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PRODUCTIVITY OF THE SPRUCE GROUSE AT THE SOUTHEASTERN LIMIT OF ITS RANGE

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Abstract.—We measured productivity of the Spruce Grouse (*Dendragapus canadensis canadensis*) in patchy black spruce (*Picea mariana*) habitat along the southeastern limit of its range in mid-coastal Maine. We captured grouse and attached necklace-mounted radio transmitters to hens prior to nesting. Of 19 females monitored, only 26% raised chicks to the late brood-rearing period. Predation was high on hens (37%) and five were killed before hatching eggs. Six (55%) entire broods were lost and only 30% of chicks survived to late summer. Production (No. of chicks/female), an index of productivity, was <1 and lower in Maine and Minnesota study areas in black spruce than areas dominated by jack pine (*Pinus banksiana*) or a mixture of jack pine and spruce with dense undergrowth. Where Spruce Grouse breed in patchy black spruce communities, immigration from neighboring populations or inter-patch movement by local individuals may be required to maintain viable populations.

PRODUCTIVIDAD DE *DENDRAGAPUS CANADENSIS* EN EL LÍMITE SURESTE DE SU DISTRIBUCIÓN

Sinopsis.—Determinamos la productividad de *Dendragapus canadensis* en un parcho de picea (*Picea mariana*) a lo largo del límite suroeste de su distribución en Maine. Capturamos hembras y polluelos y le colocamos radiotransmisores en forma de mochilas. De 19 hembras monitoreadas, tan sólo el 26% criaron a los pichones hasta el periodo más tarde de cuidado de los polluelos. La depredación fue alta para las hembras (37%) y cinco de éstas fueron eliminadas durante el periodo de incubación. Se perdieron seis (55%) camadas completas y tan sólo el 30% de los polluelos sobrevivieron hasta tarde en el verano. La producción (No. de polluelos/hembra), un índice de productividad, fue <1, y menor en hábitat de picea en Maine y Minnesota que en áreas dominadas por pino (*Pinus banksiana*) o una mezcla de pino y picea con buen desarrollo del sotobosque. Para mantener poblaciones viables de *Dendragapus canadensis* en parchos de picea, probablemente es necesario inmigración de poblaciones aledañas o movimiento entre parchos de individuos de esta especie.

The Spruce Grouse (*Dendragapus canadensis*) is distributed throughout the boreal forests of North America, and two subspecies, *canadensis* in the east and *franklinii* in the west, are currently recognized (American Ornithologists' Union 1983). The southeastern limit of the Spruce Grouse's range coincides with the transition between coniferous and deciduous forests, where suitable habitat for breeding occurs only as patches of co-

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niferous forest vegetation (Boag and Schroeder 1992). In this region, productivity has been studied in relatively large areas (0.75–6.0 km^2) dominated by jack pine, lowland black spruce, or a mixture of both conifers (Haas 1974, Keppie 1987, Robinson 1980, Szuba 1989). In areas with relatively small (<50 ha) patches of habitat, productivity data are available only from jack pine habitats in Michigan (Robinson 1980).

In the Adirondack region of New York and along the mid-coast of Maine, Spruce Grouse breed in scattered patches of lowland black spruce. Populations in these patches resemble metapopulations (Fritz 1979, Whitcomb et al. 1994), defined as a set of local populations connected by dispersing individuals (Hanski and Gilpin 1991). Research (Bouta and Chambers 1990, Fritz 1979, Whitcomb et al. 1994) has focused on patch occupancy, dispersal, and persistence in relation to individual patches where inter-patch distance and patch size are important. The number of breeding Spruce Grouse in patches in these areas is small (<14) (Fritz 1979, Whitcomb et al. 1994); therefore, productivity may be important for dispersal, recolonization of patches, and persistence of populations in individual patches.

Our objectives were to document the productivity of Spruce Grouse in a fragmented landscape near the edge of their range and compare our results to other populations of *D. c. canadensis* in the context of habitat type, quality, and patch size. Because of differences between the two subspecies in nest concealment and success, Redmond et al. (1982) recommended caution when interpreting data from a particular region to a transcontinental species. Using a similar approach, we restricted our comparisons only to populations of *canadensis* inhabiting the eastern half of North America.

STUDY AREA AND METHODS

We conducted this study on Mount Desert Island (MDI) (44°20′N, 68°19′W). Located along the mid-coast of Maine, MDI is the largest (281 km^2) island in the Gulf of Maine, and at its nearest point is <600 m from the mainland. Faunal (Crowell 1986) and floral (C. Greene, pers. commun.) diversity on MDI are similar to the mainland because of MDI's large area and close proximity to the mainland. Thus, we expected Spruce Grouse ecology on MDI to be similar to that of the adjacent mainland.

Vegetation on MDI is classified as spruce-fir (*Picea* spp.-*Abies* spp.)-northern hardwood (*Fagus grandifolia, Betula* spp., *Acer* spp.) forest (Westveld et al. 1956). A fire in 1947 changed 30% of the island to deciduous vegetation, currently dominated by birch (*Betula* spp.) and aspen (*Populus* spp.).

On MDI Spruce Grouse breed in discrete black spruce-tamarack (*Larix laricina*) communities (Whitcomb et al. 1994) usually on poorly drained soils. In addition to the dominant tree species, these communities include withe-rod (*Viburnuum cassinoides*), sheep laurel (*Kalmia angustifolia*), labrador-tea (*Ledum groenlandicum*), and black huckleberry (*Gaylussacia baccata*) (Calhoun et al. 1994). Lowbush blueberry (*Vaccinium angusti-*

folium) can be found in overstory gaps associated with small rock outcroppings. Ground cover includes leaf litter, peat mosses (*Sphagnum* spp.), and lichens.

We located female Spruce Grouse before nesting by systematically searching all patches >4 ha (n = 18) on MDI during April and May 1992–1993. We used 4 ha as a minimum size for habitat based on home range sizes reported for Spruce Grouse in Maine (Allan 1985). We located grouse with tape-recorded aggressive calls (Boag and McKinnon 1982) of female Spruce Grouse (*canadensis*). We captured individuals with noose poles (Zwickel and Bendell 1967) and equipped each female with a necklace-mounted radio transmitter weighing 11 g (Advanced Telemetry Systems, Inc., Isanti, MN). We located females with broods using a hand-held H-antenna to approach quietly and count chicks. Incubating females and those with broods were located 1–5 ($\bar{x}$ = 3.5) times a week from 1 June until 28 August (beginning of late-brood rearing period on MDI) to monitor nest success and to determine chick mortality.

We did not separate yearlings and adults for analysis because evidence of differences of productivity between age classes is inconclusive (Keppie 1982). To facilitate comparisons with other studies, we used four variables to measure productivity of radio-marked females: nest attempts (produced ≥1 egg), nest success (hatched ≥1 egg), brood size on 28 August (±8 wk old), and production (No. of chicks surviving until the beginning of the late brood-rearing period per number of females known alive at the start of nesting), considered the best index of overall productivity (Boag and Schroeder 1992). We also calculated chick survival as the number of chicks surviving to 28 August divided by the total number of chicks produced.

Herzog (1979) detected no effect of radio attachment on Franklin's Spruce Grouse (*D. c. franklinii*) and a review of other studies by Hines and Zwickel (1985) indicated little support for adverse effects of radios on galliforms. Furthermore, we used a relatively light (approximately 2.7% of female Spruce Grouse mass) transmitter and saw no evidence that our observations and brood counts disrupted activity or adversely affected birds. Although the Spruce Grouse is highly tolerant of humans (Bouta and Chambers 1990), we were cautious when approaching hens and broods to minimize disturbance.

We rank transformed annual production data obtained on MDI and four other study sites to normalize ($\alpha > 0.1$) the error distribution to test for differences in means and conducted an analysis of variance to determine a main effect interaction ($\alpha = 0.05$). We then used a Bonferroni pairwise multiple comparison test to determine differences ($\alpha < 0.05$) between studies (Milliken and Johnson 1984:33). We used t-tests to compare rainfall and temperature by month during our study to that of the previous 10 yr. All tests were performed with Systat (Systat 1992).

RESULTS AND DISCUSSION

Nest attempts and success of female Spruce Grouse on MDI were similar to other populations except in Minnesota (Haas 1974) where nest

TABLE 1. Productivity of spruce grouse (*D. c. canadensis*) on Mount Desert Island, Maine and at other sites in eastern North America.

Location year	% Nest attempts (*n*)	% Hatch success (*n*)	Brood size[a] ± SD	Young[b]/ female[c] ± SD
MDI, ME				
1992	91 (11)	80 (10)	2.3	0.6
1993	80 (5)	75 (4)	2.0	0.5
1992–1993	88 (16)	79 (14)	2.2 ± 0.21	0.64 ± 0.09
New Brunswick[d]	94 (168)	81 (37)	3.3	2.0
Ontario[e]	92 (219)	71 (219)		1.6
Minnesota[f]	100 (10)	40 (10)	2.6	0.6
Michigan[g]	88 (9)	77 (9)	3.7	1.7

[a] Late-brood rearing period, 28 August in this study.
[b] Surviving to the beginning of the late-brood rearing period.
[c] # of females known alive at the start of nesting.
[d] Keppie 1982.
[e] Szuba 1989.
[f] Haas 1974.
[g] Robinson 1980.

success was relatively low (Table 1). Predation of hens on MDI was high during spring especially prior to eggs hatching. Of the 19 females monitored, predators killed seven (38%): three at the start of nesting, two during incubation, and two with broods. Initial brood size (1–3 d posthatch) ranged from 1–6 ($\bar{x}$ = 3.4) and most chick mortality (41%) was within the first 9 d posthatch. By late summer, brood size on MDI and in Ontario (Szuba 1989) was <3.0 (Table 1). This trend can be attributed to a relatively high loss of entire broods on MDI (55%) and in Ontario (30%) (Szuba 1989) compared to either 3% in Michigan (Robinson 1980) or 5% in New Brunswick (Keppie 1982).

Based on kill-site characteristics, we identified a Red-tailed Hawk (*Buteo jamaicensis*), an unknown raptor species, and a red fox (*Vulpes vulpes*) as predators. No renesting was detected and only five (26%) females raised broods to 28 August. Predators are thought to be the primary cause of mortality of Spruce Grouse (Boag and Schroeder 1992); our results corroborate this conclusion. In a patchy environment prey may be more exposed and conspicuous (Taylor 1976, Wiens 1976).

Compared to other studies across eastern North America, only on MDI and in Minnesota (Haas 1974) was production <1 chick/female (Table 1). These areas were both lower in production (P = 0.02 and 0.03, respectively; n = 17, df = 12) than in New Brunswick (Keppie 1982). In New Brunswick, Spruce Grouse inhabited a mixture of black spruce and jack pine, whereas on MDI and in Minnesota (Haas 1974) Spruce Grouse were primarily in black spruce habitat (Table 1). Populations in Ontario (Szuba 1989) and Michigan (Robinson 1980) were located in jack pine habitat and production, although not statistically different from MDI or Minnesota, was similar (P = 1.0) to New Brunswick. Similar production

for MDI and Minnesota suggests that size of habitat patches may be less important than type and quality of habitat in as much as nesting hens were in small patches (6 of 8 were <26 ha) on MDI compared to Minnesota (≥50 ha). Productivity of Spruce Grouse in young (8–10 m) jack pine stands (Bendell and Szuba 1993) and in jack pine and spruce-pine (Redmond et al. 1982) has been directly related to diverse and abundant shrub and herbaceous cover. In contrast, Spruce Grouse breeding on MDI use black spruce habitat that is part of a maturing (>50-yr old) conifer forest characterized by sparse ground cover. We hypothesize that breeding habitat quality may be lower throughout the Spruce Grouse's range when only patches of lowland black spruce with sparse shrub or herbaceous cover are available.

Low temperature also has been correlated with lower productivity of Spruce Grouse (Robinson 1980, Smyth and Boag 1984) but no differences in mean temperature or rainfall respectively, in May ($t = 0.14$, $P = 0.9$, df = 10; $t = 1.7$, $P = 0.1$, df = 10) or June ($t = 0.8$, $P = 0.1$, df = 10; $t = 0.49$, $P = 0.6$, df = 10) were detected during our study, compared to the previous 10 yr.

Fritz (1979) modeled and explained extinction of Spruce Grouse in metapopulations in New York in terms of demographic fluctuations, but rates of chick survival were modeled from other populations and were assumed to be 0.3–0.4 in the spring following dispersal. Survival rate of Spruce Grouse chicks on MDI was 0.3 on 28 August, before fall dispersal. Although immigration, which may compensate for poor local production (Szuba 1989), or high dispersal among patches (Fritz 1985, Keppie 1987) may be important in regulating populations, periodic low productivity, as observed in MDI, may greatly influence persistence of birds in patches and the viability of local Spruce Grouse metapopulations throughout this species' range.

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