

vived to spring and 5 of 28 (18%) that survived the entire breeding period did not nest; this occurred in a steadily declining population. A substantial proportion of those that survived the entire breeding season did not nest in the first 2 yr of Hines's study (4/9), but only 1 of 19 in the last 2 yr. Thus, numbers of nonbreeders may be small or nonexistent in some years but present in others. We submit that short-term studies, such as that of Bergerud and Butler (1985), are not adequate to test general hypotheses about the presence or absence of nonbreeders as related to population regulation. Their data indicate there may have been no nonbreeding hens on Stuart Island in the years of their study (though even this is debatable), but do not confirm this for other populations or for their population in other years.

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LITERATURE CITED

- BERGERUD, A. T., & H. E. BUTLER. 1985. Aggressive and spacing behavior of female Blue Grouse. *Auk* 102: 313-322.
- HANNON, S. J., & F. C. ZWICKEL. 1979. Probable nonbreeders among female Blue Grouse. *Condor* 81: 78-82.
- , 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.
- HINES, J. E. 1986. Recruitment of young in a declining population of Blue Grouse. Unpublished Ph.D. dissertation, Edmonton, Alberta, Univ. Alberta.
- LACK, D. 1966. Population studies of birds. Oxford, Clarendon Press.
- 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 Unpublished M.S. thesis, Edmonton, Alberta, Univ.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.
- ZWICKEL, F. C. 1972. Removal and repopulation of Blue Grouse in an increasing population. *J. Wildl. Mgmt.* 36: 1141-1152.
- . 1980. Surplus yearlings and the regulation of breeding density in Blue Grouse. *Can. J. Zool.* 58: 896-905.
- , J. F. BENDELL, & A. N. ASH. 1983. Population regulation in Blue Grouse. Pp. 212-225 in Symposium on natural regulation of wildlife populations (F. L. Bunnell, D. S. Eastman, and J. M. Peek, Eds.). Moscow, Idaho, Forest, Wildl. and Range Exp. Sta., Univ. Idaho.

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Response to S. J. Hannon and F. C. Zwickel

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Two major hypotheses have been constructed to explain changes between years in the spring size of grouse populations. The territorial self-regulation hypothesis posits that numbers are limited by density-dependent territorial self-regulation and excluded (surplus) birds die quickly (Watson and Moss 1970, 1972; Watson 1985). The breeding-success hypothesis suggests that numbers of yearlings and adults change between breeding seasons in response to annual variations in breeding success (Bergerud 1970, Myrberget 1972, Bergerud et al. 1985). In the self-regulation hypothesis, mortality between the autumn and the measurement of territorial densities the next spring is density dependent and compensatory (Watson and Moss 1979); in the breeding-success model, overwinter natural mortality is density independent and additive to hunting mortality (Bergerud et al.

1985). Zwickel (1972, 1980) and Hannon and Zwickel (1979) have tested a modified version of the self-regulation model for Blue Grouse (*Dendragapus obscurus*) for nearly 15 years, primarily by means of removal experiments. They have accepted the hypothesis that spacing behavior results in large numbers of nonbreeding hens and have rejected the breeding-success hypothesis (Hannon and Zwickel 1979, Zwickel et al. 1983).

We tested the territorial model on Stuart Island, Washington, for Blue Grouse in 1975 and 1976 (Bergerud and Butler 1985) and on Moresby Island, British Columbia, for 7 years (Bergerud in press a). Our study areas were insular habitats where we could census the entire population. These populations were appropriate for testing the territorial model because adult mortality rates and breeding-success statistics were similar to those populations studied by Zwickel and Hannon and to other mainland populations. We rejected the territorial hypothesis (Bergerud and Butler 1985, Bergerud in press a).

Zwickel and Hannon studied open populations

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living in optimum habitats. We believe they could not determine the boundaries of the population, whether hens nested in marginal habitats, or whether unsuccessful females remained on the nesting range. We argued that the yearling females that moved into the vacancies created did so to improve nesting success (Bergerud 1985), but that these females generally nested elsewhere in less optimum habitat in the absence of the removal experiments. Sopuck (1979) documented that yearling hens nested in suboptimum habitat in Zwickel and Hannon's study area.

Hannon and Zwickel (1979) used oviduct mass and follicle data from yearling hens in the prelaying period to argue that many yearling hens did not nest. They arbitrarily classified females whose reproductive status in their autopsied collections indicated they would lay their first egg in the week beginning 4 June or later as "nonbreeders." The selection of the 4 June date to segregate the birds they collected into "breeders" and "nonbreeders" was based on a hatching curve of free-ranging hens ($n = 96$); but the hens they used to examine reproductive status ($n = 85$) were collected during the territorial and nesting season (Zwickel 1980) and included new hens moving in to replace hens already collected. Thus, their autopsied birds are biased toward late-nesting females that were prepared to change nesting locations.

A more conservative approach would have been to classify as nonbreeders those birds that would have laid their first egg after all the yearlings in the field had started laying. By this criteria, there would have been *no* nonbreeders. Alternatively, if they had chosen the week starting 11 June as the cut-off date, the number of nonbreeders (about 11%) would have been similar to that found by Sopuck (1979) in yearlings in the same study area. Instead, they used 4 June, one week past the peak period for start of egg laying in yearlings, and reported a nonbreeding percentage of 45%, a figure not reported before for any of the nine grouse species in North America (Bergerud in press b: table 1).

Hannon and Zwickel (1987) argued that they used additional criteria (other than that of date of the first egg) to identify nonbreeders. Their additional criteria are not independent (see Hannon 1978), and all the indices alone or in combination provide essentially the same proportion of birds they classify as nonbreeders, 37–39 of 85 birds (Hannon 1978). All birds whose reproductive development was slower than yearling females in the first half (and peak) of a normal curve of development were called nonbreeders. We believe they were the tail end of a normal distribution and were the "late breeders."

The most quoted example in Tetraonidae of the self-regulation hypothesis resulting in nonbreeding birds are the studies of Red Grouse (*Lagopus l. scoticus*; Watson and Moss 1970, 1972, 1979). In fact, these

studies are considered the best example of territorial limitation in the avian literature (Brown 1975, Davies 1978, Wittenberger 1981). However, these workers recently constructed a linear mathematical model in which the size of cyclic spring breeding numbers is based on prior breeding success (Watson et al. 1984, Moss and Watson 1985). They concluded that "Changes in spring numbers can be predicted from the observed production each year" (Watson et al. 1984: 639). This is a *de facto* rejection of their territorial-spacing model and compensatory mortality of nonbreeders because breeding success is determined before spacing. Unfortunately, these authors, who apparently now accept the breeding-success hypothesis, fail to acknowledge that it was proposed independently for cyclic *Lagopus* populations by Bergerud (1970) and Myrberget (1972). In the case of Red Grouse and ptarmigan populations, the mechanics of annual changes in numbers have now been clarified (Watson et al. 1984, Bergerud et al. 1985, Hudson 1986; but see Watson and Moss 1987).

The recent work of Hines (1986) on Blue Grouse also supports the breeding-success hypothesis. In Zwickel's newest study area, Hines documented a linear correlation between chick production (breeding success) and subsequent spring breeding numbers ($r = 0.97$ for females, $r = 0.92$ for males, $n = 4$ yr). Additionally, Hines (1986) radio-tracked 293 juvenile Blue Grouse throughout 4 winters. These juveniles died from predation at rates of 67–76% ($CV = 6\%$). These deaths were highest when the birds were shifting between summer and winter ranges and were not correlated with fall or spring numbers as required by the self-regulation model. Hines (1986) found that 5 of 28 surviving yearlings may not have nested; these hens, however, held space on the breeding ranges and continued to live. The hens were not a doomed surplus, a key component of the self-regulation model (Bergerud et al. 1985: fig. 1). Nor were these 5 females prevented from nesting by social expulsion, another criterion of self-regulation (Watson and Moss 1970). Note that because these hens did not rear chicks, their lack of progeny contributed to the mechanics of changes in numbers between seasons by lowering breeding success. As in Red Grouse, the data on Blue Grouse support the view that breeding success rather than compensatory mortality of nonbreeders is the key demographic parameter in the annual change in spring numbers.

The territorial self-regulation model was exciting 15 years ago, but has now outlived its heuristic value. One reason the hypothesis has lingered is that researchers have invested many years trying to prove a faulty model by investigating inappropriate populations living in optimum habitats where ingress and egress confounded results. In contrast, our approach was to disprove the hypothesis by investigations in more uniform habitats using insular populations.

LITERATURE CITED

- BERGERUD, A. T. 1970. Population dynamics of the Willow Ptarmigan *Lagopus lagopus alleni* L. 1955-1965. *Oikos* 21: 299-325.
- . 1985. The additive effect of hunting mortality on the natural mortality rates of grouse. Pp. 345-366 in *Game harvest management* (S. L. Beasom and S. F. Roberson, Eds.). Kingsville, Texas, Caesar Kleberg Wildl. Res. Inst., Texas A&I Univ.
- . In press a. Demography and behavior of insular Blue Grouse. In *Adaptive strategies and population ecology of northern grouse* (A. T. Bergerud and M. W. Gratson, Eds.). Minneapolis, Univ. Minnesota Press.
- . In press b. Population ecology of North American grouse. In *Adaptive strategies and population ecology of northern grouse* (A. T. Bergerud and M. W. Gratson, Eds.). Minneapolis, Univ. Minnesota Press.
- , & H. E. Butler. 1985. Aggressive and spacing behavior of female Blue Grouse. *Auk* 102: 313-322.
- , D. H. MOSSOP, & S. MYRBERGET. 1985. A critique of the mechanics of annual changes in ptarmigan numbers. *Can. J. Zool.* 63: 2240-2248.
- BROWN, J. L. 1975. *The evolution of behavior*. New York, W. W. Norton and Co.
- DAVIES, N. B. 1978. Ecological questions about territorial behaviour. Pp. 317-350 in *Behavioural ecology* (J. R. Krebs and N. B. Davies, Eds.). London, Blackwell Scientific Publ.
- HANNON, S. J. 1978. The reproductive cycle, movements and pre-nesting behaviour of adult and yearling females in a population of Blue Grouse. M.S. thesis, Edmonton, Univ. Alberta.
- , & F. C. ZWICKEL. 1979. Probable non-breeders among female Blue Grouse. *Condor* 81: 78-82.
- , & ———. 1987. Spacing behavior and population regulation in female Blue Grouse. *Auk* 104: 344-345.
- HINES, J. E. 1986. Recruitment of young in a declining population of Blue Grouse. Ph.D. dissertation, Edmonton, Univ. Alberta.
- HUDSON, P. 1986. *Red Grouse*. Bournemouth, U.K., Game Conservancy Trust, Bourne Press Ltd.
- MOSS, R., & A. WATSON. 1985. Adaptive value of spacing behaviour in population cycles of Red Grouse and other animals. Pp. 275-294 in *Behavioural ecology* (R. M. Sibly and R. H. Smith, Eds.). Oxford, Blackwell.
- MYRBERGET, S. 1972. Fluctuations in north Norwegian populations of Willow Grouse. *Proc. 15th Intern. Ornithol. Congr.*: 107-120.
- SOPUCK, L. G. 1979. Movements and breeding biology of Blue Grouse in relation to recruitment, reproductive success and migrations. M.S. thesis, Edmonton, Univ. Alberta.
- WATSON, A. 1985. Social class, socially induced loss, recruitment and breeding of Red Grouse. *Oecologia* 67: 493-498.
- , & R. MOSS. 1970. Dominance, spacing behaviour and aggression in relation to population limitations in vertebrates. Pp. 167-220 in *Animal populations in relation to their food resources* (A. Watson, Ed.). Oxford, Blackwell.
- , & ———. 1972. A current model of population dynamics in Red Grouse. *Proc. 15th Intern. Ornithol. Congr.*: 134-149.
- , & ———. 1979. Population cycles in the Tetraonidae. *Ornis Fennica* 56: 87-109.
- , & ———. 1987. The mechanics of annual changes in ptarmigan numbers: a reply to Bergerud, Mossop, and Myrberget. *Can. J. Zool.* in press.
- , ———, P. ROTHERY, & P. PARR. 1984. Demographic causes and predictive models of population fluctuations in Red Grouse. *J. Anim. Ecol.* 53: 639-662.
- WITTENBERGER, J. 1981. *Animal social behaviour*. Boston, Duxbury Press.
- ZWICKEL, F. C. 1972. Removal and repopulation of Blue Grouse in an increasing population. *J. Wildl. Mgmt.* 36: 1141-1152.
- . 1980. Surplus yearlings and the regulation of breeding density in Blue Grouse. *Can. J. Zool.* 58: 896-905.
- , J. F. BENDELL, & A. N. ASH. 1983. Population regulation in Blue Grouse. Pp. 212-225 in *Natural regulation of wildlife populations* (F. L. Bunnell, D. S. Eastman, and J. M. Peek, Eds.). Moscow, Idaho, Forest Wildl. and Range Experiment Sta., Univ. Idaho.

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