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Influence of Simulated Harvest on Iowa Wild Turkey Populations¹

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Computer models were used to simulate autumn harvest of a wild turkey (*Meleagris gallopavo silvestris*) population in Iowa. Parameters were based on estimates of survival rates, fecundity rates, and age and sex ratios from field studies in mixed forest-farmland from 1977 to 1981. Simulations with average survival and fecundity parameters resulted in a population growth rate of 4% per year. If female survival rates were reduced 4.8% or fecundity was reduced 13.9%, the population became stationary. Interaction of hunting and nonhunting mortality was incorporated according to 3 hypotheses: additive, completely compensatory, and compensatory mortality rates up to a threshold. Estimated allowable autumn harvest rates, based on the goal of a stationary breeding population, ranged from 4.7% to 9.5% of the females and from 14.8% to 28.4% of the males. At these harvest levels, female survival would have to increase approximately 5% and fecundity 16% to compensate for the harvest and return the population to former growth rates. The time required for the total population to decline by 25% of present levels ranged from more than 100 years at 5% harvest rate under additive mortality to almost 74 years at 10% harvest rate under the threshold theory.

INDEX DESCRIPTORS: Iowa, *Meleagris gallopavo silvestris*, hunting, simulation

Sport hunting of many species is based on the concept that a high reproductive capability annually produces a surplus that will not survive the winter (Errington 1934). Theoretically, mortality from hunting simply replaces mortality from "natural or nonhunting" causes; it should therefore be possible to remove the surplus without measurably affecting breeding stock. Several studies have concluded the existence of such a compensatory relationship between hunting and nonhunting mortality; Allen (1947), pheasants (*Phasianus colchicus*); Campbell et al. (1973), scaled quail (*Callipepla squamata*); Errington and Hamerstrom (1935), bobwhite quail (*Colinus virginianus*); and Mosby (1969), gray squirrels (*Sciurus carolinensis*).

The principal alternative hypothesis, that mortality due to hunting is simply additive to nonhunting mortality, has been proposed primarily on the basis of waterfowl studies (Geis and Crissey 1969). However, other authors have suggested that hunting may influence upland game populations because compensation between mortality factors is imperfect and therefore that hunting mortality does influence subsequent breeding populations (Roseberry 1979, Wagner and Stokes 1968).

An intermediate hypothesis was completely developed by Anderson and Burnham (1976). Their hypothesis states that hunting mortality is compensatory up to a threshold level, above which the effects of hunting mortality are additive. For male mallards (*Anas platyrhynchos*), they suggested that the threshold was in the range of 25% of the estimated spring population of adults (Anderson and Burnham 1976:33).

Iowa's wild turkey population has grown systematically in the last decade, and as their range and numbers have increased, the opportunity to harvest them also has increased. Spring gobblers-only seasons were successfully initiated in 1974, and since then the population has continued to increase steadily. Thus, it seems that additional hunting could be allowed. In 1980, an autumn, either-sex season was proposed by research biologists of the Iowa Conservation Commission. Justification for an autumn season includes providing opportunity for hunting recreation in both autumn and spring while maintaining the quality of the spring hunt (Little 1979). In current studies on radio-telemetered and tagged birds in Lucas County, Iowa at Stephens State Forest, a high proportion of the natural mortality of the subadult (yearling) hens occurred in the autumn (Little 1980). Thus if mortality rates were compensatory, it should be possible to harvest

additional birds without harming the population.

The percentage that can be harvested without reducing turkey populations has been debated for some time, but controlled harvest is probably the most cost-effective management practice available at this time (Williams et al. 1978). Observed harvest rates of eastern turkeys range from 2-5% for spring, gobblers-only seasons to 10-40% for autumn, either-sex seasons (Everett et al. 1978, Weaver and Mosby 1979). Allowable harvest seems to be most affected by annual reproductive success (Lobdell et al. 1972, Speake 1980), but the lack of data on the variations in the impact of mortality, especially to first-year hens, makes this conclusion debatable.

The available data for Iowa turkey populations provided the opportunity to use computer modeling to estimate allowable harvest rates. Use of models by natural resource managers is becoming accepted in both research and management decisions (Tipton 1980). Models can be used to investigate future events over a wider range of conditions than may be encountered. Thus, possibly disastrous situations, such as high harvest in years of poor recruitment, can be identified and avoided.

The objectives of this study were to:

1. Simulate wild turkey populations by using data available from field studies in Iowa.
2. Determine whether populations without additional harvest were most sensitive to changes in fecundity or natural survival rates.
3. Determine the allowable harvest mortality rate that would result in a stationary (stable age distribution and constant size) population, given the average population parameters and assuming various combinations of hunting and nonhunting mortality.

METHODS

Both models used in this study are based on population projection matrices, which are modified versions of Leslie (1945) matrices. The population was divided into 3 age classes: poults, subadults (first-year birds) and adults (birds older than 1 year). Young birds are classified as poults from the time of hatch in May to the time that they are classified as subadults before the hunting season in October. The first model, called NEWLES (Innis undated), uses a time step of 1 year, so survival values for poults were incorporated into fecundity parameters (Pielou 1977). However, the time step of 1 year did not easily allow both spring and autumn hunting seasons to be incorporated into simulations.

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This limitation led us to develop another model, TURKEY, to investigate the effect of variable harvest on the population. Harvest is incorporated by first calculating how many animals die because of nonhunting mortality before the hunting season and assuming that the annual nonhunting mortality rate applies over the period. Next, hunting mortality is incorporated with the nonhunting mortality that would occur during the hunting season, resulting in a total mortality rate for the hunting season. Finally, the number that die during the remainder of the year is calculated by assuming that the remaining mortality is due only to natural factors. Fig. 1 graphically represents what happens during 1 year of such a simulation.

TURKEY enabled us to combine hunting and nonhunting mortality rates in 3 ways. Because of the various hypotheses proposed about the possible interaction of hunting and nonhunting mortality, these combinations are represented by the following mathematical equations, where M is total mortality rate, M_n is nonhunting mortality rate, M_h is hunting mortality rate, and C is a threshold mortality rate.

1. Additive $M = M_n + M_h$
2. Completely Compensatory $M = M_n$ if $M_n > M_h$ or $M = M_h$ if $M_n < M_h$
3. Threshold $M = M_n$ if $M_h < C$ or $M = M_n + (1 - M_n)/(1 + C) + (M_h - C)$ if $M_h > C$

Fig. 2 is a representation of total mortality rate as a function of hunting mortality under the threshold hypothesis. We investigated a wide range of values of the threshold mortality rate. In addition to the parameters needed for population projection, simulations with TURKEY also required input of the following harvest parameters: hunting mortality (%), age and sex specific values), beginning date and duration of the hunting season, and threshold rate (% hunting mortality for each sex).

Validation of simulations and sensitivity tests of parameters were conducted by using the average fecundity and survival data for 1977-1981 and field estimates of the population size. Allowable harvest rate

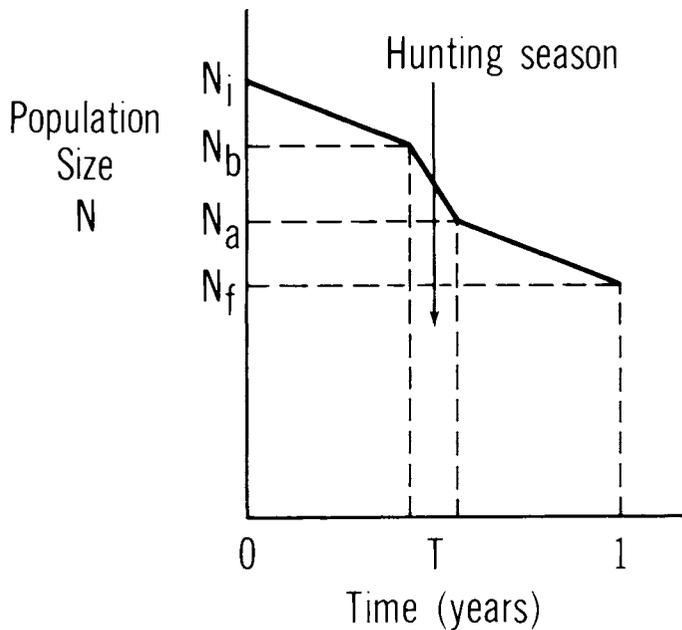


Fig. 1. Survival pattern including harvest, as it is incorporated into the simulation model TURKEY. N_i is initial population size, N_b is population size before hunting; N_a is population size after hunting; N_f is final population size.

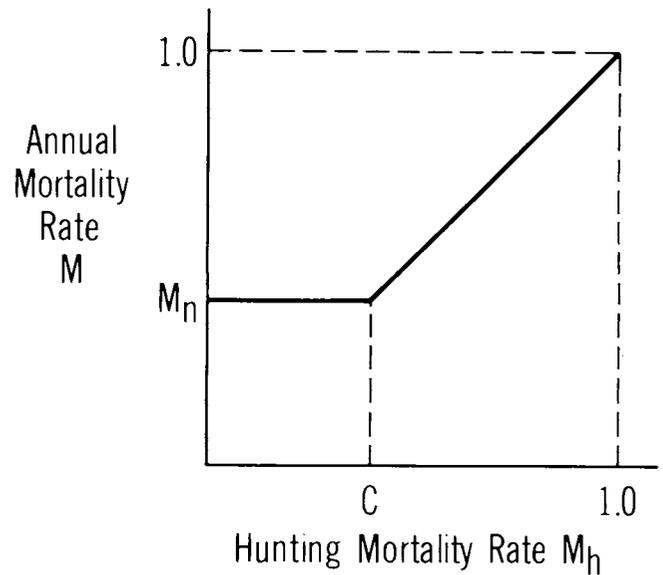


Fig. 2. Total mortality rate (M) as a function of hunting mortality rate (M_h) under the threshold hypothesis. M_n is nonhunting mortality rate; C is the threshold mortality rate.

was defined as that level of hunting mortality that resulted in a stationary population. After including the additional hunting mortality, the change in natural survival or fecundity necessary to return the population to the original rate of increase was estimated to determine if populations might realistically compensate for the harvest.

With the lack of precision in field measurements of population size of turkeys, it often is practical to detect only large declines (approximately 25%) in population level (Little 1979). Therefore, we simulated increasing levels of hunting mortality until a decline of 25% in population size resulted. The time, t_d (years), over which the decline occurred was calculated from the relationship: $t_d = \ln(0.75)/\ln(L)$, where L is the finite rate of decline of the population.

RESULTS

Basic Simulation

The values for the population parameters used in the basic simulation are listed in Table 1. Survival rates of males already reflect the influence of the spring gobblers-only harvest. Simulations were made by using data from each year separately (1977-78, 1978-79, 1979-80, and 1980-81) as well as with the average values for all 4 years. Projections were extended for 10-year periods.

The result of the simulations with the average parameter values and initial numbers of subadults and adults are graphed in Fig. 3. Although parameters would not be constant for 10 years, these simulations illustrate the expected trends with these particular combinations of reproduction and survival. Simulations using the parameter values from 1977-78 resulted in a population that declined about 7% per year, the 1978-79 estimates resulted in increases of 40% per year, the 1979-80 estimates resulted in increases of about 2% per year, and the 1980-81 estimates resulted in increases of 6% per year. The 4-year average estimates resulted in a population that increased about 4% per year.

Direct validation of projections was possible by comparing simulated population levels with data from the Stephens Forest

Table 1. Age-specific parameter values for an Iowa wild turkey population used in projection simulations. (P = poults, SA = subadults, and A = adults)

Year	Survival (%)						Fecundity (#P/female)			Numbers (initial)			Percent female (%)		
	Females			Males			P	SA	A	P	SA	A	P	SA	A
	P	SA	A	P	SA	A									
1977-78	21.9	54.7	73.8	21.9	75.0	75.0	0	0	2.8	1160	254	211	50.0	48.3	74.0
1978-79	80.4	53.1	61.8	80.4	60.0	33.3	0	2.3	3.8	466	375	158	50.0	49.4	71.6
1979-80	31.1	56.0	69.4	31.1	66.7	18.7	0	0.3	3.8	1045	325	275	50.0	64.1	61.6
1980-81	^a	90.9	72.7	^a	36.5	68.6	0	0.7	1.6	706	324	332	50.0	43.1	64.2
Average	44.5	61.6	61.0	44.5	55.2	48.1	0	0.8	2.8	720	320	245	50.0	53.5	66.1

^aNo data available.

population. A projection was made by beginning with the track count of 465 birds and the initial sex and age composition in 1977-78 (Table 1) and incorporating the observed survival and fecundity rates for each successive year. Known removals of birds for transplants were also incorporated. Winter population estimates derived from counts of tracks indicated that the real population grew about 14% per year. (465 turkeys in 1978 to 600 turkeys in 1980, Little unpubl. data). Simulated populations did not reach as high a level as that observed in field counts, but the rapid growth of the population is consistent with the observations (Fig. 4). Although both population parameters and winter population estimates may have considerable associated error, the simulation confirms the internal consistency of the data. Validation projections are a more reasonable representation of population trends when compared with the 10-year projections since they started with the actual observed population rather than the average. Validation runs reflect the sequential variation in reproduction and survival so that individual year trends in total population contradict the trends that result when parameters were held constant.

Parameter Sensitivity

We used the amount that nonhunting survival or fecundity rates must decrease before the population would become stationary as an indication of parameter sensitivity. Because the simulation with average parameters produced a population that increased slightly, we reasoned that the most sensitive parameters would be those that produced a stationary population with the smallest change in parameter value. This approach allowed us to visualize the biological

significance of such changes. A decrease of 4.8% in average female survival rate or a decrease of 13.9% in average fecundity produced stationary populations. The relative sensitivity of female survival rate is less than one-half the sensitivity of fecundity rate by using our criteria. Changes in survival rates of females have a great effect on the population's net rate of change because they affect the number of adult females surviving to breed. While in the real system poults per female may be more variable, a large breeding-female cohort may compensate for low individual productivity.

Harvest Levels

The values for the population parameters used in all simulations of harvest were the 4-year average values. The hunting season was assumed to occur during the last 2 weeks of October, with both sexes subjected to harvest (Bailey 1980). The hunting mortality rate was equal for both subadults and adults (Lobdell et al. 1972). When simulating harvest according to the threshold hypothesis, we set C, the hunting mortality rate at which the rates become additive, at the average allowable harvest level for males and females determined by assuming additive rates (Table 2).

Maximum allowable harvest rates of females ranged from 4.5 to 9.5% of the autumn population, depending on the assumption used for the interaction between mortality rates (Table 2). Maximum allowable harvest rates of males ranged from 16.7 to 28.4% of the

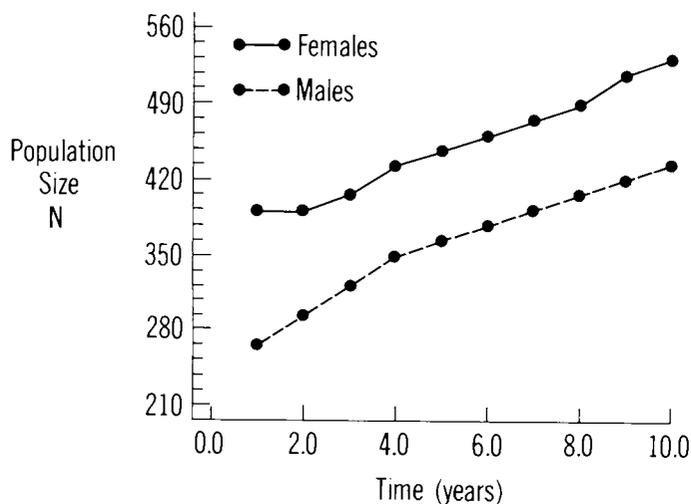


Fig. 3. Population size of Iowa turkeys simulated by assuming constant average fecundity and survival rate over 10 years.

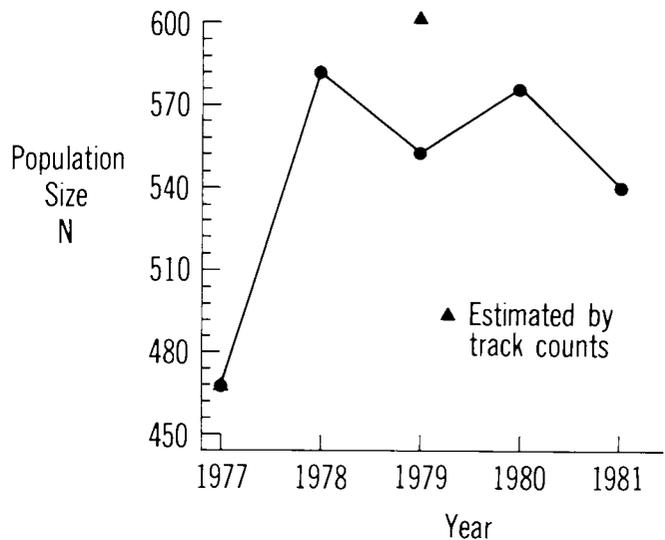


Fig. 4. Population trends of Iowa turkeys simulated by using fecundity and survival rates observed from 1977 to 1981 and comparison to field population estimates.

Table 2. Allowable fall hunting mortality rates for an Iowa wild turkey population and changes in natural survival and fecundity rates necessary to offset the effects of the harvest.

Mortality Theory			Allowable Hunting Mortality %	Fecundity increase %	Natural survival increase %
	C	Sex			
Additive		F	4.7	15.5	5.0
		M	16.7		17.0
Complete Compensatory		F	6.7	15.5	5.1
		M	17.1		17.9
Threshold	5.0	F	9.5	15.3	4.9
	16.0	M	28.4		17.0

autumn population. Harvest rates of females are lower than for males because reproductive recruitment is dependent on survival of the females through at least 1 breeding season. We also estimated the increase in nonhunting survival or fecundity necessary to offset the added harvest and return the population to a 4% annual rate of increase (Table 2). The relative change in natural survival necessary to compensate for the harvest is about 0.33 of the change required in fecundity. Because males already are being harvested during the spring gobbler season, changes in their survival rates must be much larger than those of females before an increasing population results.

Years to a 25% Decline

The number of years that it takes for a 25% decline in the total population under two alternative harvest regimes is given in Table 3. The time to decline (t_d) is listed only for the additive mortality theory (conservative allowable hunting mortality) and for the threshold mortality theory (liberal allowable hunting mortality). At a projected allowable harvest rate of 5% of the females, the population essentially would never exhibit detectable declines. At a higher rate of 10%, the effect of harvest becomes more important, and its effect is influenced by the way in which mortality factors interact. At low levels of hunting mortality, the difference between t_d values under the alternatives is large, but the difference is within 1 year at hunting mortalities above 20%. Viewed another way, for a given level of autumn harvest under each hypothesis, t_d is the number of years before a sizable decline in population level would be detectable from field measurements.

DISCUSSION

From the wildlife manager's viewpoint, one of the principal uses of population projection such as we have described is to check field data for internal consistency and similarity to other field studies. Our simulation results are consistent with the observed changes in Iowa wild turkey populations. Estimates of nonhunting mortality and fecundity are consistent with each other and with what has been observed in other studies of turkeys. Thus the model qualifies as a planning tool with which to investigate the effects of autumn harvest on the population (Romesburg 1981).

Simulation results emphasize the importance of survival of females in determining population trends. Small errors in field estimates of female survival rates could cause relatively large errors in the predicted net rate of change in the population. When combined with the expected variations in fecundity, this implies that harvest rate must be carefully adjusted to changes in both survival and fecundity.

Evaluation of the interaction of hunting and nonhunting mortality was not a primary goal of this research. However, we simulated various interactions of these mortality factors because of the obvious

importance in wildlife management (Anderson and Burnham 1976, Roseberry 1979). The concept of a threshold mortality rate, below which mortality factors are compensatory, assumes that environmental variables limit the population in a density-dependent way. For long-lived species such as turkeys, the threshold rate can be expected to be quite low (Anderson and Burnham 1976). Turkeys have relatively low natural mortality rates in the absence of hunting, so their populations have less capability to compensate for additional mortality due to hunting. Variability in spring weather conditions make reproductive recruitment highly variable from year to year. Although game populations generally are capable of responding to increased harvest, in turkey populations any compensation between hunting and nonhunting mortality is likely to be incomplete, particularly at high harvest levels. Timing of hunting losses also will be important because early autumn removal of subadults during a time when their nonhunting mortality is normally high may only replace the natural mortality, but late-season losses may have more additive effects. The isolated aspect of much wild turkey habitat in Iowa may subject some local populations to autumn harvest that is higher than anticipated. Therefore, a conservative management approach, assuming that mortality due to hunting is additive to natural mortality, is most reasonable.

It seems that an autumn harvest of both sexes of turkeys would, at most, reduce the population growth rate to zero under present conditions if the hunting mortality rate does not exceed 5% to 10% of the female birds. This rate is similar to the 9% rate observed in Texas (DeArment 1975) but lower than the 20% rate of maximum allowable harvest estimated for those populations. In New York, a minimum rate of 25% was reported for autumn harvests of study

Table 3. The number of years before a 25% decline would occur in a simulated Iowa turkey population for various levels of fall hunting mortality.

Harvest Mortality (%)	Years until 25% decline	
	Additive mortality	Threshold mortality
0	a	a
5	106.4	a
10	6.5	73.6
15	3.3	6.2
20	2.2	3.1
25	1.6	2.1
30	1.2	1.5
35		1.2

^aPopulation is increasing

populations, but maximum allowable rate was not estimated (DeGraff and Austin 1975). Lobdell et al. (1972) simulated allowable rates of hunting mortality that ranged from 10% to 40% when investigating harvest strategies for combined autumn either-sex and spring-gobbler hunting of wild turkey populations. Our simulated allowable harvest rate does not account for other factors that may have significant bearing on the hunting mortality. Factors such as crippling or the possibility of an increased illegal kill because of attitude changes about harvesting females should be an integral part of management decisions. If factors such as these are observed and estimated, they could be formally incorporated into the model system.

The simulations demonstrate that at low levels of additional hunting mortality, upward adjustment of natural survival or fecundity rates could offset the harvest, resulting in populations that would continue to increase. These adjustments could be from intrinsic responses of the population or from wildlife management techniques such as habitat manipulation. Increasing populations are especially desirable in Iowa because populations would continue to expand into available habitat.

In 1981, an additional autumn season was initiated, supported by the findings of this study. Model predictions have been made about population dynamics on the basis of specific assumptions and hypotheses that now can be validated as data is accumulated on the effects of the additional hunting mortality. Even under identical hunting regulations, the harvest of turkeys may vary greatly from the average conditions that we simulated. Continued combination of simulation and field studies over a period of 3-5 years will be valuable in assessing the influence of autumn seasons on wild turkey management in Iowa.

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