

GENERAL NOTES

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Use of space by territorial male Blue Grouse.—The social system and reproductive behavior of Blue Grouse (*Dendragapus obscurus*) have been studied in several areas of coastal British Columbia (e.g., Bendell and Elliott, *Can. Wildl. Serv. Rept. Ser.* 4, 1967; Zwickel and Bendell, *Proc. XV Int. Ornithol. Congr.*, The Hague, 15:150–169, 1972; Zwickel et al., pp. 212–225 in *Symposium on Natural Regulation of Wildlife Populations*, F. L. Bunnell, D. S. Eastman, and J. M. Peek, eds., *Forest Wildlife and Range Experiment Stn.*, Univ. Idaho, Boise, Idaho, 1983). The species has a promiscuous mating system (Wiley, *Quart. Rev. Biol.* 49:201–227, 1974) in which males establish dispersed territories on breeding ranges in spring (Bendell and Elliott 1967; McNicholl, Ph.D. diss., Univ. Alberta, Edmonton, Alberta, 1978). Occupancy of a territory is indicated when males localize their movements within a small area and advertise their presence to females and other males by hooting. These territories function primarily as areas for display and mating, although feeding and other activities also occur in them. Females do not associate with males except to breed. Most hooting is conducted from a few specific locations within the territory (McNicholl 1978); the area encompassing a male's hooting "posts" is his activity center (McNicholl 1978; Lewis and Zwickel, *Condor* 83:171–176, 1981).

In previous studies the activities of territorial males were followed by observers either working alone or with pointing dogs. These methods have a bias in that birds are more likely to be found when they are hooting than when they are silent. Consequently, they are most likely to be found within activity centers. To overcome this bias I radio-tagged territorial males and was able to address some new questions fundamental to interpretations of the function and importance of territories for male Blue Grouse: (1) where are territorial males located when they are not hooting; (2) are the same areas used consistently throughout the breeding season; (3) what portion of a male's spring/summer home range should be considered a territory? I also examined the activity patterns of males for a relationship between the size of area occupied by individuals and their hooting frequency (e.g., Falls, pp. 61–89 in *Advances in the Study of Communication and Affect*, L. Krames, P. Pliner, and T. Alloway, eds., Vol. 4, Plenum Press, New York, New York, 1975).

Study area and methods.—The study was conducted in 1981 on Hardwicke Island, a 77-km² island situated between Vancouver Island and mainland British Columbia (50°27'N, 125°50'W). The study area was ca 56 ha in size and had a vegetation structure and composition similar to that of Jamieson and Zwickel (*Auk* 100:653–657, 1983).

From 8 to 16 April 1981, 10 adult males were captured with snare poles (Zwickel and Bendell, *J. Wildl. Manage.* 31:202–204, 1967) and equipped with radio transmitters using a harness attachment (Herzog, *J. Wildl. Manage.* 43:316–323, 1979). One male was killed by a predator 1 week after being radio-tagged, so on 24 April the transmitter was placed on another bird. Transmitters weighed ca 30 g (less than 2.5% of a bird's weight), and had potential signal ranges of 3 km or more. They were applied only to males that were believed to be territorial; that is, males that were hooting prior to being radio-tagged, or if silent had been identified as adults in a previous year. Most territorial males on my study area were radio-tagged (Fig. 1).

Radio-tagged birds were located with a receiver and hand-held yagi antenna. Their exact locations were determined by taking a compass bearing and pacing to known reference points. I tried to find each male at least once every 3 days. All birds were found about the

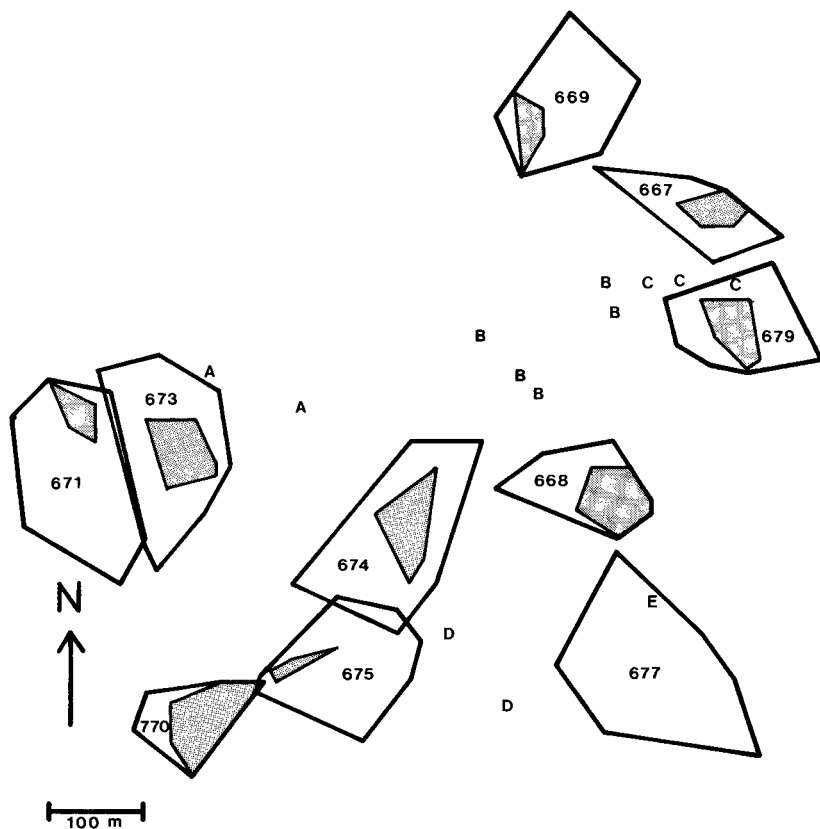


FIG. 1. Spatial relationships of territorial males on Hardwicke Island, British Columbia in 1981. Total home ranges from radio-tagging until territories were abandoned are outlined with solid lines, activity centers are shaded. Numbers identify individual radio-tagged birds and letters represent sightings of non-radio-tagged territorial males.

same number of times except for one with a faulty transmitter (no. 677) and two that were killed by predators (nos. 668 and 770, Table 1). I monitored the whereabouts of surviving birds until late August.

Home ranges were delineated by connecting outermost points of observation with a straight line (Odum and Kuenzler, *Auk* 72:128–138, 1955; Bendell and Elliott 1967). Sightings that were considered “atypical” (see below) were not used in the analyses. In all instances in which males were observed hooting, they were considered to be doing so within their activity center. Therefore, activity centers were delineated by connecting outermost locations at which males were seen hooting.

In mid-June individual males began leaving their activity centers and immediate vicinities thereof, and moved to new localities. Since they did not subsequently return to their activity centers, I considered them to be abandoning their territories. The length of time between

TABLE 1
 SIZE OF HOME RANGES AND DATES OF TERRITORY ABANDONMENT FOR RADIO-TAGGED
 TERRITORIAL MALE BLUE GROUSE ON HARDWICKE ISLAND, BRITISH COLUMBIA IN 1981

| Male | Home range size (ha) | | | Date of territory abandonment |
|------|------------------------|----------------------|--|-------------------------------|
| | Breeding period | Post-breeding period | Radio-tagging to territory abandonment | |
| 667 | 0.44 (19) ^a | 0.29 (21) | 0.91 (44) | 25 June ^c |
| 668 | 0.93 (19) | 0.36 (9) | ^b | ^b |
| 669 | 0.58 (19) | 0.16 (18) | 1.68 (72) | 11 August |
| 671 | 0.26 (16) | 1.46 (18) | 2.13 (49) | 16 July |
| 673 | 0.73 (21) | 1.55 (19) | 2.11 (48) | 4 July ^c |
| 674 | 0.64 (16) | 2.14 (20) | 2.23 (36) | 17–18 June ^c |
| 675 | 0.65 (22) | 1.53 (23) | 2.00 (63) | 20 July |
| 677 | 0.87 (8) | 1.95 (14) | 2.75 (25) | 25 June ^c |
| 679 | 0.62 (16) | 0.93 (20) | 1.31 (40) | 27 June |
| 770 | 0.60 (16) | 0.34 (11) | ^b | ^b |
| Mean | 0.63 (17.2) | 1.07 (17.3) | 1.89 (47.1) | 7 July |

^a Number of sightings in parentheses; 24 sightings obtained by observers working with dogs were included when estimating home-range size.

^b Killed by predator; 668 on 31 May, 770 on 3 June.

^c Date estimated, $\pm 1-1.5$ days.

radio-tagging and abandonment of territories differed among males, so comparisons of home range sizes during this time involve different numbers of sightings per male. I, therefore, examined and compared home range sizes of the 10 radio-tagged males within the periods 8 April–20 May and 21 May–16 June. The first period included the time from radio-tagging of the first male to the end of peak breeding on Hardwicke Island (F. C. Zwickel, unpubl.). Peak breeding is defined as the two week period during which most copulations occur (Zwickel, *Condor* 79:185–191, 1977). The second time period I examined was from the end of peak breeding to the day before the first male abandoned his territory. Although some copulations took place after 20 May (7.3%), for simplicity I will refer to the periods outlined above as the “breeding” and “post-breeding” periods, respectively.

Results.—All radio-tagged males except one were heard hooting, and some were seen displaying to females or other males. Thus, radio-packages apparently did not preclude the performance of these activities. The individual that was not heard hooting was considered to be territorial because his movements were relatively localized compared to those of non-territorial males (Sopuck, M.Sc. thesis, Univ. Alberta, Edmonton, Alberta, 1979; Jamieson and Zwickel 1983). I may have missed hearing this male hoot as most radio-tracking was done between 09:00 and 17:00 when hooting is less frequent than at other times of the day (McNicholl 1978).

Size of home ranges.—During the breeding period males occupied areas averaging 0.63 ± 0.06 (± 1 SE) ha in size (Table 1). Sixty-eight percent (117/172) of the sightings were within activity centers, and activity centers comprised an average of $48.7 \pm 9.7\%$ (range = 7.7–100%, male no. 677 excluded) of the area used during this period. Home ranges averaged 1.07 ± 0.24 ha in size during the post-breeding period, an increase of 70% over the breeding period (Table 1); the difference is significant if the two males killed by predators are excluded

TABLE 2
PROPORTION OF SIGHTINGS IN WHICH RADIO-TAGGED TERRITORIAL MALES ON HARDWICKE ISLAND, BRITISH COLUMBIA WERE HOOTING IN 1981

| Male | Proportion hooting | | |
|------|------------------------|----------------------|-------------|
| | Breeding period | Post-breeding period | Combined |
| 667 | 0.63 (16) ^a | 0.14 (21) | 0.35 (37) |
| 668 | 0.31 (16) | 0.25 (8) | 0.28 (25) |
| 669 | 0.53 (17) | 0.17 (18) | 0.34 (35) |
| 671 | 0.39 (13) | 0.11 (18) | 0.23 (31) |
| 673 | 0.33 (18) | 0.05 (19) | 0.19 (37) |
| 674 | 0.21 (14) | 0.15 (20) | 0.18 (34) |
| 675 | 0.14 (21) | 0.22 (23) | 0.18 (44) |
| 677 | 0.00 (8) | 0.00 (14) | 0.00 (22) |
| 679 | 0.33 (15) | 0.10 (20) | 0.20 (35) |
| 770 | 0.67 (12) | 0.00 (10) | 0.35 (23) |
| Mean | 0.35 (15.0) | 0.12 (17.1) | 0.23 (32.3) |

^a Number of sightings in parentheses; sightings by observers working with dogs were not included.

(paired *t*-test, $t = 2.73$, $P = 0.03$). Forty percent (70/173) of the sightings obtained from 21 May–16 June were within activity centers, and 57% (99/173) were in areas used during the breeding period. On average, 76% of the breeding period home range was used again in the post-breeding period. Total home range sizes from 21 May–16 June averaged 1.43 ± 0.21 ha. The increase in size of home ranges after 20 May did not include corresponding enlargements of activity centers. The total area within which males were observed hooting from 8 April–16 June averaged only 7.1% larger than areas used for hooting during the breeding period.

Home range size was not significantly ($P > 0.05$) correlated with the number of sightings per male for either the breeding or post-breeding period. Males were found a similar number of times in both periods (Table 1), so the increase in size of area used after 20 May did not result from the radio-tracking regime.

Up to the time they abandoned their territories, radio-tracked males occupied home ranges that averaged 1.89 ± 0.20 ha (Table 1) in size. Over this time home ranges of radio-tagged males that were adjacent to each other overlapped in only three instances (Fig. 1). Areas of overlap averaged 7.1% of the total area occupied by these males. There was no overlap of activity centers.

Home range size and frequency of hooting.—There was no correlation between the size of a male's breeding or post-breeding period home range (Table 1) and the percent of observations in which he was hooting during these times (Table 2). However, the total area used by radio-tagged males up to 16 June, and up to the time they abandoned their territories, were both inversely related to their frequency of hooting ($r = -0.940$ and -0.803 , respectively; both P 's ≤ 0.01). For the period 8 April–16 June, size of activity centers was not correlated with percent of observations in which males were hooting.

Abandonment of territories.—The exact date of territorial abandonment was known for four males; others were estimated as midway between the last sighting in the activity center, or its immediate vicinity, and the first sighting in a new locality (times between these dates

ranged from 1 to 3 days). The first and last males to abandon territories did so on 17–18 June and 11 August, respectively (Table 1). Abandonment involved direct moves to new areas, these usually being completed within 2 days of leaving the breeding territory. Three males moved to dense coniferous forest, typical of wintering habitat, whereas the other five moved to new areas on the breeding range. The latter then restricted their movements but did not behave territorially (i.e., were not seen hooting or displaying).

Prior to the time radio-tagged males abandoned their territories, I obtained seven (1.5%, 7/471) “atypical” sightings. Four involved movements in which males crossed activity centers of other males; the other three were instances in which males were found far from their usual areas of occupancy in locations uncharacteristic for territorial males. In all cases, these males were in or near their activity centers when next found. Such sightings may have resulted from males being chased by predators or from chasing conspecifics.

Discussion.—During the breeding period males spent much of their time hooting and most of their movements were restricted to areas within or near activity centers. Hooting diminished in the post-breeding period (Table 2) and there was an increase in home range size. Similarly, males that hooted the most had the smallest home ranges, possibly because their movements were more limited to their activity centers than were those of males that hooted less.

Brown (*The Evolution of Behavior*, Norton Press, New York, New York, 1975), Wilson (*Sociobiology*, Harvard Univ. Press, Cambridge, Massachusetts, 1975), and Morse (*Behavioral Mechanisms in Ecology*, Harvard Univ. Press, Cambridge, Massachusetts, 1980), among others, define territory as an essentially exclusively occupied area that is either actively or passively defended. Other less restrictive definitions also have been proposed (see Kaufmann, *Biol. Rev.* 58:1–20, 1983 for a review). What portion of a male Blue Grouse’s spring/summer home range should be considered a territory: should it consist of the activity center only, or should other areas also be included?

Home ranges of adjacent radio-tagged males overlapped only slightly even when all observations between 8 April and the time territories were abandoned were included. The small degree of overlap that did occur seems inconsequential given that 3 months of sightings were included. Also, males do expel other males from areas outside their activity centers (pers. obs.; see Falls and McNicholl, *Can. J. Zool.* 57:457–462, 1979). Thus, I suggest that the total area occupied until moving to new areas following the breeding season constitutes a territory.

Nevertheless, the activity center appears to be the focal point of the territory, especially during the breeding period. These centers usually are located on the most elevated portion of the territory, presumably facilitating the broadcasting of hooting and the detection of predators and conspecifics. Their height in relation to surrounding areas is the most critical feature distinguishing territorial sites of high and low quality (Lewis, *J. Wildl. Manage.* 45: 1048–1051, 1981). Questions that remain, however, and which relate to determining the function of territories, include, why are areas outside of activity centers defended, and why do some males stay on territories longer than others?

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