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Population Ecology of North American Grouse

A. T. Bergerud

15.1 Introduction

The first synthesis of the demography of North American grouse was thirty years ago when J. J. Hickey (1955) reviewed the then current literature. His review emphasized census methodology, the age and sex structure of populations, and the question of fluctuations and cycles in the numbers of grouse. Johnsgard (1973) also reviewed the current literature, but emphasized life-history characteristics of species. In the past ten years, wildlife biologists have been actively counting grouse, determining the sex and age composition of the living and the dead, calculating mortality rates, and searching for nests. Radiotelemetry has allowed biologists at last to find nests, to evaluate the use of space, and to investigate and document the factors that cause death. Unfortunately, many of these data on grouse are unpublished — in government reports or in doctoral and master's theses. I used these sources because not to have done so would have excluded many important findings and prohibited a current synthesis. This review chapter of the population ecology of North American grouse is my interpretation of the literature and does not, therefore, necessarily represent the views of the authors of this book nor those from whose works I have collected the statistics.

The annual change in the number of grouse can be considered to begin when yearlings and adults arrive on the breeding range in year 1. The first potential influence that could reduce the intrinsic rate-of-increase (r_m) is the percentage of hens that nest. Next, there is variability in the size of clutches and in hatching success. After hatching, some chicks die. Further, some adult birds die during the summer. Indexes to production in year 1 include the mean size of broods in autumn, and the ratio of juveniles per adult in the harvest. These indexes of
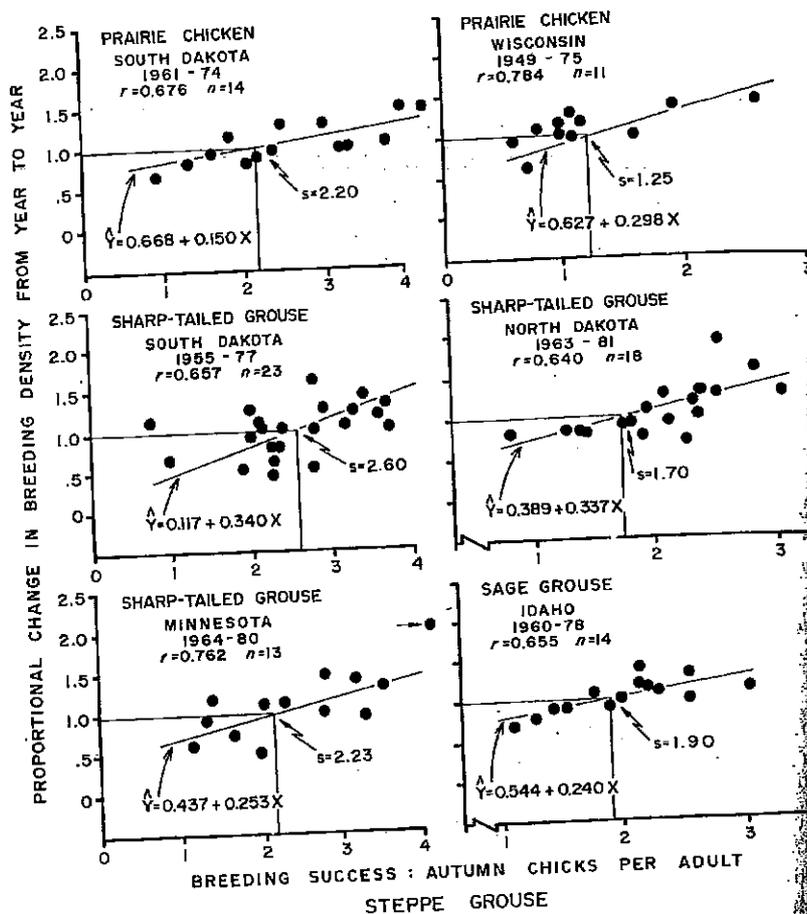
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Fig. 15.25. The proportional change in density between adjacent years is correlated with breeding success the previous year in six populations of steppe grouse; *s* equals the mean number of juveniles per adults in the autumn required to balance average overwinter losses of juveniles and adults and maintain mean population size. (Data from Hillman & Jackson 1973, Kobriger 1975, 1981, Berg 1977, Linde et al. 1978, Autenrieth 1981; some years unavailable or excluded for various objective reasons.)

nation of breeding success by assessing age ratios of harvested birds. Changes in breeding numbers are correlated with prior production in prairie chickens in Kansas (data from Horak 1971), Wisconsin, and South Dakota (Fig. 15.25). Annual changes in the density of sharp-tailed grouse males on leks are correlated with production in Montana (Brown 1966b, 1967, 1968b), Saskatchewan, Minnesota, South Dakota, and North Dakota (Fig. 15.25). Similarly, the abundance

and young and a high mortality rate of adults. The first generalization is that there is a south-north continuum for these parameters; loss of nests is greatest in the south, where there is more predation of nests. Adult mortality is probably higher in the north, where there are more effective raptors; however, there are few studies of adult mortality in the south to verify this. The southern distribution of grouse is probably limited by nest predation, and the northern distribution limited by protective cover to avoid predators.

A second generalization is that grouse die primarily from predation. There is no substantial evidence that grouse of North America, other than young chicks, starve or succumb to disease in normal populations. The vulnerability of grouse to predation changes seasonally. They are most susceptible when they must compromise their inconspicuousness to advertise and to nest and rear chicks. It should be expected that the mortality rates of males and females will be different, because they differ in their investment in offspring.

A third principle is that individuals of each species are preadapted to a specific predator-escape cover complex, i.e., their species-specific habitat. Willow ptarmigan are found in the tall-shrub zones of the tundra. Gyrfalcons also occupy this zone and ptarmigan depend on willow shrubs for cover to escape this raptor (Chap. 10). Each habitat has its own array of coevolved predators and vegetation with unique morphological characteristics used by grouse to escape these predators. Birds of each grouse species, indeed of each *population*, will be subject to a unique mortality rate that is extrinsically determined by resident predators and cover.

Annual mortality rates are more constant than breeding success rates. But mortality can be expected to vary if predator abundance changes, or if the searching pattern of predators varies with changing, alternate-prey abundance. Mortality rates may vary among years if the inconspicuousness of the grouse is altered. Grouse behavior will add another dimension—density-intolerant birds have a suite of behaviors that improves their fitness in some intraspecific competitive situations, but at the same time may increase their vulnerability to predation.

If mortality rates change among years, they must alter breeding numbers. But mortality rates are only about half as variable as changes in breeding success. Mortality is induced by predator populations in which individual grouse have evolved their own adaptations to maximize fitness. This coevolution lends stability to the mortality rates of grouse. Breeding success, in contrast to mortality rates, varies more in response to the extrinsic environment, outside biological adaptation, and without lag effects or buffers.

I can find little evidence of density-dependence in the mortality rates of adult grouse. A relatively constant proportion of the population dies between breeding seasons. There were exceptions—the death of prairie chicken hens in summer increased with numbers as did the mortality of advertising, male ruffed grouse. A major predator like the goshawk generally hunts ruffed grouse, regardless of

population size, but the goshawk may change its range in response to encounter rates.

It is the breeding-success side of the population equation that most influences changes in breeding numbers of grouse. Nearly all hens nest; clutch size varies among species and populations, but it shows little variation between years that is correlated with population change. Nesting success varies markedly in relation to: (1) changes in nesting cover, (2) predator pressure, (3) age structure (experience of the hen), and (4) female behavior. Nesting success of grouse is the most variable parameter in the dynamics of their populations, and through its influence on breeding success, contributes more to changes in population size between years that any other parameter.

The survival of chicks also has a fairly large coefficient of variation (Table 15.6). As in other bird species, very young grouse are the weakest link in the life-history of a cohort; chicks die from many causes before they can thermoregulate. Apparently no populations do not lose at least 25% of the chicks that hatch (Fig. 15.1). The major variables that likely alter chick survival are spring temperature, insect abundance, intrinsic viability, predation, concealing cover, and maternal condition. Also, the parental solicitousness may change between cohorts in cyclic species and affect chick survival.

We can recognize at least five extrinsic patterns and one intrinsic pattern to breeding success. (1) Chick survival can be influenced by the viability of young at hatch, which in turn is affected by maternal nutrition or parasitism mediated through weather and food in the prelaying period. Red grouse are an example (Fig. 15.40). (2) Breeding success can be influenced by nesting cover, which is influenced by rainfall. Sharp-tailed grouse in South Dakota are an example. (3) Breeding success can vary with stages of plant succession, as for blue grouse on Vancouver Island. When birds first colonize a newly logged area, nesting success and breeding survival are low (Zwickel & Bendell 1967). When after a period of years the forest grows too dense and homogeneous relative to the food for chicks, recruitment declines. (4) Breeding success can vary in relation to cycles in mouse populations and cover and predators switching to nesting grouse. The willow ptarmigan in Norway is an excellent example. (5) Breeding success can vary with June temperatures that affect insect abundance and the need to thermoregulate; the ruffed grouse at Watch Lake (Chap. 3) is an example. (6) The one intrinsic pattern is that breeding success can vary with density-dependent selection between genotypes. Rock ptarmigan in Scotland may be an example. These annual changes in productivity are the driving forces of population changes (Fig. 15.41).

The density of grouse, in turn, is a function of the species-specific habitat (space) prorated to the total number of birds alive (Fig. 15.41). It is an effect of last year's population demography; however, the density of birds is the arena in which density-tolerant and density-intolerant morphs compete for forthcoming

sponse to a shortage of time, as explained in the random-walk theory of An-drewartha and Birch (1954). To study these populations is to never secure an an-swer to the question of the ultimate check of population growth. But there are a few insights. The ultimate limit of natural, *noncyclic* populations coexisting with undisturbed predators is density-dependent nesting success. If the environment is benign and natural populations continue to increase, the first requisite in short supply is adequate space so that hens can nest at sufficient distances from each other such that predation is reduced and sufficient progeny are hatched to equal natural, adult losses. Potts (1980) and Angelstam (1983) have reached a similar conclusion—that nesting success is the density-dependent damping mechanism in Hungarian partridge and black grouse. The inverse relationship between popula-tion growth and density in grouse comes down, in the end, to nesting success as it is influenced by space, cover, and predators. In those cases where there are in-sufficient predators in the environment to cause negative, density-dependent nest-ing success—the *cyclic* populations—density-dependent selection between geno-types at high densities can result in chicks of insufficient viability to maintain the population, and again population growth is limited.

15.10 Summary

The number of breeding grouse in a population constantly changes between years. Documentation of the mechanics of this change is the primary aim of this chapter. Parameters that could influence annual changes in the number of grouse are: percentage of hens that nest, variations in clutch size and nesting success, survival of chicks in summer, survival of juveniles in winter, and variations in annual mortality rates of adults. Nearly all hens attempt to nest. Clutch size is relatively constant between years and is also insufficient to account for the large, annual changes in the number of grouse. There are, however, large differences in clutch size between populations of the same species. The characteristic clutch size of each population is hypothesized to have arisen from selection with respect to lifetime fitness as influenced by the characteristic longevity of individuals in specific populations. Clutch size may have been further modified in some popula-tions from that predicted by the expected longevity of an individual female be-cause of directional selection from nest predators against females that lay large clutches. Nesting success of grouse is generally low; as a group only about 58% of the nests hatch. Predation accounts for an average of 79% of nest failures. Mortality of chicks is also high; on average 44% of chicks die before fall. But chick mortality is not correlated with clutch size and occurs regardless of the pres-ence or absence of predators. Abundant insect food appears to be a necessary precondition for high survival of chicks. Mortality rates of juveniles and adults show large differences among populations, ranging from 18% to 81%. The differ-ences can be attributed to the unique, predator-cover complex in which each

population lives. Birds in some populations are quite secure from predato... populations that show this low mortality mode ($< 45\%$ annual $q.$), sel... favors females that lay small clutches. In noncyclic populations with a prepo... ance of males, mortality of females is high during the nesting period. The g... proportion of males in cyclic ptarmigan populations is possibly explained ... increased mortality of female chicks during population declines. The mo... the 10-year cycle proposed by Bergerud (1970a) is further refined by the hy... sis that the switching mechanism between density-tolerant and density-into... phenotypes and population increases and declines is mediated by female c... of aggressive males with large territories when the density of birds is high... by choice of docile males that control high-quality nesting cover when po... tions are low and birds are spaced far apart. The major conclusion of this ch... is that variations in breeding success drive population changes between y... overwinter mortality is relatively constant. The ultimate damping mechani... the growth of noncyclic populations is postulated to be density-dependent... predation; that to the growth of cyclic populations, density-dependent chang... mate choice between genotypes that provide chicks with differing intrinsic... bilities.

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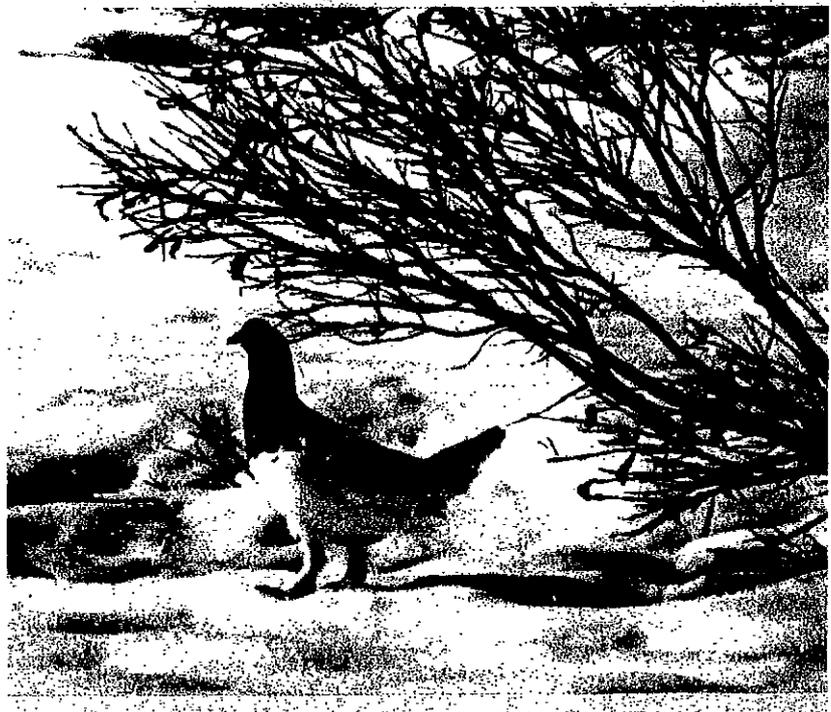
Arthur T. Bergerud
and Michael W. Gratson, Editors