 34 |
| 2 | 11 | 21 |
| 3 | 15 | 15 |
| 4 | 10 | 10 |
| 5 | 11 | 6 |
| 6 | 8 | 5 |
| 7 | 6 | 2 |
| 8 | 3 | 1 |
| 9 | 1 | 0 |
| 10 | 3 | 0 |
| 11 | 1 | 0 |
| Mean | 4.25 | 2.60 |
| N | 81 | 94 |

because some of the newly banded males may have been unbanded individuals that were there previously; including these would have underestimated survival. Survival as reported here is minimal, however, because males occupying territories at the end of the study (1978) were included in the estimates and considered to have died by 1979 even though most would not have done so. Males occupying persistent sites survived longer than those using transient sites (Mann-Whitney U-test, U = 5,304.5, 2-tailed, $P < 0.001$; Table 2).

Sites may have been occupied persistently merely because males on these areas survived a relatively long time (Table 2). We therefore compared numbers of males using persistent and transient sites. Newly banded males were considered as new individuals even if the site they used had been occupied by an unbanded male in the previous year. If an area was occupied by an unbanded male for a series of years, this bird was considered as one individual. Overall, because survival of males is greater on persistent than on transient sites, this may result in an overestimation of the number of males on persistent sites relative to the number on transient sites. However, we assume that any bias produced by this is slight and inconsequential. The mean number of males per persistent site was 3.20 while the value for transient sites was 2.16. Thus, each persistent site had, on average, at least as many different males occupying them over the 10 years as did transient sites. Therefore, continuous occupancy of persistent sites was not due solely to the high survival of males using them.

## LOCATIONS OF FEMALES

As noted above, males can increase their breeding success by mating with more than one female each year. Copulations, however, are rarely observed and it is difficult to determine if some males are breeding more than others. We plotted the locations of all females sighted prior to 16 May for each year in order to test the hypothesis that males on persistent sites attract, and potentially breed with, more females than those occupying transient sites. Locations prior to 16 May were used because most breeding on this area is completed by this date (Zwickel 1977). For each location, we determined whether the hen was nearer the activity center of an occupied persistent site or transient site. Over the period of study, 444 females were nearer persistent sites and 301 were nearer transient sites. The number of females nearer each occupied persistent site ($\bar{x} = 1.24 \pm$ SE of 0.19) was greater than that for each occupied transient site ($\bar{x} = 0.88 \pm 0.10$; Wilcoxon's Signed Rank Sum T, T = 2, 2-tailed, $P < 0.01$).

Even though more females were found near persistent than transient sites, this may not be because males on the former attract more females. Persistent sites could simply represent habitat that is most suitable and, hence, preferred by females. Since a primary requirement of females in spring is to secure a nesting area (S. J. Hannon, pers. comm.), more nests should be found near persistent than transient sites if the former areas are also more suitable for females. Between 1969 and 1978, 113 nests were found on Comox Burn. Thirty-nine were nearer activity centers of persistent sites, 74 nearer activity centers of transient sites. This does not differ significantly from a ratio of 1:2 (41 persistent sites, 82 transient sites; $P > 0.05$) that one would expect if habitat near transient sites was equally as good for nesting as that near persistent sites. Thus, the greater number of females near persistent sites during the breeding season was not due to these areas being preferred by females for nesting.

## WEIGHTS OF MALES

Weights of males occupying persistent and transient sites were compared to see if body weight might relate to which type of site was obtained. Average weights of newly banded males from persistent sites (1,287 ± 16 g, N = 17) did not differ significantly from those of newly banded males on transient sites (1,293 ± 13 g, N = 39; $t = 0.236$, 2-tailed, $P > 0.05$). When weights of males

banded as yearlings and which subsequently returned as adults were compared, those that obtained persistent sites weighed less (1,102 ± 23 g, N = 12), on average, as yearlings than those that acquired transient sites (1,164 ± 15 g, N = 24; $t = 2.307$, 2-tailed, $P < 0.05$).

### DISPERSION OF ACTIVITY CENTERS

Gullion (1967, 1976) and Boag (1976) noted that activity centers of Ruffed Grouse tended to occur in groups or clusters, although each postulated different reasons for this arrangement (structure of habitat and social interaction, respectively). A similar phenomenon in Blue Grouse seems possible since McNicholl (1978) showed that males tend to sing in groups. To test this idea, we measured the distance from the activity center of each territory to the activity center of the nearest adjacent territory. All territorial sites were used in these measurements even if they were not occupied every year. We then calculated an $R$ value (Clark and Evans 1954), which gives a measure of the dispersion of activity centers. There was a significant tendency for uniform spacing of activity centers (see Fig. 1; $R = 1.3346$, c = 4.68, $P < 0.01$). The distribution of activity centers of occupied territories also showed a significant tendency toward uniformity when compared year by year (all tests, $P < 0.01$). A similar conclusion was reported by Bendell and Elliott (1967).

Boag (1976) further suggested that transient centers were grouped around perennial centers. Although activity centers on Comox Burn tended to be uniformly distributed, transient sites could be located principally around persistent sites. We therefore plotted 82 random points on a map of the study area (equivalent to the number of transient sites) and determined whether the activity center of a transient site or a random point was nearer the activity center of a persistent site. If transient sites are spaced randomly in relation to persistent sites a similar number of transient sites and random points should be found nearer to persistent sites. This was the case (18 vs. 23, respectively, $P > 0.05$). Thus, transient sites were not located preferentially around persistent sites.

## DISCUSSION

Males occupying persistent sites survived longer and had more females near their territories in early spring than those using transient sites. Thus, as Boag (1976) suggested, persistent sites are apparently better than transient sites for territories. These attributes of persistent sites could arise as a result of the quality of the areas, the quality of the individuals occupying them, or a combination of both. At present the relative importance of these factors in making persistent sites better for territories is unknown. However, since some individuals apparently delay breeding because persistent sites are not obtained and because males seem to prefer these areas (Lewis and Zwickel 1980), we think that the sites differ in quality and that these differences do, at least in part, make persistent sites better than transient sites.

Over the 10-year period of this study, vegetative structure on Comox Burn changed greatly. In 1969, Douglas-fir plantations were at early stages of regeneration. By the final two years of study some areas were entering "very dense" stages (Fig. 1). Because recruitment to populations of Blue Grouse is not affected by density of conifers until "very dense" stages are reached (Redfield et al. 1970), we believe that changes in vegetative structure from 1969 to 1978 likely had little effect on a site's suitability as a territory. Transient sites were not more often located in areas where vegetative structure had become most dense (Fig. 1). This contrasts with Boag's (1976) report for Ruffed Grouse in which changes in vegetative structure around perennial centers, occurring over short periods of time, resulted in some sites becoming transient. At present, the only difference that has been found between persistent and transient sites is that the former tend to be located on relatively higher areas (Lewis 1981).

On Comox Burn there were only 41 persistent sites and males may have competed for these areas. What determines which males obtain persistent sites? In Red Grouse (*Lagopus lagopus*), heavier individuals may have better chances of being recruited into breeding populations than lighter ones (Lance 1978). However, male Blue Grouse securing persistent sites did not weigh more, either as yearlings or adults, than those procuring transient sites. Thus, greater body weight did not give a male an advantage in acquiring a persistent site.

Yearling male Blue Grouse seldom hold territories (Bendell and Elliott 1967; this study), but tend to have home ranges encompassing the territories of several males (Sopuck 1979). Yearlings may evaluate the suitability of these sites for territories at this time, for as young adults most males return to the same general areas they occupied as

yearlings (Sopuck 1979). When two-year-old males arrive on breeding range in spring some territorial sites will be vacant because previous owners have died. These new adults should attempt to secure the best sites available and once secured these sites are unlikely to be lost to intruders (McNicholl 1978). Whether or not a two-year-old acquires a persistent site will depend, to some degree, on how many are vacant in the area he occupied as a yearling. It may also depend on his being the first to find and recognize that a site is not occupied.

On Comox Burn between 1969 and 1978, 141 banded yearling males were identified and only one was territorial. This almost complete absence of territorial behavior in yearling males needs to be explained since they are physiologically able to breed (Hannon et al. 1979) and vacant transient sites always were available. Most yearling males must delay breeding. Wiley (1974a, b) suggested that if early survival and later reproduction are enhanced by delaying breeding, such a system can evolve. Males occupying persistent sites survived longer and had more females near their territories than those using transient sites. Thus, occupancy of a persistent site seems to enhance a male's reproductive potential. Yearling males probably cannot compete with adults for persistent sites. Rather than select transient sites, to which they may be committed for the rest of their lives (Lewis 1979), it may be advantageous to delay breeding until they are adults, when chances of obtaining persistent sites are presumably increased. Indeed, results from a removal experiment demonstrated that some yearlings will become territorial on persistent sites if they are available (Lewis and Zwickel 1980). Nevertheless, life expectancy declines with age. Thus, it may not be advantageous for adult males to delay breeding, so some individuals not securing persistent sites would settle on transient sites and attempt to breed there.

Other workers have suggested that territorial behavior is not involved in determining the breeding density of male Blue Grouse (Bendell and Elliott 1967, Zwickel 1972). This conclusion was based on the finding that all adult males appeared to be territorial. The fact that vacant transient sites were present on Comox Burn each year seems to support this conclusion. However, Lewis and Zwickel (1980) provided strong experimental evidence that surplus adult males are present among Blue Grouse. As well, earlier removal experiments demonstrated that yearling males will occupy territories if adult males are not present (Bendell et al. 1972, Zwickel 1972). Presence of potential breeders that are prevented from breeding by residents is one requirement that must be satisfied in order to show that territorial behavior limits the numbers of breeders (Watson and Moss 1970, Klomp 1972).

Klomp (1972) also suggested that all suitable space must be filled before territorial behavior limits breeding density. If transient sites are considered suitable for territories, even though marginal, then this requirement does not seem to be satisfied in Blue Grouse. However, since territorial behavior seems to limit numbers of males occupying optimal areas (e.g., persistent sites) and, hence, may be a factor causing some males to delay breeding, it cannot be ruled out as a factor determining numbers of breeding males.

Our results demonstrate that some sites used by males for territories are occupied continuously and that males using these areas have better survival than individuals using less frequently occupied sites. We conclude that persistent sites are of higher quality than transient sites and that males occupying them have enhanced opportunities for reproducing. That yearling males delay breeding seems to be at least partially explained by the fact that they cannot acquire persistent sites for territories (Lewis and Zwickel 1980, this study). Several questions remain, however, one of them being why some males are successful in obtaining persistent sites while others use poorer areas.

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