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John L. Roseberry
Southern Illinois University

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SUSTAINED HARVEST OF BOBWHITE POPULATIONS

JOHN L. ROSEBERRY, Cooperative Wildlife Research Laboratory, Southern Illinois University, Carbondale, IL 62901

Abstract: Sport hunting is an important aspect of wildlife management, yet the principles of game harvesting seem not to be particularly well understood or accepted by many in the wildlife profession. This paper examines the two major harvest theories as they apply to the bobwhite. The sustained yield approach is considered conceptually superior to the popular annual surplus theory. Wildlife management admittedly involves practical as well as theoretical considerations; nevertheless, it is important that harvest policy be based on sound scientific principles and guided by clear objectives. To do otherwise puts both the resource and our own professional credibility at risk.

Virtually all professional wildlifers agree that the regulated harvest of certain species is biologically justifiable. In fact, maintenance of huntable populations is often the primary objective of management. Despite this emphasis, relatively little attention is given to the principles of harvesting. Upland game management in particular stresses habitat manipulation rather than population theory, the rationale being that given adequate food and cover, these prolific species can usually take care of themselves. However, as perspectives broaden and resources shrink, wildlife officials are taking a closer look at traditional harvest policies. To do this requires a valid model or conceptual image of how population exploitation works--and therein lies the problem. According to some (Scott 1954, Gross 1969, Wagner 1969, Caughley 1976, McCullough 1979), the wildlife profession has too long adhered to a convenient, but simplistic view of hunting.

This paper examines the two major approaches to game harvesting as they apply to the bobwhite (*Colinus virginianus*). The treatment is purposely general and not intended to provide harvest strategies for specific situations or localities. W. D. Klimstra, David Joyner, Alan Woolf, and Scott Yaich critically read the manuscript and offered helpful suggestions.

ANNUAL SURPLUS VS. SUSTAINED YIELD

The annual surplus concept (Leopold 1933, Errington and Hamerstrom 1935) has traditionally served as the biological justification for hunting. This argument is based on the premise that more individuals are produced each year than can survive. Therefore, it should be possible to remove this "already-doomed" surplus without affecting standing density (Figure 1). Indeed, several studies of upland game species, including the bobwhite (Baumgartner 1944, Vance and Ellis 1972), appear to show that hunting has little if any effect on abundance. However, certain aspects of the annual surplus theory are not supported by other population data (Wagner 1969). For example, the notion that numbers of breeders will be about the same each year regardless of fall population size is not correct. Bobwhite breeding densities are strongly related to previous fall abundance and are no less variable (Roseberry and Klimstra 1983). More important, hunting and nonhunting losses do not appear to be entirely compensatory. I concluded from a long-term bobwhite population study that fall-to-spring mortality rates (and thus breeding densities) were influenced by hunting (Roseberry 1979, 1981; but see also Anderson and Burnham 1981). This assertion does not imply that hunting is detrimental to quail as a species. On the contrary, given their naturally high rate of population turnover, bobwhites are quite resilient to hunting losses. The point here is not that the annual surplus concept is entirely wrong, just that it is incomplete. It says nothing about the size of the harvestable surplus, or its relation to population density or rate of harvest.

In the opinion of many, a more tenable basis for game harvesting is the sustained yield approach. This model of exploitation, pioneered in fisheries management, is based on the interactions of density, production, and rate of increase. According to this view, density-dependent birth and/or death rates (Figure 2a) result in the familiar S-shaped growth curve (Figure 2b), which shows generally how a population would increase if a few individuals were placed into a suitable but empty habitat.

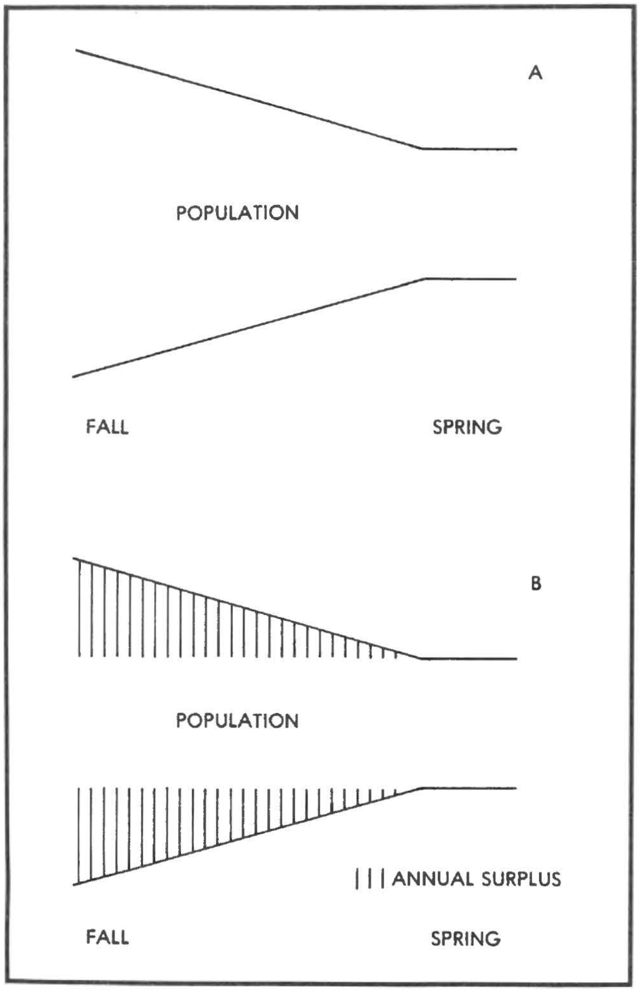

Fig. 1. Traditional view of an "annual surplus".

Growth is initially slow, but accelerates much like compound interest as the breeding stock expands. As numbers approach carrying capacity, the density-dependent birth and death rates begin to converge, thereby slowing and finally halting growth. At this point, the population is said to be at its equilibrium level (K), and though numbers may continue to fluctuate, there can be no further permanent increase unless living conditions improve. The number of new individuals added to the population each year represents net production, or the excess of births over deaths. If this annual growth increment is plotted against numbers already present, a characteristic dome-shaped curve results (Figure 2c), showing production lowest at both population extremes and highest at some intermediate density corresponding to the steep part of the growth curve.

Obviously, real populations are not as neat as diagrammatic charts. There is always a certain amount of variation, random or otherwise. And density dependence refers to general tendencies, not precise, automatic annual adjustments. Nevertheless, population behavior over time often conforms surprisingly well to these textbook generalities, whether the population is mealworms or white-tailed deer. Furthermore, a knowledge of the principles governing population behavior is

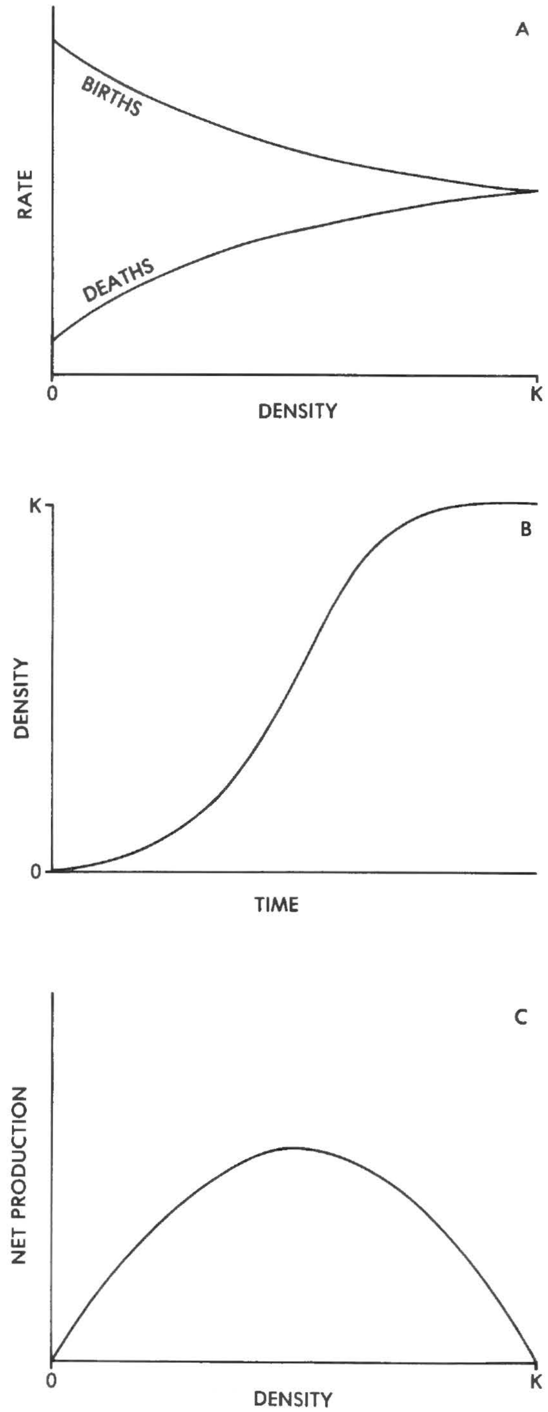

Fig. 2. Interactions of population density, production, and growth.

necessary before specific performance can be interpreted. Be that as it may, some may still be wondering what all this has to do with harvesting game.

For one thing, it would seem that a population at carrying capacity would have little if any harvestable surplus. At K, births and deaths are necessarily balanced and the average rate of increase is zero. Excess annual production is characteristic only of populations that are below their maximum density; in other words, those which would normally be increasing. This is the basis for sustained yield harvesting. By maintaining breeding densities at a more productive level below K, we can in effect induce the population to produce a harvestable surplus year after year (what would otherwise be its annual growth increment). The amount that can be taken annually from a population without causing further decline is called the sustained yield (SY) and corresponds to the net production at that level. Thus, populations of game animals do not have a single harvestable surplus; rather, the allowable harvest depends on where density is in relation to carrying capacity. Yields can, therefore, be manipulated by harvesting to maintain population density at a particular level (Figure 3). Generally, a harvest that holds density in the steep part of the growth curve will produce the maximum sustained yield (MSY). Permanently increasing the number removed annually from a population already producing MSY would ultimately extirpate it. Increasing just the rate of harvest though, would simply depress density to the point where adjustments in reproduction and mortality could again accommodate the increased losses due to hunting. When this occurred, the population would stabilize at a new, lower level (Figure 4).

Computer studies indicate that the MSY harvest rate for one southern Illinois quail population might be as high as 55 percent of prehunt densities (Roseberry 1979). This simulated annual harvest maintained average spring and fall populations at about 50 and 70 percent of their respective nonhunted levels. Theoretically, the sustained yield from any particular density should approximate the expected net production. In the case of these simulations, however, sustained yields were considerably greater than this, mainly because the model (and presumably the real population on which it was based) achieved most of its compensation to exploitation within the same year as it occurred.

Bobwhites are able to absorb as much hunting as they do because (1) the impact of fall shooting on breeding densities is numerically less than the actual number of birds removed, and (2) the loss of potential breeders that does occur is partially compensated by density-dependent recruitment the following summer. As noted earlier, the relationship between hunting and nonhunting mortality does not appear to be entirely compensatory; neither, however, is it entirely additive. For example, unhunted midwestern quail populations normally suffer about 50 percent mortality from fall to spring. Even removing half the fall population by hunting would likely increase this figure to no more than about 70 percent. For one thing, some of the birds shot would have died anyway from natural causes. Thus, the number dying naturally is less in a hunted population simply because they are no longer

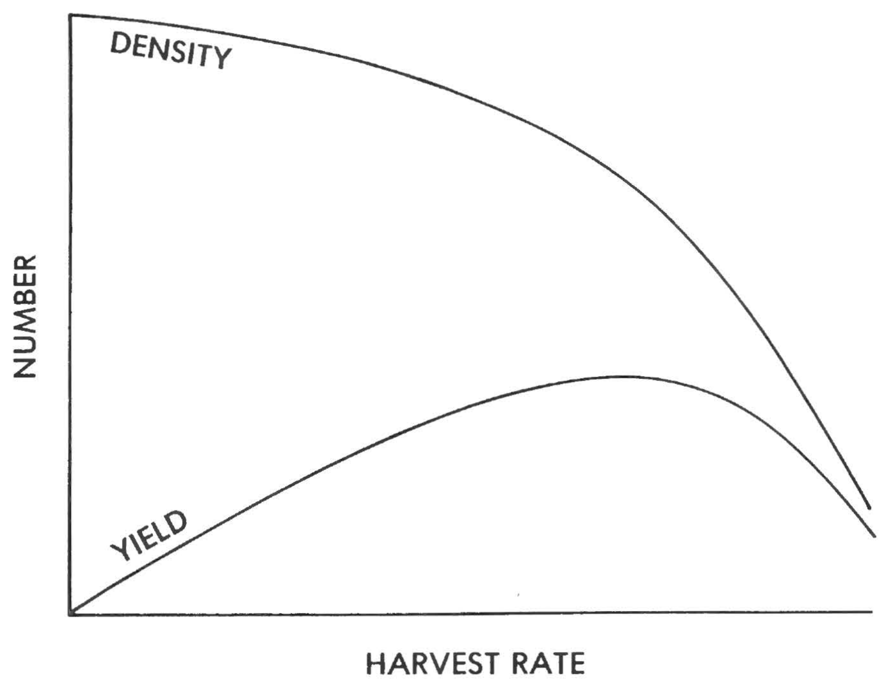

Fig. 3. Relationship of harvest rate to standing density and sustained yield.

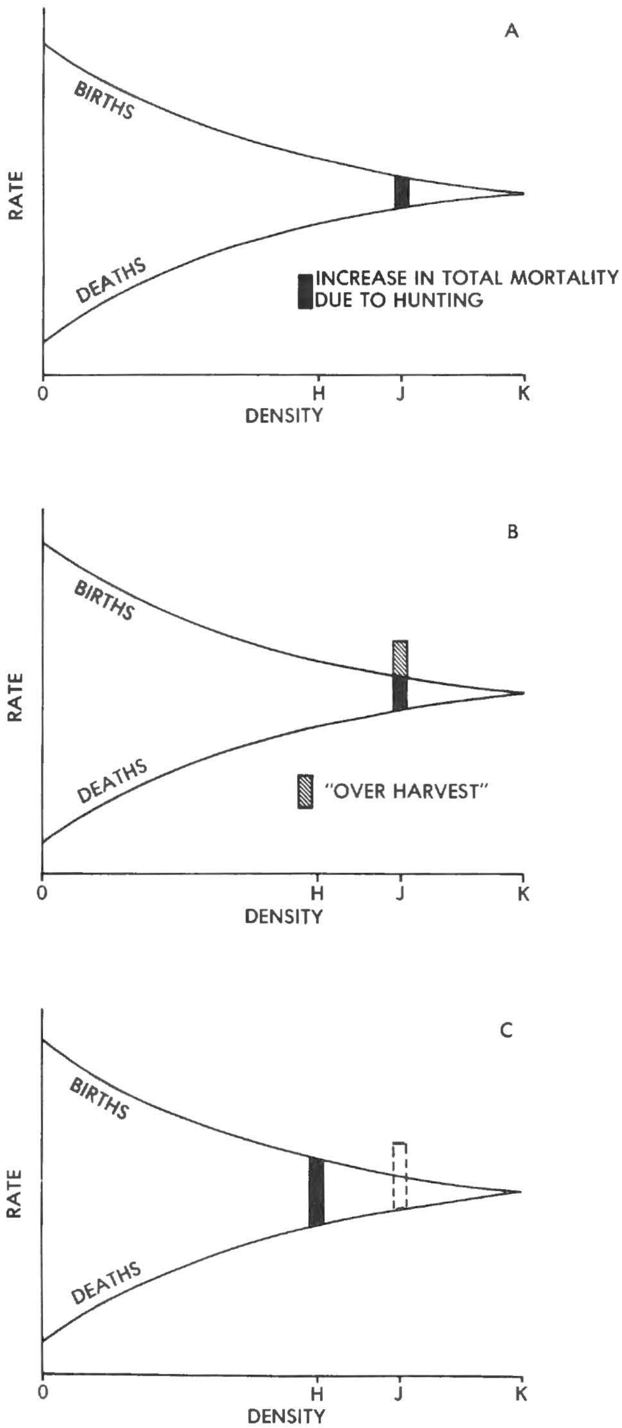

Fig. 4. Diagrammatic population response to increased harvest rate:
A - hunted population stabilized at density J;
B - increase in harvest rate temporarily exceeds net production;
C - population declines to and stabilizes at density H.

available. In addition, hunting season survivors generally suffer a lower percentage of posthunt mortality because of density dependence. Obviously though, the later in the season that hunting losses occur, the more additive they become to natural mortality. Furthermore, as the percentage of fall-to-spring mortality increases linearly, the percentage of summer gain necessary to offset it increases exponentially (Roseberry 1979). For this reason, the density-dependent nature of bobwhite recruitment plays an important role in the species' ability to absorb hunting. It is particularly significant that the positive response to reduced breeding density is essentially immediate, rather than delayed. This, plus the fact that bobwhite offspring are recruited into the huntable population their first autumn, permits relatively high prehunt densities to be maintained even in heavily hunted situations.

SOME IMPLICATIONS

We have thus far considered the interactions of harvest, density, and yield as if they occurred in a vacuum. In reality, habitat conditions dictate the upper limits of abundance on both hunted and nonhunted areas, and short-term fluctuations are influenced by weather and possibly even cycles (Roseberry and Klimstra 1983). I discussed in a previous paper the harvesting of bobwhites in a fluctuating environment (Roseberry 1979). There are additional reasons why a strictly sustained yield approach is perhaps not as appropriate for quail or other upland game species as it is for big game. For one thing, precise harvesting is difficult except on controlled shooting areas, and hunting pressure itself may vary inversely with game abundance. Certainly, quail management cannot be based solely on theoretical considerations; excellent results are sometimes achieved using a purely pragmatic, common sense approach. Nevertheless, officials must at least be cognizant of the basic principles underlying population dynamics and harvesting. To completely ignore theory in favor of intuition and tradition can lead to some very practical problems (Gross 1972, Caughley 1977, McCullough 1979). The remainder of this paper offers some examples.

A commonly expressed management goal is to maintain target populations at their highest possible level, ostensibly to provide maximum recreational opportunities. Actually, however, these goals are not congruent. Achieving maximum sustained yields requires that spring densities be held well below carrying capacity. Therefore, managers might wish to harvest at a somewhat lower rate if nonconsumptive use of the resource is also a consideration. Of course, improving habitat conditions would benefit both types of users.

Upland game biologists traditionally consider high young:adult ratios indicative of thriving, productive populations. Owing to density-dependent reproduction, however, such ratios are often associated with relatively low breeding densities and are not necessarily characteristic of high autumn populations (Roseberry 1974). Consistently extreme young:adult ratios may be symptomatic of chronically low breeding densities, possibly due to overshooting.

Another problem involves interpretation of population status. Stable numbers are generally considered evidence that management is successful and/or that hunting is having "no effect" on abundance. In reality though, most populations will ultimately stabilize at almost any level under a relatively constant harvest, and this density and associated yield may or may not be consistent with management objectives.

There is also the question of what constitutes a "safe" harvest. Early recommendations ranged from about 30 to 55 percent of prehunt densities (Errington and Hamerstrom 1936, Baumgartner 1944, Hickey 1955). Later, Vance and Ellis (1972) suggested that a 70 percent annual take might not be excessive, whereas Rosene (1969) cautioned that winter losses from all causes should not exceed 45 percent. In my opinion, this lack of consensus reflects an inadequacy of the annual surplus model, namely that its only criterion for judging a particular harvest regime is a supposed absence of population reduction. The common analogy that hunters must take only the "interest" and not touch the "principal" stems from a misconception that the harvestable surplus is a static figure, i.e., that it represents a fixed proportion of each population. In reality, even moderate hunting probably affects the "principal" or breeding stock to some extent. However, under a sustained yield approach, this is not necessarily undesirable. In summary, the question "How much can we hunt a population without 'hurting' it?" is meaningless unless we first establish objectives in terms of densities and yields. Under normal circumstances, it is not a matter of what harvest is "safe," but what is consistent with the overall plan for use of the resource. With game harvesting, as with any management program, agencies should identify and consolidate objectives before implementing policy.

Finally, there is a matter of public image. As stated earlier, most of us support the consumptive recreational use of renewable wildlife resources. Not surprisingly, this support has drawn criticism from anti-hunting groups who publicly question both our professional competence and integrity. As these attacks become more sophisticated (e.g. Favre and Olsen 1982), it is imperative that we maintain credibility. Too often, however, we fail to adequately articulate the scientific rationale for game harvesting, resorting instead to paradoxical cliches such as "Hunting has no effect on healthy wildlife populations, and besides, if we didn't hunt them they would overpopulate and all starve to death." To offer such half-truths and oversimplifications as state-of-the-art wildlife management, or to permit outdoor writers to do so, does a disservice to our profession and, in my opinion, plays right into the hands of the anti-hunting groups.

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