

- CARTAR, R. V., AND R. D. MONTGOMERIE. 1985. The influence of weather on incubation scheduling of the White-rumped Sandpiper (*Calidris fuscicollis*): a uniparental incubator in a cold environment. *Behaviour* 95:261-289.
- DAVIS, S. D., J. B. WILLIAMS, W. J. ADAMS, AND S. L. BROWN. 1984. The effect of egg temperature on attentiveness in the Belding's Savannah Sparrow. *Auk* 101:556-566.
- DIXON, W. J. [ED.]. 1981. BMDP statistical software. Univ. of California Press, Berkeley.
- DRENT, R. H. 1972. Adaptive aspects of the physiology of incubation. *Proc. XV Int. Ornithol. Congr.* (1970):255-280.
- DRENT, R. H., K. POSTUMA, AND T. JOUSTRA. 1970. The effect of egg temperature on incubation behaviour in the Herring Gull. *Behav. Suppl.* 17: 237-261.
- DRENT, R. H., J. M. TINBERGEN, AND H. BIEBACH. 1985. Incubation in the Starling, *Sturnus vulgaris*: resolution of the conflict between egg care and foraging. *Neth. J. Zool.* 35:103-123.
- FRANKS, E. C. 1967. The responses of incubating Ringed Turtle Doves (*Streptopelia risoria*) to manipulated egg temperature. *Condor* 69:268-278.
- FROST, P.G.H., AND W. R. SIEGFRIED. 1977. The cooling rate of eggs of Moorhen *Gallinula chloropus* in single and multi-egg clutches. *Ibis* 119: 77-80.
- GIESEN, K. M., AND C. E. BRAUN. 1979. Nesting behavior of female White-tailed Ptarmigan. *Condor* 81:215-217.
- HAFTORN, S. 1978. Egg-laying and regulation of egg temperature during incubation in the Goldcrest, *Regulus regulus*. *Ornis Scand.* 9:2-21.
- HAFTORN, S. 1979. Incubation and regulation of egg temperature in the Willow Tit, *Parus montanus*. *Ornis Scand.* 10:221-234.
- KLUIVER, H. N. 1950. Daily routine of the Great Tit, *Parus major*. *Ardea* 38:99-135.
- LENNERSTEDT, I. 1966. Egg temperature and incubation rhythm of the Capercaillie (*Tetrao urogallus* L.) in Swedish Lapland. *Oikos* 17:169-174.
- MAXSON, S. J. 1977. Activity patterns of female Ruffed Grouse during the breeding season. *Wilson Bull.* 89:439-455.
- MCCOURT, K. H., D. A. BOAG, AND D. M. KEPPIE. 1973. Female Spruce Grouse activities during laying and incubation. *Auk* 90:619-623.
- MORTON, M. L., AND M. E. PEREYRA. 1985. The regulation of egg temperatures and attentiveness patterns in the Dusky Flycatcher (*Empidonax oberholseri*). *Auk* 102:25-37.
- PULLIAINEN, E. 1971. Behaviour of a nesting Capercaillie (*Tetrao urogallus*) in northeastern Lapland. *Ann. Zool. Fennica* 8:456-462.
- PULLIAINEN, E. 1978. Behaviour of a Willow Grouse, *Lagopus l. lagopus*, at the nest. *Ornis Fenn.* 55: 141-148.
- RINGLEMAN, J. K., J. R. LONGCORE, AND R. B. OWEN, JR. 1982. Nest and brood attentiveness in female Black Ducks. *Condor* 84:110-116.
- SHALLENBERGER, R. J., G. C. WHITTOW, AND R. M. SMITH. 1974. Body temperature of the nesting Red-footed Booby (*Sula sula*). *Condor* 76:476-478.
- SKUTCH, A. F. 1976. Parent birds and their young. Univ. Texas Press, Austin.
- THOMPSON, S. C., AND D. G. RAVELING. 1987. Incubation behavior of Emperor Geese compared with other geese: interactions of predation, body size, and energetics. *Auk* 104:707-716.
- WHITE, F. N., AND J. L. KINNEY. 1974. Avian incubation. *Science* 189:107-115.
- ZERBA, E., AND M. L. MORTON. 1983. Dynamics of incubation in Mountain White-crowned Sparrows. *Condor* 85:1-11.

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## NONTERRITORIAL MALES IN POPULATIONS OF SPRUCE GROUSE<sup>1</sup>

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*Key words:* Spruce Grouse; *Dendragapus canadensis*; nonterritorial; males; removal experiment.

Nonterritorial males have been observed in populations of several species of grouse (e.g., Herzog and Boag

1978, Zwickel 1980, Gullion 1981, Watson 1985, Dunn and Braun 1986). In addition, removal experiments have revealed a large number of males capable of breeding that replaced territorial birds when they were shot (e.g., Watson and Jenkins 1968, Lewis and Zwickel 1980, Hannon 1983). These studies suggest that many birds may be prevented from establishing territories, and thus that territorial behavior may limit the number of breeding males.

Nonterritorial yearling males were found in popu-

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lations of Spruce Grouse (*Dendragapus canadensis*) in Alaska (Ellison 1971) and Alberta (Herzog and Boag 1978). However, because nonterritorial adults were not found in either study, Herzog and Boag (1978:863) proposed that only a small proportion of birds may be prevented from breeding, and only in preferred habitats where population density is high. Here we report that a large number of yearling males, and some adults, may be without territories in both sparse and dense populations of Spruce Grouse in Ontario. In addition, we removed a small number of territorial males to see if nonterritorial birds would replace them. Once replacements appeared, we returned the original occupants to their former territories and radio-tagged the territorial and replacement males. This allowed us to determine if the replacements came from a pool of nonterritorial birds, and to compare the behavior and movements of both.

## STUDY AREAS AND METHODS

The study was conducted near Gogama, Ontario, Canada (47°30'N, 81°40'W) in two homogeneous jack pine (*Pinus banksiana*) plantations that were 15 km apart. One (Area 1) was 75 ha in size and 12 years old (in 1981); the other (Area 2) was 200 ha and 33 years old. Their boundaries were marked by highways and large blocks of different habitat such as bog, alder (*Alnus rugosa*), and willow (*Salix* spp.) swale, deciduous forest, or mature mixed conifer forest. Vegetation on the study areas is described in more detail in Szuba and Bendell (1983; where Area 1 = GO-VB, Area 2 = GO-G).

Grouse were found on the study areas during daily search with trained pointing dogs between mid-April and August 1981 to 1985. We also found males without the aid of dogs by locating those performing "flutter flights" (Lumsden 1961) in the morning and evening during the period of peak display in late April and early May. Grouse were captured with snare poles (Zwickel and Bendell 1967), banded with unique combinations of colored leg bands, and weighed to the nearest 5 g with Pesola spring scales. Age (yearling  $\leq 15$  months of age, or adult) was determined using characteristics of primary feathers (Szuba et al. 1987).

A male was considered to be a resident if found within the boundaries of the study area  $\geq 3$  times in May when most territorial and courtship display occurred, and, for nonterritorial males (see below), at least once more between June and August. We believe these criteria excluded possible migrants present only in April or in August (see Herzog and Keppie 1980), and, considering the intensity of our searching effort, produced accurate counts of territorial males present in the spring display period. However, the number of nonterritorial males may be underestimated since mortality of males on our study areas is high in May (unpubl. data). Territorial birds localized on small areas and performed flutter flight and strutting displays (Lumsden 1961) when alone, in the presence of hens, in response to displays of neighbors, or to tape-recorded calls of hens. In contrast, some males moved widely and were never observed doing flutter flights, although they were occasionally observed strutting in the presence of hens. As they did not appear to have

areas of exclusive use that were advertised or defended in any way (see Wilson 1975:256), such residents were considered to be nonterritorial. Herzog and Boag (1978) used similar criteria to classify males.

We considered all residents to be marked when searches with dogs and display counts yielded no new unbanded birds. All resident males were banded by about 30 May in 1981 and the second week of May in subsequent years. Area 1 had a dense Spruce Grouse population (mean = 31.7 males/km<sup>2</sup>, range = 28.0–36.0 per year), and Area 2 had a sparse population (mean = 4.0/km<sup>2</sup>, range = 3.5–4.5).

Between 8 and 10 May 1985 we removed three males from Area 1 and two from Area 2 from territories that could be checked easily for replacements. The males were captured while doing flutter flights and were immediately taken to a holding area  $> 5$  km away. Each was released in its own wooden pen (60 × 60 × 90 cm) which was covered in fine mesh screen. The pens were shaded and separated by a thick layer of conifer branches. Captive males were given fresh water and jack pine branches once daily. Despite never eating more than 30% of what was supplied, after 2 to 4.5 days in captivity all had lost weight (mean = 17.4 g, range = 10–30,  $n = 5$ ).

We checked the identity of all males performing flutter flights within 400 m of removal territories each morning and evening after removal of residents. Males judged to be replacements were those performing flutter flights  $\leq 20$  m from where a territorial male was removed in Area 1, and  $\geq 50$  m in the more sparsely populated Area 2. We attempted to capture and radio-tag a replacement as soon as it was observed. Within 6 hr (three birds) or the subsequent morning (one bird) the captive male was radio-tagged and released where first captured on its former territory. Radios were attached as backpacks (Herzog 1979) that weighed 14 g. We could not capture one of the replacements, so the original territorial male was released without a radio. We used dogs to locate these two birds and identified the replacement subsequently by his unique pattern of facial and breast plumage.

We used telemetry equipment to visually locate territorial and replacement males at least once every 2 days in May, and less frequently thereafter. At each sighting we noted the type of displays performed (flutter flight or strutting), and determined the bird's location by pacing from where it was first observed along a compass bearing to staked grid lines. Sightings were plotted on maps (scale: 1 mm = 2 m), and home range or territory size was determined by using the modified minimum area method (Harvey and Barbour 1965; peripheral locations  $\leq$  half the distance between the two most extreme points were connected). Males were followed until early August when they were recaptured to remove radios.

## RESULTS

### DESCRIPTIVE STUDIES

On average, each year from 1981 to 1985, 71% of the resident males were adults in the dense (Area 1: 87/120) and sparse (Area 2: 27/40) populations (years pooled), and 29% were yearlings. During that period, 82% of the males were territorial (98/120 in Area 1,

33/40 in Area 2) and 18% were nonterritorial. A larger proportion (39%) of yearlings (13/33 in Area 1, 5/13 in Area 2) than adults (10%) (9/87 in Area 1, 2/27 in Area 2) was nonterritorial (heterogeneity  $G$  test with William's correction, Area 1:  $G = 11.84$ ,  $df = 1$ ,  $P < 0.001$ ; Area 2:  $G = 5.07$ ,  $df = 1$ ,  $P < 0.025$ ). In all the above comparisons, the proportion of males in each category did not differ between populations ( $P > 0.05$ ).

We identified 18 different nonterritorial resident males in Area 1, and seven in Area 2. Approximately half (12/25; nine in Area 1, three in Area 2) of these males obtained territories on the study areas in a later year. Of the remaining nonterritorial birds, three were found dead (predation, in Area 1) and the rest disappeared. Some may have obtained territories elsewhere (see below).

Some males did not obtain territories on the study areas until they were adults. Between 1982 and 1985 there were eight new territorial adults in Area 1, and two in Area 2. None was seen on the study areas or their periphery in previous years. On our study areas, only one male in 5 years was known to abandon its old territory and move to another in a subsequent year, and this movement was  $< 300$  m (see also Robinson 1980). As well, no resident was known to become nonterritorial after spending one season as a territorial bird (see also Herzog and Boag 1978). Thus, these 10 new territorial adults must have been immigrants, and likely were nonterritorial before they appeared on the study areas. We combined these males believed to be immigrants (eight in Area 1 and two in Area 2) with the territorial yearlings (20 in Area 1, eight in Area 2) and the nonterritorial birds that eventually obtained territories on the study areas (nine in Area 1, three in Area 2). The resulting proportion of resident males that did not obtain territories on the study areas until they were adults was 44% (17/37 in Area 1, 5/13 in Area 2).

Some males were nonterritorial for  $\geq 3$  years. For example, one resident moved widely on Area 1 for 2 years as an adult before establishing a territory. Another wandered for 3 years, then disappeared. Finally, a chick banded in 1983 on Area 1 was not seen on the study area in 1984, was found only once in 1985 (late July), and established a territory there as a 3-year-old in 1986.

#### REMOVAL EXPERIMENT

In the following results, replacement males are designated as R1, R2, etc., the numbers corresponding to those of the territorial males (T1, T2, etc.) they attempted to replace. Replacement males were observed performing flutter flights on the removal territories within 48 hr in three cases, and 56 hr in another. One territory in Area 1 remained vacant for 108 hr, whereupon we released the original resident. Judging by repeated checks on the identity of displaying males and daily searches with dogs before the experiment, the replacements were not neighbors that had expanded their territories.

All four replacements appeared to leave removal territories soon after the original territorial males were released. R3 moved  $> 1$  km within 48 hr out of Area 2 into a black spruce (*Picea mariana*) bog where he stayed. R4 (also from Area 2 but without a radio tag)

was found approximately 400 m from the removal territory 2 and also 10 days later but never thereafter. On the first 2 days after territorial males were released in Area 1, R1 was 318 m and 260 m respectively, from T1, and R2 was 112 m and 246 m from T2.

In some ways the replacements differed from territorial males (Table 1). Replacements were lighter in weight at first capture in May (no overlap between groups; all males weighed within 4 days of each other). They periodically made longer movements than territorial males in May (see maximum movement on consecutive days and maximum displacement), and their home ranges were 3.8 to 9.5 times larger. They did not differ from territorial males in mean daily movements or home-range size in June to August. Although the replacements were first captured within the territories of original residents, there was generally little overlap between home ranges once residents were released. In May, 8.1% of the home range of R2 was contained within that of T2. Overlap increased to 43% in June to August and may partly reflect the early loss of R2 (killed by a predator on 16 July). Overlap was  $< 1\%$  for R1 and T1, and for R3 and T3 in both periods. Similarly, the home ranges of T4 and R4 (no radio tags) may have been disjunct (see R4 locations above). The replacements had performed flutter flights when territorial males were removed, but only R1 was seen displaying after the original males were returned to their former territories (Table 2). This occurred on the afternoon of 7 August; the fresh remains (avian predation) of T1 were found earlier that day. In contrast, all original residents displayed after release from captivity.

#### DISCUSSION

Nonterritorial male Spruce Grouse appear to exist in a variety of habitat types and population densities. Such males were first described by McLachlin (1970) and later by Herzog and Boag (1978) in a lodgepole pine (*Pinus contorta*) forest in Alberta with a moderately dense Spruce Grouse population (7.5 to 10.5 males/km<sup>2</sup>; calculated from Herzog and Boag 1978: 863 assuming a 1:1 sex ratio). Ellison (1971) also found nonterritorial males in a sparsely populated spruce (*Picea* spp.) forest in Alaska (2.7 to 3.9 males/km<sup>2</sup>). The present study reveals nonterritorial resident males in sparse (3.5 to 4.5/km<sup>2</sup>) and dense populations (28.0 to 36.0/km<sup>2</sup>) in jack pine forests in Ontario.

In our study, an average of 18% of the resident males was nonterritorial each year in both the sparse and dense populations. The proportion may have been even higher if nonterritorial birds were secretive and more difficult to census than territorial birds (e.g., Zwickel 1980, Jamieson 1985). There is some evidence for this from our removal experiment. The replacements appeared quickly ( $\leq 56$  hr) but were not found before territorial males were removed even though we believe the study areas were searched thoroughly. They might have been present but not detected, for once the original residents were released, the replacements had large home ranges, made periodic long-distance movements, and did not display.

Zwickel (1980) suggested that there are two types of nonterritorial male Blue Grouse (*Dendragapus obscu-*

TABLE 1. Physical characteristics and movements of territorial (T) and replacement (R) male Spruce Grouse. R1 replaced T1, R2 replaced T2, and R3 replaced T3. R4 (no radio tag) was found only twice after T4 was released and is not included. There was no replacement for T5. (Sample size is in parentheses.)

	Male <sup>1</sup>							
	T1	T2	T3	T4	T5	R1	R2	R3
Age (adult or yearling)	A	A	Y	Y	A	Y	Y	Y
Body weight (g) at first capture)	515	500	510	495	490	465	485	450
Mean and maximum movements (m) on consecutive days in May <sup>2</sup>	60.1 <sup>ab</sup> (9)	85.1 <sup>ab</sup> (8)	75.3 <sup>ab</sup> (6)	19.4 <sup>c</sup> (4)	42.4 <sup>bc</sup> (9)	128.0 <sup>a</sup> (10)	96.3 <sup>ab</sup> (11)	161.7 <sup>a</sup> (6)
Maximum displacement (m) in May <sup>3</sup>	250	256	276	144	94	367	1,270	1,210
Home-range size (ha) in May	0.96 (13)	1.42 (13)	1.85 (13)	0.58 (8)	0.42 (13)	3.63 (15)	13.47 (15)	9.03 (12)
June to August	2.89 (26)	5.02 (20)	6.50 (17)	0.71 (10)	2.16 (25)	9.21 (23)	1.15 (11)	3.22 (16)

<sup>1</sup> Males T3 and T4 were from Area 2; T1, T2, and T5 were from Area 1.

<sup>2</sup> One-way ANOVA on log-transformed data ( $F = 3.47$ ,  $df = 7, 48$ ,  $P < 0.01$ ), and Duncan's multiple range test. Means sharing the same letter are not different ( $P > 0.05$ ).

<sup>3</sup> Maximum straight-line distance moved from the point of first capture in May.

rus), unrecruited or "surplus" birds, and nonterritorial residents or "standby" birds which may obtain territories locally in a later year. The replacement male Spruce Grouse that left Area 2 was thus a surplus bird. The nonterritorial resident males present on our study areas each year (and the replacements that became residents) may be equivalent to standby birds. Almost half of them obtained territories on the study areas in a subsequent year. Similarly, Herzog and Boag (1978) noted that some nonterritorial males present in spring moved in autumn into vacancies created by the death of residents. Lewis and Zwickel (1982) reported that 46% of the nonterritorial yearling male Blue Grouse identified on their study area eventually obtained territories there.

In our study most (62%) nonterritorial males were yearlings, as were the three replacements captured in the removal experiment. Yearlings generally weigh less than adults (Szuba and Bendell 1984) and the replace-

ments weighed less than the territorial birds. We estimate that 44% of the males that obtained territories on the study areas did not do so until they became adults. Thus, as has been proposed for Blue Grouse (see review in Jamieson 1985), immaturity resulting in an inability to compete successfully for territories seems a likely explanation for the lack of territorial behavior in yearling males. In our study, yearling replacements quickly occupied the vacancies we created and performed displays typical of territorial males, but once the original occupants were returned to their territories, the replacements ceased displaying, moved away, and behaved as nonterritorial birds. However, the following suggests that nonterritoriality cannot be fully explained by immaturity. Many yearlings are clearly capable of holding territories; 61% of those on our study areas were territorial (see also Ellison 1971). Moreover, as in Blue Grouse, *Dendragapus obscurus* (Lewis and Zwickel 1980, 1982), we identified some nonterritorial adults, a few of which were without territories for at least 3 years.

Boag et al. (1979) proposed that the territorial behavior of adult Spruce Grouse in spring may force excess yearlings to disperse, thereby regulating the local density of breeding birds. If all dispersing birds establish territories elsewhere, territorial behavior might space them out but not prevent any from breeding (Bergerud et al. 1985). Our data, with that of Ellison (1971) and Herzog and Boag (1978), suggest that a substantial number of males may be at least temporarily prevented from holding territories in sparse and dense populations and in a range of habitats. If birds without territories do not breed, territorial behavior may have an important role in limiting the number of breeding males.

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TABLE 2. Frequency of display by territorial (T) and replacement (R) male Spruce Grouse after territorial males were released. ( $n$  = total number of observations between May and August.)

Male	$n$	Display type <sup>a</sup>		
		Flutter flight	Strutting and tail-flick	
			To hen	To observer
T1	39	2	4	1
T2	33	1	3	0
T3	30	1	0	1
T4	18	0	2	1
T5	38	0	1	1
R1	38	1	0	0
R2	26	0	0	0
R3	28	0	0	0

<sup>a</sup> Displays are described in Lumsden (1961).

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## LITERATURE CITED

- BERGERUD, A. T., D. H. MOSSOP, AND S. MYRBERGET. 1985. A critique of the mechanics of annual changes in ptarmigan numbers. *Can. J. Zool.* 63: 2240-2248.
- BOAG, D. A., K. H. MCCOURT, P. W. HERZOG, AND J. H. ALWAY. 1979. Population regulation in Spruce Grouse: a working hypothesis. *Can. J. Zool.* 57: 2275-2284.
- DUNN, P. O., AND C. E. BRAUN. 1986. Late summer-spring movements of juvenile Sage Grouse. *Wilson Bull.* 98:83-92.
- ELLISON, L. N. 1971. Territoriality in Alaskan Spruce Grouse. *Auk* 88:652-664.
- GULLION, G. 1981. Non-drumming males in a Ruffed Grouse population. *Wilson Bull.* 93:372-382.
- HANNON, S. J. 1983. Spacing and breeding density of Willow Ptarmigan in response to an experimental alteration of sex ratio. *J. Anim. Ecol.* 52: 807-820.
- HARVEY, M. J., AND R. W. BARBOUR. 1965. Home range of *Microtus ochrogaster* as determined by a modified minimum area method. *J. Mammal.* 46: 398-402.
- HERZOG, P. W. 1979. Effects of radio-marking on behavior, movements, and survival of Spruce Grouse. *J. Wildl. Manage.* 43:316-323.
- HERZOG, P. W., AND D. A. BOAG. 1978. Dispersion and mobility in a local population of Spruce Grouse. *J. Wildl. Manage.* 42:853-865.
- HERZOG, P. W., AND D. M. KEPPIE. 1980. Migration in a local population of Spruce Grouse. *Condor* 82:366-372.
- JAMIESON, I. G. 1985. Behavior of yearling male Blue Grouse and its relation to delayed breeding. *Wilson Bull.* 97:71-77.
- LEWIS, R. A., AND F. C. ZWICKEL. 1980. Removal and replacement of male Blue Grouse on persistent and transient territorial sites. *Can. J. Zool.* 58:1417-1423.
- LEWIS, R. A., AND F. C. ZWICKEL. 1982. Survival and delayed breeding in male Blue Grouse. *Can. J. Zool.* 60:1881-1884.
- LUMSDEN, H. G. 1961. Displays of the Spruce Grouse. *Can. Field-Nat.* 75:152-160.
- McLACHLIN, R. A. 1970. The spring and summer dispersion of male Franklin's Grouse in lodgepole pine forest in southwestern Alberta. M.Sc. thesis, Univ. of Alberta, Edmonton.
- ROBINSON, W. L. 1980. Fool hen: the Spruce Grouse on the Yellow Dog Plains. Univ. of Wisconsin Press, Madison.
- SZUBA, K. J., AND J. F. BENDELL. 1983. Population densities and habitats of Spruce Grouse in Ontario, p. 199-213. *In* R. W. Wein, R. R. Riewe, and I. R. Methven [eds.], Resources and dynamics of the boreal zone. Assoc. of Canadian Univ. for Northern Studies, Ottawa, Canada.
- SZUBA, K. J., AND J. F. BENDELL. 1984. Weights of Ontario Spruce Grouse by sex, age, and breeding success. *Can. J. Zool.* 62:788-792.
- SZUBA, K. J., J. F. BENDELL, AND B. J. NAYLOR. 1987. Age determination of Hudsonian Spruce Grouse using primary feathers. *Wildl. Soc. Bull.* 15:539-543.
- WATSON, A. 1985. Social class, socially-induced loss, recruitment and breeding of Red Grouse. *Oecologia (Berl.)* 67:493-498.
- WATSON, A., AND D. JENKINS. 1968. Experiments on population control by territorial behavior in Red Grouse. *J. Anim. Ecol.* 37:595-614.
- WILSON, E. O. 1975. *Sociobiology*. Harvard Univ. Press, Cambridge, MA.
- ZWICKEL, F. C. 1980. Surplus yearlings and the regulation of density in Blue Grouse. *Can. J. Zool.* 58:896-905.
- ZWICKEL, F. C., AND J. F. BENDELL. 1967. A snare for capturing Blue Grouse. *J. Wildl. Manage.* 31: 202-204.