

AGGRESSIVE AND SPACING BEHAVIOR OF FEMALE BLUE GROUSE

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ABSTRACT.—Female Blue Grouse (*Dendragapus obscurus*) on Stuart Island, Washington were found to interact aggressively with female dummies in the prelaying period when a taped cackle call was played. Interactions included: tail fanning, wing dragging, everting the white patagium feathers to display a shoulder patch, head bobbing, neck stretching, jump attacking, pecking, and diving attacks. Threatening and aggressive calls included: cackling calls with inflections, a Nee-uk call, and attack and scream whinny calls. The frequency of aggressive interactions was greatest in the latter half of April, a period when hens were selecting nesting sites. The prelaying ranges of 12 hens were mostly mutually exclusive and showed a dispersed distribution relative to each other. However, there were interspaces sufficient for other grouse to nest. We suggest that aggressive behavior and mutual avoidance of females resulted in a dispersed distribution of nest sites. Such spacing should enhance the reproductive fitness of females by reducing predation rates on hens, eggs, and young. Received 24 August 1983, accepted 16 November 1984.

THERE has been disagreement among biologists on whether territoriality in birds primarily served to disperse the breeding population (Lack 1966, 1968), or whether, in addition to this spacing function, it regulated numbers by excluding some individuals from securing breeding space (Wynne-Edwards 1962). Even after 20 years, the argument continues (Davies 1978, Patterson 1981, Wittenberger 1981). Recently, the territorial limitation hypothesis has been expanded to include the mutual exclusion of yearling females by other females in polygynous Blue Grouse (*Dendragapus obscurus*; Zwickel 1972, 1980; Hannon and Zwickel 1979). The primary evidence for surplus nonbreeding females was that, following the removal of localized females in the prelaying period, additional yearling females occupied the vacancies created (Zwickel 1972, 1980). However, this replacement does not constitute unequivocal evidence of socially induced nonbreeding in yearling females, since these females might have bred elsewhere (cf. Watson and Moss 1970). The newcomers could have shifted their ranges to improve their fitness as proposed in the Fretwell-Lucas habitat model (Fretwell and Lucas 1969). Such redistribution is consistent with theoretical considerations that animals should space themselves to reduce predation risk (Taylor 1976).

The resolution of this perennial question requires documentation of the dispersion pattern

of all females in a population where emigration cannot confound results. We measured aggressiveness and described the distribution of female Blue Grouse on Stuart Island, Washington during the breeding cycle in 1975 and 1976. Our hypothesis was that social interactions between females in the prelaying period resulted in mutually spaced ranges but that the spacing and ensuing social interactions did not prevent any female from nesting. Subordinate females could either nest between the ranges of other females or delay nesting until adults were egg-laying and/or incubating their eggs.

METHODS

Blue Grouse were introduced to Stuart Island in 1970 (Bergerud and Hemus 1975). From 1971 to 1976 territorial males numbered 9–11 individuals. Hen counts were not made prior to 1975. On 30 April 1975 we tape-recorded a series of cackle calls given by a hen in response to taped whinny calls during a mirror-arena test of a territorial male (see Stirling and Bendell 1970 and Hannon 1978 for details on calls, and Mossop 1971 and Bergerud and Hemus 1975 on the mirror-arena). We subsequently used this recording to elicit cackles from females and to attract them to mirror-arena tests, thus making possible a study of female aggressive behavior.

In May 1975 we conducted mirror-arena tests of hens within the territories of 10 territorial males. A triangle of mirrors was set up on the forest floor within sound of the hooting male, with a dummy hen placed 30 cm in front of and facing away from

TABLE 1. Description of females that fought a dummy hen or a like hen on Stuart Island.

Case	Date and time	Stimulus	Behavior
1	3 May 1975, A.M.	Female dummy, cackle call, mirrors	Female cackled continuously 1:45 after start of tape, advanced 18.6 m/min, and gave 17 attack whinnies/min; from 5:41 to 12 min she attacked, with 10.5 whinnies/min, 1.6 pecks at dummy/min, 1 peck at mirror, 1 jump attack at mirror, 1.1 tail fans and lateral runs with wing drag at dummy per minute, and 1.1 cackles/min. She attacked until observer was 3 m away.
2	4 May 1975, 0715	Female dummy, cackle call, mirrors	Female cackled 8 min after start of tape, flew in 9.44, male flutter flights, and hooted; she was on the ground at 11:30 min and gave tail fan with white showing on shoulders. From 13 to 18 min she attacked, cackling continuously, with 2.2 pecks/min and 6.8 jump attacks/min at mirror and 1.2 pecks/min and 1 diving attack at dummy. Male hooted at both dummy and hen. Female continued attack until snared.
3	16 April 1976, 1300	Cackle call while holding tape recorder	A cackle heard immediately. Found 2 females 18 m in tree 1 m apart. Banded resident bird jumped from branch to branch, following unbanded female and giving attack whinny calls. Unbanded hen cackled. Unbanded female flew; banded female followed and repeated display in second and third trees. Unbanded female flew uphill and landed with flutter flight. Both birds had cackle duel from respective trees. I flushed unbanded female; she flew downhill, giving cackles, and returned to tree, where banded female cackled. Both sat quietly.
4	17 April 1976, 0700	Female dummy, cackle call	Banded female immediately flew from tree near Case 3 encounter, approached dummy rapidly with sleek, horizontal posture, giving attack whinnies and whinny screams, and dived at neck of dummy. She continued attack until snared.
5	19 April 1976, 0840	Female dummy, cackle call	Three females responded and advanced to cackle. Banded resident ♀ ₁ landed in tree 18 m from dummy and cackled. Unbanded ♀ ₂ landed in tree 5.5 m from dummy, and unbanded ♀ ₃ landed 3 m from dummy. ♀ ₁ flew to tree of ♀ ₂ , and both flew to ♀ ₃ 's tree; ♀ ₃ flew to second tree and ♀ ₁ followed while cackling. ♀ ₂ left area, ♀ ₁ returned to ♀ ₃ , and both cackled and gave hard whinnies. Birds fought 2 s, then both flew to second tree and remained quiet. One male was present and displayed to ♀ ₁ .

one mirror. A tape recorder was placed inside the mirror triangle, and the cackle call was played for 15 min while we hid nearby. If a female answered the cackle and came to the arena, we recorded the rate of advance (m/min), vocalizations/min, aggressive interactions (e.g. pecks and wing strikes per minute), and whether attacks were directed at the dummy or the mirror image.

The focus in 1976 was on determining the chronology of elicited cacklings in April and May and relating the frequency of cackling responses to the annual breeding cycle (copulation, egg-laying, and incubation). We determined the frequency of cackling by visiting 17 listening posts at 2-3-day intervals and listening for cackling responses to a 2-min recording of the taped cackle call. After tests, areas were

searched intensively with a pointer dog to verify that hens were present. Nesting chronology was determined by searching for hens with young broods in June. A chick was captured from each brood when possible, and the approximate date of hatch was determined from feather development (Zwicker and Lance 1966).

We mapped the ranges used by females and territorial males in 1976 prior to incubation. Females were located both by playing the cackle call and noting the location of answering females before they advanced and by intensive searches with pointer dogs. We also put radio transmitters on two hens to facilitate relocation. Males were located by searching from 0500 to 1000 for males that were hooting, and by tracking with dogs. On Stuart Island 10 of the 11

territorial males had leg bands in 1976. There were 9 banded hens and at least 5 unbanded females.

We evaluated breeding success in 1975 and 1976 by counting the chicks per brood in August. We wished to know if there was adequate production for a valid test of the territorial limitation hypothesis.

RESULTS

Aggressive behavior of hens.—Three females answered the cackle call during the 10 mirror-arena tests conducted on male territories in May 1975. All 3 hens advanced to the arena, and 2 attacked the female dummy (Table 1, Cases 1 and 2). In 1976 we observed 3 aggressive interactions (Table 1, Cases 3–5). On 16 April, 2 females answered the cackle. Both birds had been sitting silently near each other in adjacent trees; one female chased the other (Case 3). The next day the dominant bird returned and attacked the female dummy (Case 4). On 19 April, 3 females responded to the cackle call, advanced, and interacted. Two of the females fought in a tree for approximately 2 s (Case 5).

These attacks, plus 5 attacks on dummies that we observed on Vancouver Island, can be placed in two categories: hesitant attacks (Cases 1, 2) and more direct, hard attacks (Case 4). During a typical hesitant attack, females advanced slowly, often stopped and gave cackling calls and a Nee-uk call (Fig. 1), fanned their black retrices, dragged the wing adjacent to the dummy, and displayed a patch of white feathers on the shoulder region of the wing (cf. Lumsden 1970). As these females neared the dummy, their calls changed from cackling calls with inflections to attack whinnies or whinny screams (Fig. 1). Attacks were frequently brief, involving a jump upward and a downward blow with wing and bill, followed by a jump away. During a hard attack, the challenging hen advanced quickly on the ground, giving rapid attack whinnies. These hens approached the dummy with body horizontal and neck extended. The tail was closed and the white shoulder spot was not displayed. In 3 observations of this type, hens attacked immediately with a hard, diving attack. Blows came rapidly, and in one case the female stood on the dummy and pulled hard on the neck region. Attacks commonly continued until our taped call ended.

All of the 10 fights observed were elicited by the cackling call. The whinny call (graphed by Stirling and Bendell 1970) that we played in

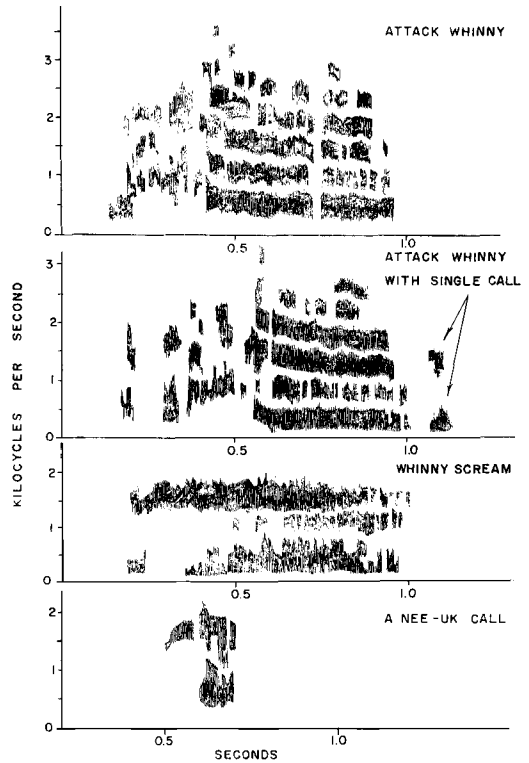


Fig. 1. Spectrograms of aggressive calls. The second attack whinny ends with a single Ca (the Ca of the cackling calls). The Nee-uk call was often heard before the attack whinny. We heard many combinations of whinny and cackling calls.

mirror-arena tests for males often attracted females, but none attacked. Hemus (1972) heard the whinny call on several occasions when hens were together and interacting nonaggressively. Thus, the presence of an intruding hen (our dummy) giving the whinny call was not sufficient cause for an attack response.

The frequency of cackling was high throughout April 1976 (Fig. 2), but the peak of activity of 4 banded hens was in the last 2 weeks of April (Table 2). Three of the 4 hens showed their peak response approximately 42–49 days before their eggs hatched.

The interval between copulation and hatching has been estimated at about 39 days (Zwicker 1977). Thus, female response to cackling peaked about a week before breeding. Three banded hens would not respond to the taped calls at about the time they bred. Hannon (1978) reported that cackling ceased in her study area before all copulations had occurred, and call-

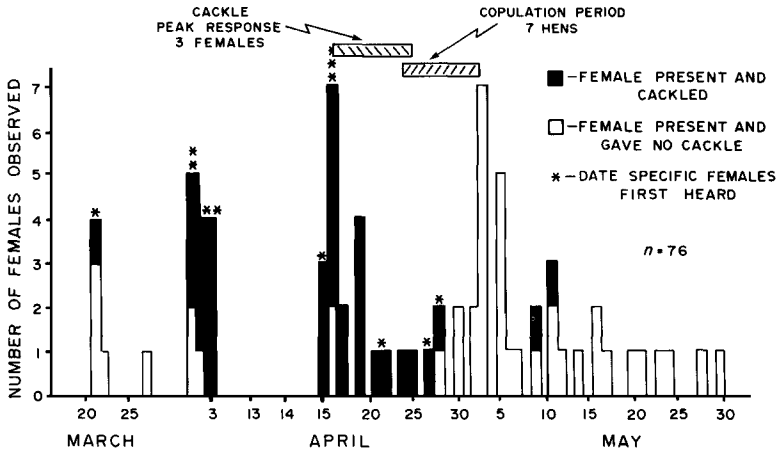


Fig. 2. Frequency of observations of banded and unbanded females that cackled on Stuart Island, 21 March to 30 May 1976. (Excludes 14 radio fixes where females were not seen.)

ing coincided with the period when the birds were localized on their prelaying ranges (Hannon et al. 1982).

In March and April on Stuart Island, 63% of the hens located, especially those that cackled, were in trees (Table 2). This percentage is conservative since we usually searched for hens on the ground using pointer dogs. Further, during March and April, more hens (63%, $n = 33$) were in trees than were territorial males (24%, $n = 34$); males, in our experience, usually sit high in trees when they hoot. Since the mean height of females in trees (13.4 ± 1.32 m, $n = 15$) was similar to that for males (12.6 ± 1.26 m, $n = 16$), females also appeared to be seeking high vantage points.

Spacing of hens prior to incubation.—We determined the location of 9 banded hens on Stuart Island 73 times prior to incubation in 1976 (Fig. 3). Eight banded hens gave cackling responses to our taped call one or more times. We also observed unbanded hens at 6 locations on 22 occasions (Fig. 3).

The number of sightings of banded hens was not related to the size of their prelaying ranges (Fig. 3). The slope of the regression of range size on number of sightings of 8 banded hens (seen 3 or more times) was not significant ($t = 0.896$, $P > 0.40$). During the 2 months of our study the females were always found in these localized ranges, as has been noted by others in Blue Grouse (Hannon 1978, Sopuck 1979) and Spruce Grouse (*Dendragapus canadensis*, Herzog and Boag 1978). Also, the sizes of these

prelaying ranges were not significantly different from that found with intense radio tracking in the vicinity of Comox Burn, British Columbia by Sopuck (1979): for yearlings, 6.7 ± 2.6 ha on Stuart Island ($n = 2$) vs. 12.9 ± 8.8 ha at Comox Burn ($n = 27$), and for adults, 5.5 ± 1.9 ha on Stuart Island ($n = 6$) vs. 4.6 ± 2.7 ha at Comox Burn ($n = 10$). However, the mean number of sightings of the unbanded hens, most of which were probably yearlings, were not adequate to determine the size of their ranges. Yearling hens usually travel more widely than adults (Lance 1970, Hannon 1978).

The frequency distributions of sightings of 13 hens considered separate birds (excluding the 2 hens with radios located 17 and 20 times; Fig. 3) did not differ from a Poisson distribution ($\chi^2 = 2.827$, $P < 0.10$). This suggests that we searched for birds in a random manner. The expected Poisson percentage for a rare event of 0 frequency (a female overlooked) was 0.032. Hence, we may not have overlooked the range of any hens.

We can also evaluate whether we found nearly all the hens by comparing the observed number of hens (15) with an expected number based on the number of males in the population. The normal sex ratio in Blue Grouse is 50:50 (Zwickel and Bendell 1967). There were 11 hooting males on Stuart Island. Researchers agree that adult hooting males can be accurately counted. The ratio of hooting males to silent yearling males is commonly 75:25 (Zwickel and Bendell 1967, Zwickel et al. 1983). For Stuart

TABLE 2. Frequency of cackling and females in trees in 1976. Sample sizes are given in parentheses.

	Cackle tests		
	Percentage that elicited female responses	Number of times females advanced	Percentage of females in trees ^a
21-31 March	7 (43)	3 (43)	67 (6)
1-14 April	14 (43)	6 (43)	70 (10)
15-30 April	18 (90)	16 (90)	53 (17)
1-14 May	2 (106)	3 (106)	35 (17)
15-31 May	—	—	44 (9)

^a Significant difference 21 March to 30 April vs. May, $t = 2.722$.

there should be 15 males ($1.00 \times 11 \div 0.75$) and, with a balanced sex ratio, 15 adult and yearling hens—the same number as we found (Fig. 3).

There was no overlap of ranges of females that cackled except one, and one of these birds was expelled. The range of the noncackling yearling, Y/R, overlapped the adult Y/G (Fig. 3); however, Y/R moved into the range of Y/G when the latter had disappeared and was probably incubating.

The ranges of hens were well scattered across the island (Fig. 3). The mean nearest-neighbor measurement for 12 hens that cackled (measured from center to center of ranges) was 472 ± 69.8 m. The index of dispersion (calculated after Clark and Evans 1954) indicates a population more uniformly distributed than chance ($R = 1.45, c = 3.157, P < 0.01$).

The mean distance between the centers of the ranges of 12 females that cackled and the center of the nearest male territory was 188 ± 37.6 m. These females were significantly clumped around the males ($R = 0.578, c = 2.906, P < 0.01$). There were 6 females adjacent to the 4 males on Tiptop Ridge. The remaining 9 hens were scattered across the island, as were the remaining 7 territorial males (Fig. 3).

Most females probably visit the territories of males to copulate (4 females showed movement uphill towards males as expected copulation date approached). Our distribution data (Fig. 3), however, suggest that females did not choose male territories for movement prior to incubation, even though they were closer to males than expected in a random distribution (cf. Lance 1970).

The vegetation types within the female ranges varied widely, with no indication of

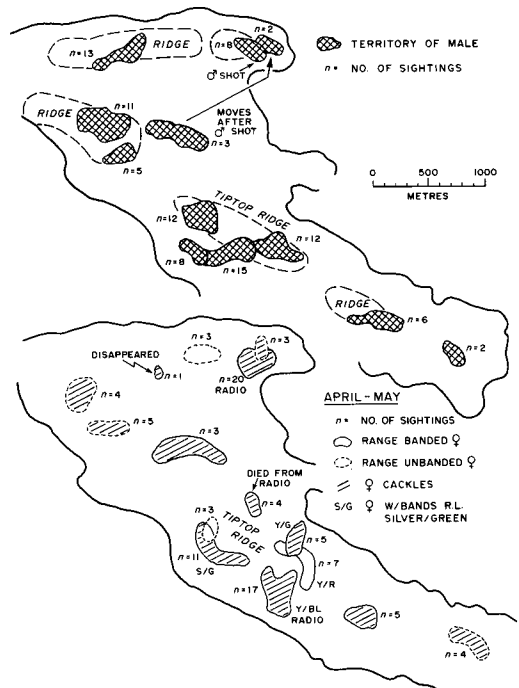


Fig. 3. Dispersion patterns of cocks (top) and hens (bottom) on Stuart Island in the preincubation period in 1976.

clear preferences within the selections available (Table 3). Seven of the 11 hens (64%) had ranges that included the arbutus-Douglas fir type (type 6), and their combined ranges included 8.2 ha (13%) of the 65 ha available. Eight of the 11 hens (73%) had some of their ranges on rock outcrops (type 14), the habitat type most heavily utilized by males. However, these females occupied only 3.1 ha (6%) of the total rock outcrops available (Table 3). Extensive areas of these two most highly utilized types were available (Fig. 4). But it is questionable that any specific habitat that we could map was required. Two adult hens did not frequent either type 6 or 14.

Habitat types 3 and 10, which were widely scattered across the islands (Fig. 4), may be marginal habitats for hens because there are few openings in the canopy. We passed through these habitats daily on our searches. Sopuck (1979) found that some yearling hens at Comox Burn settled in marginal habitats outside the recently logged areas where he usually searched; he would not have found those birds

TABLE 3. Habitat types on Stuart Island found in 11 preincubation ranges of females that cackled and in the ranges of 11 territorial males.^a

Type no.	Habitat type	Openings in forest floor	Hectares on island ^b	Frequency in ranges (females/males)	Percent of total available that was occupied	
					Fe-males	Males
3	Second-growth Douglas fir	None	117 (21)	36/36	3	1
10	Douglas fir logging mosaic	Rock outcrops (15%)	87 (16)	45/45	5	7
6	Arbutus/Douglas fir	Very open	65 (12)	64/73	13	18
14	Rock outcrop	100% open	50 (9)	73/100	6	22
16	Pasture	100% open	40 (7)	27/18	8	<1
9	Alder-sword fern	<5%	36 (7)	45/9	4	3
21	Mature Douglas fir/salal	Some openings	29 (5)	36/36	15	13
15	Dry pasture	100% open	25 (5)	9/18	6	12
20	Mixed trees, steep slopes	None	21 (4)	27/27	31	19
Remaining 12 types			86 (15)		19	15
Total			556 (101)		9	10

^a All types described are from Donaldson and Bergerud (1974) except 20 and 21; 20 is a mixture of dry- and moist-site trees on steep slopes, and 21 is similar to type 2 in Donaldson and Bergerud (1974), but with openings in shrub layer.

^b Percentage of the area given in parentheses.

without the aid of radiotelemetry. However, we searched all the island vegetation types, and birds made themselves known and came long distances in response to the cackle-call recording we played.

Territorial males on Stuart Island sought more open habitats (types 6 and 14, Table 3) and higher elevations than did females. The mean elevation of the territories of 11 males was 105 ± 12.8 m, and the elevation of 13 prelaying ranges of hens was 82 ± 10.3 m.

In August 1975 we located 10 different hens with a total of 25 chicks. Nine hens located in 1976 were accompanied by 19 chicks. This production is comparable to other Blue Grouse populations in British Columbia (Zwicker and Bendell 1967) and is sufficient to replace adult losses. The annual survival for the 10 original males provided an annual mortality rate of 30%, again normal for Blue Grouse (Zwicker and Bendell 1967).

DISCUSSION

Female grouse displayed a wide variety of calls and postures while interacting with the taped cackle call and female dummy. We interpret the cackling call as a threat and not sexual advertisement, as did Stirling and Bendell (1970). The attack and scream whinny calls and

the Nee-uk calls were more intense and expressed intention to attack.

In contrast to Bendell and Elliot (1967) and Lance (1967), we think females are aggressive in some populations prior to laying. In 1976 we observed two females fighting. In 1975, two other females attacked their mirror image or the female dummy. Further, we witnessed 5 attacks of females on dummy hens on Vancouver Island. Thus, some females engage in physical combat. This probably seldom happens in natural situations since adult females probably avoid each other early in their search for nest sites. When they finally settle and are prepared to be aggressive, a dispersion has already occurred. Yearlings commonly do not settle until adults are laying (Hannon et al. 1982) and are no longer cackling (Fig. 2).

Females displayed the same black and white colors as males for threat, but these colors were usually well concealed prior to display. In females the black rectrices are under the brown upper tail coverts, and the white shoulder feathers are on the patagium, under the wing. The presence of the elaborate displays seen in tested females suggests selection for aggressive behavior tempered with a need for crypticness.

The aggressive behavior of females ceased quite abruptly prior to copulation and egg-laying. Thus, this aggressiveness was associated

with the dispersion of ranges used in the nest searching and before females visited males; it was not associated with the ranges females used during egg-laying and incubation (Hannon 1978, Sopuck 1979).

The prelaying ranges of hens on Stuart Island appear to qualify as territories (Noble 1939). Further, both Blue Grouse and Spruce Grouse nest within their prelaying territories (Hannon 1978, Herzog and Boag 1978, Sopuck 1979). The territories of hens on Stuart showed a dispersed distribution. Our results of non-overlapping ranges of females are similar to the findings of Herzog and Boag (1978), who showed mutually exclusive prelaying territories in female Spruce Grouse. However, the territories of Blue Grouse were spatiotemporal (Schoener 1971); defense shifted when the hen moved. Such a system is characterized for vertebrates in general as having moderate defense and moderate dispersal of yearling invaders (Wilson 1975). This aggressive system suggests defense of space rather than of some other resource. The defending hens did not advertise their presence but sat high in trees from which invaders could be seen.

Did the aggressive behavior (and mutual avoidance) of females space females so that some were prevented from breeding, and hence was it a means of population regulation by the criteria of Brown (1969) and Watson and Moss (1970)? There were large interspaces between the prelaying territories on Stuart Island (Fig. 3). If each female had a maximum range of 10 ha (the largest observed), then 130 ha of the approximately 300 ha of Douglas fir habitat available would have been occupied. Thus, there appeared to be available space for other hens to nest in suitable habitat (Table 3), even considering that the ranges we documented were minimal because of lack of observations.

The prelaying territories of the females were dispersed from other hens but aggregated relative to males. Each female could reach the territory of a male for breeding without traveling through the range of other females, and she could thus avoid eliciting overt behavior from another hen that would compromise her inconspicuousness. It would also be disadvantageous for a hen to nest too near a male because she would attract his attention when away from her nest and increase her conspicuousness to predators (Wittenberger 1978). It would be to her advantage to be dispersed from other hens

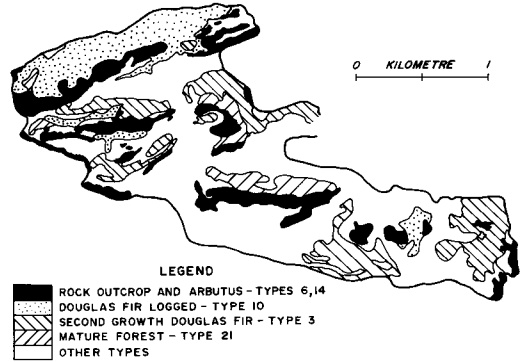


Fig. 4. Distribution of the major habitat types used by grouse.

relative to predation, so she may expel or avoid other hens while selecting her nest site within her territory. Because spontaneous cackling is seldom heard, mutual avoidance must be a major aspect of this dispersed distribution.

Ellison (1971), Herzog and Boag (1978), and Lance (1970) have shown a dispersed distribution of nests located between male territories for Blue and Spruce grouse. Nugent and Boag (1982) reported aggressive calling by Spruce Grouse, with calls similar to those reported here, and their hens also used trees as vantage points to detect intruders. They described these behaviors as spacing displays that reduce the functional and numerical response of predators.

Our population was sufficiently viable to test the self-regulation hypothesis. In 1975 there should have been at least 12 female juveniles alive in the fall. According to Zwickel (1980) these birds should live until spring, when many are expelled and become surplus. We found only 4 or 5 yearling females in the spring and saw some of these birds several times. A more parsimonious hypothesis is that the missing birds died over winter from natural causes.

The findings of this study support the view that territorial behavior functions to disperse birds, thereby reducing predation risk. Our findings are not consistent with the view that female territoriality in Blue Grouse also regulates numbers by preventing some yearling females from breeding (Zwickel 1972, 1980; Hannon 1978; Hannon and Zwickel 1979).

Zwickel's (1972, 1980) primary evidence of territoriality resulting in surplus, nonbreeding females was that after removal of resident fe-

males, replacement birds appeared and settled on the vacated territories. In both studies he did not know where the replacements came from or if they would have bred in their former location if they had stayed there. This knowledge is necessary to test the surplus-nonbreeding hypothesis (Watson and Moss 1970).

Comox Burn, B.C. was used as a control area by Zwickel (1972, 1980) to see if birds would move from Comox Burn to Tsolum Main, where vacancies were created. Sopuck (1979) found 15% (7 of 46) of the female yearlings that appeared early at Comox Burn eventually settled in extensive second-growth forests (suboptimum habitat) around the burn. Six of the 7 hens nested, but only 1 raised a brood. Zwickel did not search the second-growth forests around Tsolum Main in his removal experiment, but he searched his control area, Comox Burn, which was optimum habitat similar to the removal area, Tsolum Main.

Thus, the removal experiments did not test the Fretwell-Lucas (1969) territorial model of an ideal-dominance habitat distribution in which birds may shift from suboptimum to optimum areas to improve their fitness when competitors are removed. Such a shift was documented thoroughly in Krebs' (1971) classic territorial study of the Great Tit (*Parus major*). Nesting success appeared to be much higher at Comox Burn than in the suboptimum area. If territorial birds had been removed at Comox Burn in 1976 and 1977, the yearling birds from the suboptimum habitat might have filled the vacancies. As it was, they remained in the suboptimum habitat and *did* nest, but with reduced success.

We question another interpretation used by Hannon and Zwickel (1979) in arguing that yearling females were prevented from breeding. They arbitrarily classified birds at Comox Burn that would lay their first egg in the week of 4 June or later as "nonbreeders." By this method, they converted a normal curve of first egg-laying dates to one skewed to the left. However, hatching curves of grouse populations not subject to reneating (no nest predation) are normally distributed (Mercer 1967, Hannon 1982).

Hannon's (1978) definition of a nonbreeding hen included the criteria: (1) calculated first-egg date was on or after the last day of peak laying of brood hens, (2) largest follicle was less than 6 mm in slow phase at recrudescence,

and (3) both largest follicle diameter and oviduct weight were less than the mean for all individuals captured the same week. These criteria define a late-breeding bird, not a non-breeder. In fact, Hannon found that all yearling hens had developed mature follicles. Earlier, Zwickel and Bendell (1967) reported that nearly all the hens they found at Comox in the summer had developed brood patches.

Zwickel (1980) reported that few yearling females were seen from 1969 to 1977 at Comox Burn when hens were incubating. If there were "surplus" hens, it seems unreasonable that they would suddenly disappear at the time of incubation; it is more likely that they also were incubating. Sopuck (1979) radio-tracked 46 yearling females at Comox Burn in the same years as Hannon's (1978) study; Sopuck found that 83% of the yearling hens definitely nested, 11% probably nested, 2% died, and 4% did not nest. Sopuck also found that no females left the breeding range in late May, which was Hannon and Zwickel's (1979) explanation for the lack of sightings of "surplus females" when hens were incubating (see Zwickel 1980: Fig. 3).

The delayed breeding of yearling Blue Grouse females (Hannon et al. 1982) may actually be a tactic wherein returning yearlings benefit by evaluating habitat through the location of adults (Oring 1982). By waiting to settle and search for nest sites until after adult females are laying and no longer defending space, yearlings could search for nest sites with less visibility.

Blue Grouse females have a rich repertoire of potential vocalizations and aggressive postures that can assist them in keeping other females from their nesting area. However, the displays are seldom resorted to in natural situations and usually cease immediately before breeding and egg-laying. The tempered use of these displays suggests an overriding need to remain inconspicuous, avoiding detection by raptors and predators of nests after hens have committed themselves to nesting locations.

The view that territorial behavior of hens functions to space nests and reduce nest predation can be partially tested by using dummy nests. Clutches can be distributed near nesting hens to ascertain if nesting success is density dependent. Clutches can also be placed near the advertising location of males to test whether females remain apart from males because displaying males attract predators. Dummy fe-

males and taped calls can be used inside the prelaying range of females to see if they will shift location or if nest-site locations will be altered. Further, conspicuous female dummies should attract predator attention, resulting in reduced nesting success for nearby females.

LITERATURE CITED

- BENDELL, J. F., & P. W. ELLIOT. 1967. Behavior and the regulation of numbers in Blue Grouse. Can. Wildl. Serv. Rept. Ser. No. 4.
- BERGERUD, A. T., & H. D. HEMUS. 1975. An experimental study of the behavior of Blue Grouse (*Dendragapus obscurus*). I. Differences between the founders from three populations. Canad. J. Zool. 53: 1222-1237.
- BROWN, J. L. 1969. Territorial behavior and population regulation in birds. Wilson Bull. 81: 293-329.
- CLARK, P. J., & F. C. EVANS. 1954. Distance to nearest neighbours as a measure of spatial relationships in populations. Ecology 35: 445-451.
- DAVIES, N. B. 1978. Ecological questions about territorial behaviour. Pp. 317-350 in Behavioural ecology: an evolutionary approach (J. R. Krebs and N. B. Davies, Eds.). Oxford and London, Blackwell Scientific Publications.
- DONALDSON, J. L., & A. T. BERGERUD. 1974. Behavior and habitat selection of an insular population of Blue Grouse. Syesis 7: 115-127.
- ELLISON, J. N. 1971. Territoriality in Alaskan Spruce Grouse. Auk 88: 652-664.
- FRETWELL, S. D., & H. L. LUCAS, JR. 1969. On territorial behavior and other factors influencing habitat distribution in birds. I. Acta Biotheoretica 19: 16-36.
- HANNON, S. J. 1978. The reproductive cycle, movements and prenesting behaviour of adult and yearling females in a population of Blue Grouse. Unpublished M.S. thesis, Edmonton, Alberta, Univ. Edmonton.
- . 1982. Female aggressiveness, breeding density, and monogamy in Willow Ptarmigan. Unpublished Ph.D. dissertation, Vancouver, British Columbia, Univ. British Columbia.
- , L. G. SOPUCK, & F. C. ZWICKEL. 1982. Spring movements of female Blue Grouse: evidence for socially induced delayed breeding in yearlings. Auk 99: 687-694.
- , & F. C. ZWICKEL. 1979. Probable nonbreeders among female Blue Grouse. Condor 81: 78-82.
- HEMUS, H. D. 1972. A behavioural and demographic comparison of three Blue Grouse populations released on Moresby Island. Unpublished B.S. honours thesis, Victoria, British Columbia, Univ. Victoria.
- HERZOG, D. W., & D. A. BOAG. 1978. Dispersion and mobility in a local population of Spruce Grouse. J. Wildl. Mgmt. 42: 853-865.
- KREBS, J. R. 1971. Territory and breeding density in the Great Tit *Parus major* L. Ecology 52: 2-22.
- LACK, D. 1966. Population studies of birds. Oxford, Clarendon Press.
- . 1968. Ecological adaptations for breeding birds. London, Methuen.
- LANCE, A. N. 1967. A telemetry study of dispersion and breeding biology in Blue Grouse. Unpublished M.S. thesis, Vancouver, British Columbia, Univ. British Columbia.
- . 1970. Movements of Blue Grouse on the summer range. Condor 72: 437-444.
- LUMSDEN, H. G. 1970. The shoulder display of grouse. Living Bird 9: 65-74.
- MERCER, W. E. 1967. Ecology of an island population of Newfoundland Willow Ptarmigan. Newfoundland and Labrador Wildl. Serv. Tech. Bull. No. 2.
- MOSSOP, D. H. 1971. A relation between aggressive behavior and population dynamics in Blue Grouse. Unpublished M.S. thesis, Vancouver, British Columbia, Univ. British Columbia.
- NOBLE, G. D. 1939. The role of dominance in the social life of birds. Auk 56: 263-273.
- NUGENT, D. P., & D. A. BOAG. 1982. Communication among territorial female Spruce Grouse. Canad. J. Zool. 60: 2624-2632.
- ORING, L. W. 1982. Avian mating systems. Pp. 1-92 in Avian biology, vol. 6 (D. S. Farner, J. R. King, and K. C. Park, Eds.). New York, Academic Press.
- PATTERSON, I. J. 1981. Territorial behaviour and the limitation of population density. Pp. 53-62 in The integrated study of bird populations (H. Klomp and J. W. Woldendorp, Eds.). Amsterdam, North-Holland Publishing Company.
- SCHOENER, T. W. 1971. The theory of feeding strategies. Ann. Rev. Ecol. Syst. 2: 369-404.
- SOPUCK, L. G. 1979. Movements and breeding biology of Blue Grouse in relation to recruitment, reproductive success and migration. Unpublished M.S. thesis, Edmonton, Alberta, Univ. Alberta.
- STIRLING, I. G., & J. F. BENDELL. 1970. The reproductive behavior of Blue Grouse. Syesis 3: 161-171.
- TAYLOR, J. 1976. The advantage of spacing out. J. Theor. Biol. 59: 485-490.
- WATSON, A., & R. MOSS. 1970. Dominance, spacing behavior and aggression in relation to population limitation in vertebrates. Pp. 167-200 in Animal populations in relation to their food resources (A. Watson, Ed.). Oxford, Blackwell Scientific Publications.
- WILSON, E. O. 1975. Sociobiology: the new synthesis. Cambridge, Massachusetts, Belknap Press.
- WITTENBERGER, J. F. 1978. The evolution of mating systems in grouse. Condor 80: 126-137.

- . 1981. *Animal social behavior*. Boston, Duxbury Press.
- WYNNE-EDWARDS, V. C. 1962. *Animal dispersion in relation to social behavior*. New York, Hafner.
- ZWICKEL, F. C. 1972. Removal and repopulation of Blue Grouse in an increasing population. *J. Wildl. Mgmt.* 36: 1141-1152.
- . 1977. Local variations in the time of breeding of female Blue Grouse. *Condor* 79: 185-191.
- . 1980. Surplus yearlings and the regulation of breeding density in Blue Grouse. *Canad. J. Zool.* 58: 896-905.
- , & J. F. BENDELL. 1967. Early mortality and the regulation of numbers in Blue Grouse. *Canad. J. Zool.* 45: 817-851.
- , ———, & A. N. ASH. 1983. Population regulations in Blue Grouse. Pp. 212-235 in *Symposium on natural regulation of wildlife populations* (F. L. Bunnell, D. S. Eastman, and J. M. Peek, Eds.). Moscow, Idaho, Forest, Wildlife and Range Exp. Station, Univ. Idaho.
- , & A. N. LANCE. 1966. Determining the age of young Blue Grouse. *J. Wildl. Mgmt.* 30: 712-717.

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than half-way admission of all that is implied in the modern interpretation of instinct, or the 'blind instinct' of the non-scientific writer. If we interpret [sic] instinct as 'inherited habit,' what better explanation do we need of the ability of young birds to build a nest like that of their parents or of their species? In view of the slight evidence available as to how much a nestling bird can take cognizance of its surroundings, and make mental note of them for purposes of imitation at a remote future, does not the assumption of such extraordinary powers of imitation and memory border upon absurdity? To extend the theory, which it is perfectly legitimate to do, to other classes of animals, does the tadpole, or the embryo fish (in the case of the nest-building species) also remember the exact position, structure and materials of its maternal nest? Does the young turtle remember throughout the long years of its adolescence the precise nature of the spot from which it emerged, so as to select a similar place for its own eggs? Or does the larva of an insect remember, through its various stages of metamorphosis, the exact arrangement of the egg from which it was hatched

in relation to the eggs of its brother larvae so distinctly as to be able to deposit its own eggs in a similar situation and similar order of arrangement? Why, indeed, the idea that birds are guided by 'instinct,' taking the term as interpreted by modern science, is so repugnant to a certain class of minds, or why they will persist in denying that *any evidence in its favor exists*, is to me at least incomprehensible. In short, I agree exactly with Mr. Seebohm in his footnote appended to Mr. Dixon's essay, in which he says: 'I regard the word Instinct as the popular term for the mysterious impulses which scientific men call Hereditary Habit; and I think that it plays a great part, an overwhelmingly great part, not only in Bird-nest building, but in every other action of every animal, man included . . . If Hereditary Habit have the lion's share in the production of a birds' [sic] nest, we must allow that Memory, Imitation, and a rudimentary form of Reason also play their subordinate parts.' In these few words, it seems to me, we have the sum of the whole matter, and a rational answer to the question of how young birds build their first nest."