

COMMENTARIES

Spacing Behavior and Population Regulation in Female Blue Grouse

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David Lack's (1966) views on the role of territoriality in population regulation of birds have engendered much controversy. Does spring territoriality serve to space individuals remaining after regulation has occurred over winter, as Lack insisted, or does it set an upper limit to breeding density by the exclusion of some individuals from breeding? Bergerud and Butler (1985) have added to the controversy with data from a 2-yr study of Blue Grouse (*Dendragapus obscurus*) on Stuart Island, Washington, that they claim support Lack's view. We suggest that their population may not be a good model for other populations of Blue Grouse and examine their major criticisms of our earlier work (Zwickel 1972, 1980; Hannon and Zwickel 1979).

The population of Blue Grouse on Stuart Island probably is not typical of other populations on the west coast. It was introduced recently onto a small island (556 ha). The density was low (5 females/km²) compared with those reported in a summary of 32 yr of work on two populations on nearby Vancouver Island (approx. 500 km long, 100 km wide), British Columbia (Zwickel et al. 1983). The population on Stuart Island appears to have stabilized at a low density, and may be in suboptimal habitat.

The exact size of the Stuart Island population was unknown because 6 of 15 reported females were unbanded. A principal census technique for females used by Bergerud and Butler was response to playbacks of the "cackle," a female call. Nonbreeders easily could have been missed because they are not likely to respond to this call (Hannon et al. 1982). In addition, the large interspaces found between home ranges of hens could be due to low sample sizes.

Bergerud and Butler took issue with interpretations of past removal studies on Vancouver Island (Zwickel 1972, 1980). Here, Blue Grouse were removed from a 625-ha area in 1970 and from 1974 to 1976, and were replaced by large numbers of yearling birds. Zwickel suggested that the replacements represented "surplus" birds, presumed nonbreeders. Bergerud and Butler criticized this interpretation because the specific origin of replacements and their potential fates if residents had not been removed were not known. They suggested that these birds were likely to breed elsewhere. They stated (p. 320), "Zwickel did not search the second-growth forests around Tsolum Main in his removal experiment, but he searched his control area, . . ." In fact, virtually

all the young second-growth forest (less than 20 yr postlogging) in an area up to 1 km wide around the removal plot was searched in all years from 1971 to 1977, and there were no significant differences in the proportions of yearling females in removal years as compared with nonremoval years or with the population on the control area. We believe the large number of replacements probably was not drawn from birds that normally would have settled in the surrounding area. One cannot rule out, of course, that some yearlings might have nested in marginal areas (mature and mid- to late-successional forest) beyond the area of search, but the large numbers identified during the removal (2 times those found on the control) and the low breeding densities normally found in such forest make it unlikely that all would have done so.

Bergerud and Butler (1985) also questioned our techniques in an analysis of the ovaries and oviducts of yearlings removed in 1974-1976 (Hannon and Zwickel 1979). They said we arbitrarily classified birds that might have developed oviducts sufficiently to have laid their first egg on or after 4 June as "nonbreeders." The use of 4 June was not arbitrary, but identified yearlings that would have begun laying after peak laying of yearlings with broods. In addition, not all hens predicted to lay after 4 June were classed as nonbreeders because some yearlings (13%) do lay after this date. We required two additional criteria to identify probable nonbreeders (Hannon and Zwickel 1979). Bergerud and Butler (1985: 320) stated that ". . . Hannon found that all yearling hens had developed mature follicles." This statement is untrue. One of the criteria used to identify potential nonbreeders was that the largest ovarian follicle was less than 6 mm in diameter, i.e. not mature.

Sopuck's (1979) 2-yr radio-tracking study (1976-1977) was used by Bergerud and Butler to support a contention that all females breed. In fact, Sopuck found that 6 of 46 (13%) females did not nest. Although the proportion of nonbreeders found by Sopuck was low, both he and Zwickel (1980) noted that production of young was relatively poor in 1975 and 1976 and that the number of nonbreeders may fluctuate with the success of the previous breeding season. Sopuck also realized that he may have underestimated the number of nonbreeding hens if "unsettled" females were more difficult to capture than those that are settled (all his birds were caught in spring).

Recently, Hines (1986) radio-marked juvenile females in autumn. Seventeen of 40 (43%) that sur-

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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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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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