INTRODUCTORY POPULATION DYNAMICS

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Abstract: Changes in the number of bobwhites (*Colinus virginianus*) from year to year depend on loss (egress and death) and gain (ingress and production) between years. An important but usually overlooked sources of loss is death from old age and accidents, which may take from 20 to 40% of a population annually. Bobwhite population dynamics differ between northern and southern latitudes: northern populations are poor survivors and good producers, whereas southern populations are poor producers and good survivors. Self-adjustment mechanisms (density dependence) within populations cushion the effects of weather catastrophes and harvest. Winter and summer weather explains most of the variation in year-to-year trends of quail populations. Bobwhite populations at bust levels require 2-3 years of favorable weather to reach boom levels.

Introduction

The number of quail on an area at any time, say the start of hunting season, depends on loss and gain in the past year. Loss includes death and movement out of the area (egress). Gain includes production and movement into the area (ingress). When loss exceeds gain, populations decline, and when gain exceeds loss, populations increase. In this paper, I discuss how loss and gain interact and lead to the populations dynamics observed on farms and ranches. I also discuss density dependence and weather catastrophes, factors that influence rates of loss and gain.

Loss

Egress

Individual bobwhites and other quails may move considerable distances away from the area where they hatched. Movements of more than 20 miles (32 km) are documented through banding and radiotelemetry studies (Snyder 1978, DeMaso et al. 1997). Kiel (1976) reported a banded bobwhite moved 65 miles (104 km) from point of banding to point of recovery. However, at least 87% of banded bobwhites moved 5 miles (8 km) or less in Kiel's study.

An important but seldom mentioned source of loss is death from senescence (old age) and accidents. These types of losses place limits on expectations of population behavior in response to changes in harvest management or predator control.

Death from senescence and accidents is difficult to measure in the field, because quail that die are quickly scavenged or they quickly disintegrate. Errington and Hamerstrom (1936) estimated senescence and accidents take about 6% of a population every 3 months. This estimate extrapolates to an annual mortality rate of 22.2% in the absence of all other forms of mortality. Stoddard (1931:89) reported a bobwhite living for 7 years in captivity. Under some assumptions, we can infer an annual mortality rate of 44% from Stoddard's observation. Japanese quail (*Coturnix coturnix*) held in captivity died at annual rates of 43% (males) to 48% (females) in the absence of predators and hunters and in the presence of ample food supplies and disease and parasite prevention (Woodard et al. 1973). In summary, bobwhites would die at annual rates of about 20-40% in perfect environments. Such high rates of death from senescence typify native animals with high metabolic rates (Gould 1980).

Wild bobwhites in southern latitudes (e.g., Texas) typically die at annual rates of about 70%, whereas those in northern latitudes (e.g., Wisconsin) typically die at annual rates of about 80% (Guthery 1997). Thus, predators, pathogens, weather catastrophes, and hunters, among other factors, roughly double or triple the mortality rate expected from senescence and accidents.

It must be noted that the "typical" rates of annual mortality are subject to considerable variation from year to year. The typical rates represent averages and in any year, the actual rate almost certainly will be higher or lower than the typical rate, given latitude. Bobwhite populations are likely to go extinct if the annual mortality rate exceeds about 82%. Production, which is limited by bobwhite physiology and time, cannot neutralize the effects of mortality with annual rates exceeding about 82%.

Biologists and hunters express considerable interest in the percentage of mortality attributable to different factors such as birds, mammals, and hunters. For example, "hawks were responsible for 50% of total mortality." These percentages are of no value in understanding population dynamics--more directly, these percentages are meaningless. If, say, hawks are responsible for 50% of total mortality, this could result in declining populations, stable populations, or increasing populations. The key issue in understanding dynamics is the total mortality rate, not the percentage of mortality attributable to various sources. If you receive promotional materials asking you to contribute to predator control campaigns, and if you see phrases like "varmints were responsible for 80% of mortality," you can rest assured that the solicitor is ignorant of quail dynamics, desirous of your money, or (most likely) both.

Gain

Ingress

In that quail move out of areas, they must also move into areas. Accordingly, ingress affects the behavior of populations on areas. There is limited evidence that bobwhites have a tendency to disperse uniformly in suitable habitat at the beginning of breeding season (Ellis et al. 1969). This tendency, to the extent that it exists, would foster ingress-egress dynamics that would stabilize populations among areas, providing bobwhites have the cover necessary to move among areas. Modern, fragmented landscapes may prevent dispersal to and from areas. Such fragmentation eliminates and important population process.

Production

Annual production usually is measured at the start of September or October. Variables used to gauge production include the percentage of young in the population, the percentage increase in the population from spring to fall, and the age ratio in juveniles/adult. Juveniles are birds hatched in the immediate past breeding season and adults are breeders. Juveniles, even if hatched early, cannot produce in the same summer they hatch (Kulenkamp and Coleman 1968). It makes no difference which of these gauges is applied, because any one is derivable from any other. That is, knowing the percent juveniles, we could calculate the percentage spring-fall gain and the age ratio. I will use the age ratio in further discussion.

Just as annual mortality varies with latitude, so does production. Bobwhites in northern latitudes, being poorer survivors, must be better producers (Fig. 1). Bobwhites in southern latitudes, being poorer producers (Fig. 1), must be better survivors. The age ratio (R) and annual survival (S) in stable populations (those that show no trend through time) are related (Guthery 1997) as

$$R = 1/S -$$

and

$$S = 1/(1 + R).$$

Suppose, for example, the age ratio is 3 juveniles/adult. Then the annual survival rate is

$$S = 1/(1 + 3) = 0.25.$$

Based on the mortality rates given above, which translate to 20% survival for northern populations and 30% survival for southern populations, the stabilizing age ratios are 4 juveniles/adult (north) and 2.3 juveniles/adult (south).

Several factors influence production in any year (Guthery and Kuvlesky 1998):

The proportion of hens that participates in reproduction. A high percentage usually participates, but heat loads associated with drought may reduce the percentage.

The number of nesting attempts per hen. Hens typically make 2-4 attempts if nests are loss.

The probability of nest success on any attempt. Success rates of 30-35% (loss rates of 65-70%) are perfectly normal. Renesting counteracts the high loss rate.

The average number of eggs in a nest (usually 12-14 on the first nest of the season).

The survival rate of breeders

The survival rate of chicks.

The number of days in the breeding season (80-150, depending on the weather).

·The number of days committed to laying and incubation on a nesting effort. A successful nest requires a time commitment of 47-55 days (Rosene 1969:71).

·The rate at which hens in a population initiate first nesting attempts.

Production in quail populations is a complex process, because it involves so many variables.

The confirmation of multiple-brooding in bobwhites (Sermons and Speake 1987) changed the biological perspective on quail production. Multiple-brooding occurs when 1 hen is responsible for the laying and hatching of 2 or more nests (up to 4). While this behavior is interesting, it does not add much to total production in comparison with single-brooding (Guthery and Kuvlesky 1998).

Density Dependence

Density dependence occurs when the number of animals in a population influences the survival and production (or both) of individuals in a population. Density dependence is a self-regulating mechanism for populations. If survival is density dependent, then populations with higher density (more individuals per unit area) suffer higher mortality than populations with lower density (Roseberry and Klimstra 1984). If production is density dependent, then populations at lower density experience higher production than populations at higher density (Errington 1945).

Density independent factors act on populations independent of the density of individuals in a population. Weather catastrophes, in particular, act largely in a density-independent manner.

The astute reader might have surmised by now that density dependence acts differently on northern- and southern-latitude populations of quail. This, indeed, seems to be the case. Winter weather catastrophes, which act more or less independent of density, reduce fall-spring survival in bobwhites (Leopold 1937). However, rather strong density dependent production (Roseberry and Klimstra 1984) reverses the effects of winter weather catastrophes. Southern populations, like those in Texas, are vulnerable to summer catastrophes (drought and heat waves) that reduce production. Based on computer simulations, southern populations react to summer catastrophes with density dependent fall-spring survival. However, this speculation has not been submitted to field tests.

Whereas density dependent population process cannot be seen, felt, or tasted, they are crucial for the persistence of quails and other native animals. Density dependence is like a shock absorber: it cushions the effects of weather catastrophes and harvest. It is impossible to imagine how quail populations could be harvested, or how they could persist, in the absence of density dependence.

Weather Catastrophes

Within the framework of density dependent survival and reproduction, 2 types of variability influence the populations trends of quails. One type is inherent in the processes that influence survival and production. This variability is more or less random and can be illustrated by flipping a coin. Given 4 flips, we would expect 2 heads and 2 tails. However, we would have a chance for other outcomes ranging from 4 heads to 4 tails. In a like, random manner, the probability of predation, of harvest, and of accidents, among other sources of loss, varies randomly from year to year. This type of random process explains some of the year-to-year variation in quail populations. However, these random processes are rather weak, and they are easily counteracted by density dependent production and survival.

Weather catastrophes, on the other hand, powerfully influence quail dynamics. Subfreezing temperatures, high winds, and extended periods of snow cover may be devastating to northern-latitude populations (Errington and Hamerstrom 1936, Leopold 1937, Roseberry 1964). Bobwhites starve to death in 2-3 days if temperatures are freezing and they cannot eat (Robel et al. 1974). Bobwhites may die from hypothermia within a few hours under severe weather conditions (Gerstell 1939).

Just as quail are vulnerable to heat underloads, so are they vulnerable to heat overloads. Temperatures too high have several adverse effects survival and production:

·Reduce the length of the laying season and the number of nesting attempts.

·Prevent hens from entering laying condition or cause them to go out of laying condition earlier than normal.

·Cause males to stop manufacturing sperm.

·Kill embryos in eggs, chicks, and adults.

·Cause eggs to begin incubation at different times, leading to staggered as opposed to simultaneous hatching of a clutch. The attending adult usually leaves with the first few chicks that hatch, leaving the remainder to perish.

The weather factors, cold and heat, primarily govern year-to-year trends in quail abundance. Quail dynamics seem to be more an issue of physics than an issue of biology.

Population Growth

The growth multiplier in any 2 consecutive years is defined as this year's population in autumn divided by last year's population at the same time. For example, if we had 100 birds last year and we have 50 this year, the growth multiplier is 50/100 = 0.5. If the growth multiplier is <1, a population has declined between years, if it equals 1 the population is the same, and if it is >1 the population has increased.

If a population shows no trend through time, even if it varies from year to year, the average growth multiplier will be about 1.0. Declining populations will show average growth multipliers <1, whereas expanding populations will show average multipliers >1.

By virtue of the average growth multiplier in nontrending populations, the number of birds this year is a reasonable estimate of the number next year. If populations have reached a low level, an extremely optimistic expectation for the next year is a doubling of population size (growth multiplier of 2, 100% increase between years). Growth multipliers of 2 or more are rare in northern-latitude populations and extremely rare in southern-latitude populations. Sometimes in newspaper articles and magazines, one sees reference to populations multiplying themselves by five between years. This is pure fiction for large areas. The bottom lines is that when quail populations reach bust levels, it will take at least 2-3 years of good weather for them to reach boom levels.

Combined Effects of Density Dependence and Weather Catastrophes

In this section, I illustrate the effects of density dependence and weather catastrophes on quail dynamics with computer simulations (Fig. 2). I executed these simulations at a fixed demographic capacity of 1,000 bobwhites on 1 October. Demographic capacity is the density about which populations exhibit positive or negative density dependent influences.

Populations subject to strong density dependent processes and no weather catastrophes exhibit small fluctuations about demographic capacity from year to year (Fig. 2A). These fluctuations are associated with the random processes in populations dynamics described above. The simulated population in Fig. 2A averaged 1,003 birds and ranged between 907 and 1,115 birds.

Weak density dependence in the absence of weather catastrophes is associated with substantial variation in annual populations (Fig. 2B). This simulated population averaged 762 birds and ranged between 54 and 1,626 birds. Populations subject to this degree of random variation would be quite vulnerable to extinction, especially on small areas.

Populations with strong density dependence subject to winter (Fig. 2C) or summer weather catastrophes (Fig. 2D) exhibited boom-bust population behavior. Populations subject to winter catastrophes averaged 895 birds and ranged between 300 and 1,090 birds, whereas those subject to summer catastrophes averaged 893 birds and ranged between 350 and 1,100 birds. Winter catastrophes reduced fall-spring survival, whereas summer catastrophes reduced production.

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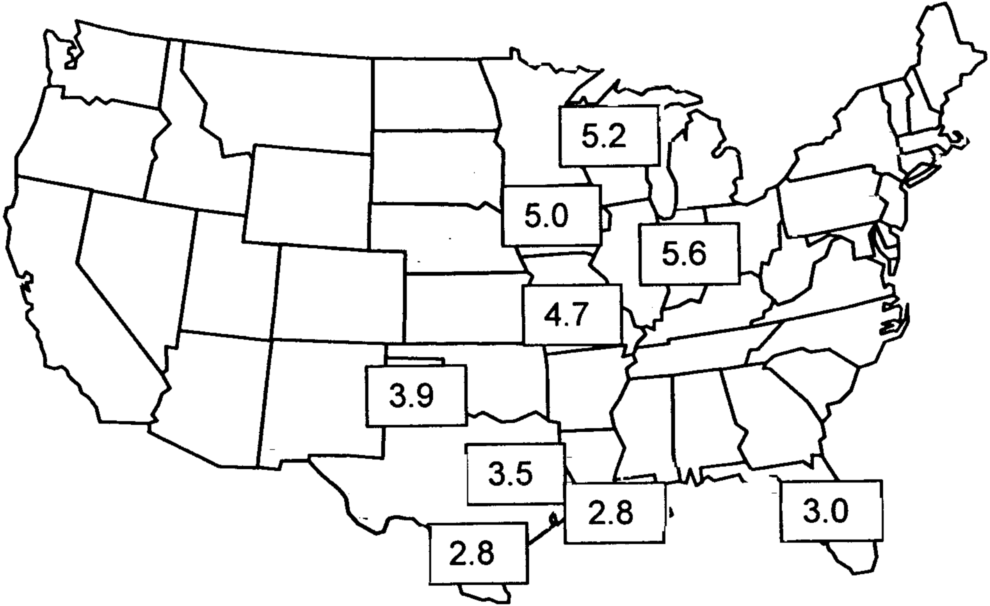

Figure 1. Mean age ratios (juveniles/adult) of bobwhites in the United States based on time series published by Jackson (1969), Rosene (1969:385-386), Lehmann (1984:133), and Roseberry and Klimstra (1984:218).

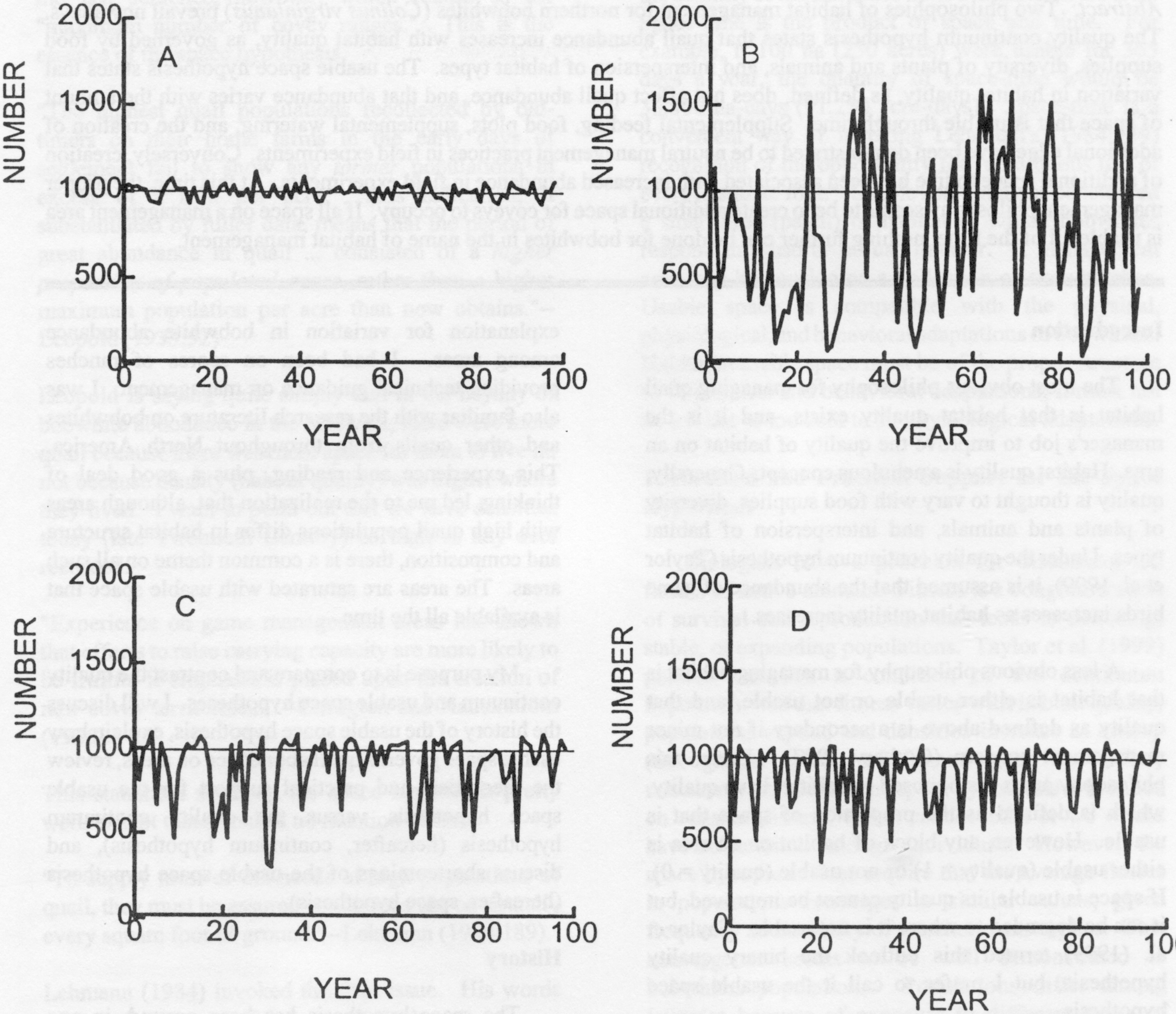

Figure 2. One-hundred-year computer projections of bobwhite populations subject to strong density dependence and no weather catastrophes (A), weak density dependence and no weather catastrophes, (B) strong density dependence and winter weather catastrophes that reduce fall-spring survival (C), and strong density dependence and summer weather catastrophes that reduce production. The horizontal line in each graph represents demographic capacity in autumn (1,000 quail).