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PERIODIC HARVEST AS A METHOD OF INCREASING BIG GAME YIELDS

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Abstract: Using theoretical arguments and a computer simulation model, we have concluded that increased yields may be obtained from some big game populations by harvesting only once every several years. Since productivity per female increases with age in most big game populations, and since hunting shifts the age distribution towards younger animals, annual harvest may result in lowered mean productivity. Periodic harvest may help prevent changes in productivity. Computer simulation suggests that yield may be increased by 10 to 20 percent by periodic harvest and that the best interval between harvests is usually 2–4 years.

Annually sustainable harvests have long been considered a basic objective of wildlife management, and recent studies have shown theoretically how annual harvests in big game populations can be maximized (Scott 1954, Gross 1969). However, no attention has been devoted to the possibility that periodic harvests, in which animals are taken only in every second, third, or fourth year, may produce higher yields in the long run than annual harvests.

In the management of big game populations, it has been assumed that potential annual harvest is equal to, or closely related to, potential population recruitment in the absence of hunting (Leopold 1933: 171). Moreover, this assumption has been applied to hunted populations so that expected annual yield is equated to the observed annual rate of increase. The cumulative effects of hunting on age structure, and hence on population increase, have been ignored.

The intent of this paper is to show that higher yields may be obtained from some big game populations by harvesting only once every several years, and to provide guidelines to expected gains when periodic harvesting is used in management. The guidelines are based on results obtained from computer simulation studies using typical population parameters from the literature.

THEORETICAL BASIS FOR PERIODIC HARVESTS

The argument that periodic harvests will produce higher sustained yields than annual harvests of big game populations is based...
on four common observations: (1) reproductive potential generally increases with age, and the contribution of any given age-class is a function of age-specific reproductive rates and the numbers of survivors in that age-class, (2) harvesting usually shifts the age distribution towards younger animals, (3) mortality rates for intermediate age-classes are low and relatively constant, and (4) population change tends to follow a pattern wherein productivity reaches a maximum and then decreases with further increases in density.

The combination of these premises has lead to the concept that exploitation reduces the density of animals and moves the population away from a senescent structure towards a more youthful and productive condition. It has been then construed that, with animals having reached a more productive state, annual exploitation is required to maintain the population at this productive level. However, the intermediate age groups contribute most to population recruitment, because they are relatively numerous and have the highest reproductive potential. The relative abundance of these age groups is decreased by harvesting, and though the annual removal of individuals is equal in number to the recruitment, the contribution of the harvested stock to future reproductive periods is lost to the population. This would not be true if the harvested animals contained those individuals that would be lost through natural mortality prior to the next period of reproduction, or if the removal of productive individuals permits the survival of a comparable number of animals, with the same reproductive capacities (complete compensatory survival). However, if the harvest contains a significant number of individuals capable of surviving and contributing to one or more future periods of reproduction, and if compensatory survival does not occur or is only partially complete, then the harvest reduces the potential of the population to reproduce in the next period. Mean age, and thus mean productivity, is reduced by harvesting. By hunting at intervals greater than 1 year and thereby capitalizing on low rates of natural mortality in intermediate age groups, the recruited portion plus the initial breeding stock can contribute significantly to the numbers of animals available in the next hunting period.

To put this in another way, suppose that through nonselective hunting, the population is reduced along its growth form to a position near the maximum rate of increase. If the population is allowed to grow from this base in the absence of harvest for at least one whole year, and is reduced to the base level in one season, a greater net gain may be realized than if the population is harvested annually. If this policy is continued, a more productive age structure will be achieved. Each periodic harvest thus takes the sum of the net population gains since the last harvest. Through reinvestment and higher productivity, the harvest may be greater on a per-year basis than an annual harvest equal to the production derived from the base population. The yield can thus be increased by periodic harvests as long as there is a cumulative net gain in population size. However, if the period between harvests is too long, population growth will decrease near the end of each period, thereby reducing the average yield.

**SIZE OF BASE POPULATION AND LENGTH OF PERIOD**

Inferences about best population size to be left after each periodic harvest (base population size) and best interval between harvests can be obtained by assuming a general sigmoid pattern of population growth. In Fig. 1, cumulative population change (CPC) after periodic harvest is
harvest if the remaining population were small. The sigmoid growth assumption is not critical; we need only assume that growth rate will steadily decrease for population sizes above some inflection point. The cumulative sustained yield (CSY), in terms of either annual or periodic harvests, is dependent upon the position of the population along its curve of growth. A base population situated near the inflection point will produce the most rapid increase in CSY corresponding to high CPC. Similarly, low or high base populations, situated near the extreme ends of the growth curve, will produce low CSY (Fig. 1). Thus, both annual and periodic harvests and their corresponding CSY are materially influenced by the base level from which harvests are taken.

Also, the most suitable interval between harvests varies for different base levels along the curve. As is shown in Fig. 1, the best period between harvests for a low base population is long, because almost all of the cumulative population change is rapid relative to cumulative annual yield. At the other extremes, the best period between harvests for a high base population is relatively long, but the CPC is relatively low so that no significant numerical advantage is gained by extending the period. Thus, a light annual harvest equivalent to the annual recruitment is probably suitable for a high base population.

For intermediate base populations, the best period between harvests is dependent upon the innate capacity of the population to increase from the base, and the period will differ for each species and each population. The optimum period between harvests will be the one that maximizes the difference between CPC in the absence of harvest and the cumulative sustainable annual yield (Fig. 1), and at the same time permitting the development of a more productive age structure.

represents as segments of a general sigmoid growth curve that might be realized if population age structure were not affected by harvest to the degree expected under annual harvesting. Longer segments of the growth curve would be realized after
In Fig. 1, the CSY curve is below the CPC curve, because we expect the periodically harvested population to have a more productive age structure. If, however, natural mortality is compensatory or can be replaced by harvest, then the CSY curve can be above the CPC curve, and periodic harvest should produce lower yields than annual harvest. When compensatory or replacement mortality occurs, sustainable annual yield can be greater than the increase in population size that would occur in the absence of hunting, because harvest can take all of the net gain plus some animals that would otherwise have died naturally.

In summary, we predict some general relationships between base population size and best time interval between harvests, sustainable periodic harvest associated with the best interval, and corresponding average annual yield (harvest per period length). From low base populations, large harvests can be obtained, but only at long intervals; hence the average annual harvest is low. Similarly, only low average harvests can be obtained at high base population size, because both the sustainable yield and the optimum period are small. For intermediate base populations, average annual yields are relatively high, because the best period between harvests is short and annual gains (CPC) are highest.

**EXAMPLES USING SIMULATION**

The theoretical arguments presented above give no basis for the calculation of numerical benefits and effects from periodic harvest, and no actual data on periodically harvested herds are available in the literature. Since computers can rapidly perform the basic bookkeeping of population dynamics, it was decided to use simulation experiments as a means to evaluate some possible effects of periodic harvest management. The results presented are no substitute for real experience; the intent of this section is to provide management guidelines for use until data become available.

The computer studies were made with a model described by Walters (1969), which uses age-specific birth and death rates to keep track of age and sex structure over time. Critical assumptions of the model are that (1) age-specific survival rates are constant over time and are independent of population density, (2) age-specific production rates in any year (birthrate per female x survival rate through the first summer of life) are functions only of total density at the time fawns are born that year, and (3) the sex ratio of the fawns is constant at 50:50.

Thus, the model ignores possible changes in survival rates due to environmental factors. Moreover, the effects of predators, diseases, and similar factors on survival are assumed constant and are implicitly accounted for in age-specific survival rates. Changes in fawn mortality with density are treated as a component of production. Total density at the time when fawns are born is viewed as an index to social and nutritional conditions encountered during the previous fall and winter; for simplicity, it was assumed that age-specific production rates are constant when spring densities are low but that these rates decrease linearly when spring densities are high (Gross 1969). That is, we assumed that food and other factors act to lower production at high densities but that production can respond after one winter to sudden decreases in density during the previous fall.

Simulation studies were made with an IBM 1130 computer for two hypothetical populations of deer (*Odocoileus* spp.) and elk (*Cervus* spp.), representing a range of reproductive potentials and mortality rates.
Table 1. Productivity and death rate parameters used in computer simulation of deer and elk populations subjected to periodic harvest.

<table>
<thead>
<tr>
<th></th>
<th>0–1</th>
<th>1–2</th>
<th>2–3</th>
<th>3–4</th>
<th>4–5</th>
<th>5+</th>
</tr>
</thead>
<tbody>
<tr>
<td><strong>DEER</strong></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Annual death rate</td>
<td>0.4</td>
<td>0.2</td>
<td>0.1</td>
<td>0.1</td>
<td>0.2</td>
<td>0.3</td>
</tr>
<tr>
<td>Maximum productivity</td>
<td>0.1</td>
<td>1.0</td>
<td>1.6</td>
<td>1.8</td>
<td>1.8</td>
<td>1.7</td>
</tr>
<tr>
<td>Population above which productivity drops</td>
<td>14</td>
<td>200</td>
<td>500</td>
<td>500</td>
<td>500</td>
<td>528</td>
</tr>
<tr>
<td>Slope of population versus productivity</td>
<td>-0.0070</td>
<td>-0.0050</td>
<td>-0.0036</td>
<td>-0.0036</td>
<td>-0.0036</td>
<td>-0.0036</td>
</tr>
</tbody>
</table>

|                |     |     |     |     |     |    |
| **ELK**        |     |     |     |     |     |    |
| Annual death rate | 0.30 | 0.15 | 0.06 | 0.06 | 0.06 | 0.15 |
| Maximum productivity | 0.00 | 0.30 | 0.60 | 0.80 | 0.80 | 0.75 |
| Population above which productivity drops | 0 | 500 | 500 | 500 | 500 | 560 |
| Slope of population versus productivity | 0.0000 | -0.0006 | -0.0012 | -0.0016 | -0.0016 | -0.0015 |

*Productivity for the ith age-class is assumed to follow the equation \( P_i = p_i + b_i (N - N_a) \) where \( p_i \) is maximum productivity, \( b_i \) is the slope of the productivity–population curve, \( N \) is the total spring population size, and \( N_a \) is the total population above which productivity begins to fall. \( P_i \) is assumed equal to \( p_i \) for \( N < N_a \).*

for big game animals. Data from several deer, elk, and moose (Alces alces) studies, (Taber and Dasmann 1957, Robinette et al. 1957, Brown 1961, Murphy 1963, Simkin 1965, Nellis 1968, Eberhardt 1969, McCullough 1969) were used to generate parameters for the populations (Table 1). Preliminary test runs with different parameter values revealed that the most critical parameters were those associated with production and juvenile mortality. The production values shown in Table 1 were obtained by multiplying fertility rates by estimates of mortality during the first summer of life. We used optimistic estimates of productivity for young females to insure that any conclusions would apply even in cases where age structure has a minimum effect on productivity. Test runs also indicated that conclusions about periodic harvests are not greatly affected by estimates of the rate of decline in productivity with increasing density.

Each simulated population was subjected to a different 30-year harvest regime, with a constant percentage harvest rate and period between harvests during each regime. Equilibrium population size and yield were determined for each regime by examining output for near the end of the 30-year period. Simulated spring populations of deer resulting from some typical management regimes are shown in Fig. 2. An annual harvest of 15 percent per year reduced the spring population to about half its original size, whereas periodic harvests of 20 percent every second year nearly maintained the base population. On the other hand, a 15 percent harvest every third year appeared to restrict the natural rate of increase only slightly and limited the population numbers below the unharvested asymptotic level.

Equilibrium yields for the two populations (Fig. 3) are shown as functions of harvest rate and period between harvests. For deer, the simulation studies suggest that the optimum period between harvests
is around 2 years and that 15–18 percent of the typical population can be taken in each harvest. By harvesting every 2 years instead of every year, average sustainable yields of deer might be increased by 15–17 percent. For elk and other less productive species, the studies suggest that the optimum period between harvests is about 3 years and that the increase in average yield over that obtained by annual harvest is approximately 10 percent.

In general, it appears that the optimum period between harvests is inversely proportional to annual productivity. For more productive species (such as deer), sustainable harvest rates and potential effects of hunting on age structure are likely to be greatest. Thus, increases in yields realized from periodic harvests are likely to be greatest for more productive species. For both deer- and elk-type species, it appears that the optimum base population (density in the spring after each periodic harvest) is about one-third to one-half of the carrying capacity level; however, this observation depends strongly on the simulated patterns of linear decrease in production with density.

**DISCUSSION**

The foregoing theoretical and simulation results suggest that periodic harvests from suitable base population sizes can provide greater yields than annual harvests when hunting is nonselective towards age and
when natural mortality is not replaced by harvest. This is possible because the harvested population is permitted to regain its more productive state in the interval and because advantage is taken of the cumulative net gain in population size. Still greater yields might be achieved by age-selective hunting designed to preserve annually the most productive breeding stock. Annual culling practices employed in Great Britain and continental Europe thus produce greater yields on an annual basis than can be achieved by the nonselective methods of hunting employed in North America.

Although no distinction was made between sexes in the foregoing, the increased yields obtained are the result of effects on the abundance and age structure of the most productive age-classes of females. Thus, periodic harvest of females and annual harvest of males may produce almost the same results. However, periodic harvest of males also takes advantage of a cumulative gain in numbers available to the hunters at the start of each hunting period. Furthermore, as mean age and body size are increased during the closed periods, biomass yield and the quality of the hunt may be improved by periodically hunting both sexes. In cases where hunters normally take a disproportionately large number of juveniles, periodic harvest should improve yields even more than if hunting is not selective; productivity (and thus juvenile density) should be higher, and population age structure should be less affected by hunting.

These advantages could be partially offset by the possibility that populations managed for periodic harvest may accommodate less total hunting effort than those managed for annual yields. This would be true if animals become more vulnerable when hunted less frequently, so that the same total yield might be taken by fewer hunters. Also, large numbers of hunters may be required to reduce the enlarged population to the base level in one season. Thus, unless hunting is spread out across a lengthy season by regulations, unacceptable or unattractive concentrations of hunters may result in a reduction in recreational quality. A management program based on periodic harvests may be more acceptable from the hunter's point of view when alternative places to hunt each year are abundant.

LITERATURE CITED


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