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OPTIMAL EXPLOITATION STRATEGIES FOR AN ANIMAL POPULATION IN A MARKOVIAN ENVIRONMENT: A THEORY AND AN EXAMPLE¹

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Abstract. Optimal exploitation strategies were studied for an animal population in a Markovian (stochastic, serially correlated) environment. This is a general case and encompasses a number of important special cases as simplifications. Extensive empirical data on the Mallard (*Anas platyrhynchos*) were used as an example of general theory. The number of small ponds on the central breeding grounds was used as an index to the state of the environment. A general mathematical model was formulated to provide a synthesis of the existing literature, estimates of parameters developed from an analysis of data, and hypotheses regarding the specific effect of exploitation on total survival. The literature and analysis of data were inconclusive concerning the effect of exploitation on survival. Therefore, two hypotheses were explored: (1) exploitation mortality represents a largely additive form of mortality, and (2) exploitation mortality is compensatory with other forms of mortality, at least to some threshold level. Models incorporating these two hypotheses were formulated as stochastic dynamic programming models and optimal exploitation strategies were derived numerically on a digital computer.

Optimal exploitation strategies were found to exist under the rather general conditions. Direct feedback control was an integral component in the optimal decision-making process. Optimal exploitation was found to be substantially different depending upon the hypothesis regarding the effect of exploitation on the population. If we assume that exploitation is largely an additive force of mortality in Mallards, then optimal exploitation decisions are a convex function of the size of the breeding population and a linear or slightly concave function of the environmental conditions. Under the hypothesis of compensatory mortality forces, optimal exploitation decisions are approximately linearly related to the size of the Mallard breeding population.

Dynamic programming is suggested as a very general formulation for realistic solutions to the general optimal exploitation problem. The concepts of state vectors and stage transformations are completely general. Populations can be modeled stochastically and the objective function can include extra-biological factors.

The optimal level of exploitation in year t must be based on the observed size of the population and the state of the environment in year t unless the dynamics of the population, the state of the environment, and the result of the exploitation decisions are completely deterministic. Exploitation based on an average harvest, or harvest rate, or designed to maintain a constant breeding population size is inefficient.

Key words: *Anas platyrhynchos*; dynamic programming; exploitation; harvest; Mallard; maximum sustained yield; model; optimal; population ecology; stochastic environments; strategies.

INTRODUCTION

One of the greatest challenges of modern ecology is to place resource management on a scientific basis (Krebs 1972). This study examines optimal exploitation strategies for an animal population in an environment where the environmental variables are stochastic and are serially correlated. It is a theoretical study based on an analysis of empirical data. A number of hypotheses are formulated, tested, and their implications examined.

The optimum yield problem is to determine the maximum number of individuals that can be removed from a population without impairing the ability of

the remainder to produce the maximum on a sustained basis. The problem of optimal yield arises whenever a population of living organisms is subjected to systematic exploitation by man, whether this is in the form of fishing, hunting, harvesting, or lumbering (Watt 1955). In the process of exploiting a population of organisms, man assumes the role of a predator. He differs from a nonhuman predator in his ability to attempt to calculate his strategy of predation to maximize both the harvest and the likelihood that the exploited population will persist on a sustained basis (Slobodkin and Richman 1956).

Previous studies

Four laboratory studies of exploitation conducted during the mid-1950's provided the basis for much

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of the present theory of exploited animal populations. The results of the studies indicate a significant homeostasis in the population response to exploitation pressure. Nicholson (1954) investigating the effects of exploitation on the Australian sheep blowfly (*Lucilia cuprina*) found that blowfly populations could sustain a 99% removal of emerging adults because of a compensatory mortality process. As the exploitation rate increased, pupal and adult mortality decreased. In addition, the birth and replacement rates increased as exploitation rates increased. Nicholson demonstrated that these compensatory mortality processes represent an evolutionary result allowing the blowfly population to withstand stress. Watt (1955) studied optimal exploitation of the flour beetle (*Tribolium confusum*) and found that productivity increased with increased exploitation rate up to a point. Beyond this point, the population fell rapidly to extinction. He suggested that the number of individuals remaining after harvest is a key element in optimal exploitation theory.

Slobodkin and Richman (1956) found similar results in a laboratory study of exploitation of newborn *Daphnia pulicaria*. The size of exploited *Daphnia* populations was reduced but not in direct proportion to either the number or the percentage of the newborn animals removed. Median life expectancy and reproduction rates of survivors increased as the rate of exploitation increased. Maximum yield occurred when approximately 90% of the newborn *Daphnia* were removed.

Silliman and Gutsell (1958) studied exploitation of guppies (*Lebistes reticulatus*) and found the equilibrium yield was approximately 30%–40% of the population per 6 wk; this occurred when the population was at approximately one-third the level of the unexploited control population (Watt 1968:91, disagrees with this conclusion). Silliman and Gutsell noted a resilience to exploitation through increased survival and growth rates of the remaining guppies. The optimum yield problem is much more complex when mortality and recruitment rates are not uniform.

Methodological approaches

Comparatively little research has been done toward the development of a general quantitative theory of optimal exploitation. Watt (1956), Beverton and Holt (1957), and Ricker (1958) have taken a classic approach to the general problem. The fisheries literature contains numerous examples and extensions of this type of approach.

Bellman and Kalaba (1960) were the first to suggest a general outline to a realistic approach to the optimal yield problem. They suggested the formulation and analysis, either analytically or nu-

merically, of optimal exploitation problems using the recursive optimization theory of dynamic programming. This theory seems to be the most promising and general approach, but not a single application of this theory has been found in the literature to date.

Mann (1970, 1971a, b, and c) has studied exploitation from a theoretical viewpoint. His results are based on a combination of differential equations for sex-specific population growth and Markov transition matrices, which allow birth and death rates to vary randomly or as functions of environmental variables. Mann's work is particularly important because of the tenable assumptions made and the generality of the approach. Deriving numerical solutions to the equations may prove to be extremely difficult except in the simplest cases.

A number of other approaches to the quantitative theory of optimal exploitation of animal populations have appeared in the literature. Several appear to exclude important concepts and variables and may be useful only in specific, and usually fairly simple, population processes. Darwin and Williams (1964), Lefkovitch (1967), Dunkel (1970), and Beddington and Taylor (1973) discussed exploitation for populations with age-specific birth and death rates based on a study of Leslie's (1945, 1948) population projection matrices. Davis (1967) used linear programming to study optimal management plans for deer (*Odocoileus virginianus*). Lomnicki (1972) suggested a nonlinear programming approach to exploitation of big game populations. Clark (1971, 1972) presented an econometric treatment of the commercial exploitation of animal populations using a very simple deterministic model. He derived several analytical results and noted possible extensions using dynamic programming.

Present theory

At present, there is no single, explicit exploitation theory or population model for exploitation (Slobodkin and Richman 1956, Wagner 1969). Any theory for the biological aspects of exploitation must be powerful enough to account for at least the minimum of biological complexity that might be expected to arise in the natural world.

I have synthesized a brief summary of the present theory of exploitation of animal populations from the literature using the principles of Silliman and Gutsell (1958) as a base:

- 1) Any exploitation of an animal population, however mild, somewhat reduces its abundance.
- 2) Below a certain level of exploitation, animal

populations may be resilient, increasing their survival and/or growth rates and production rates to compensate for the individuals removed.

- 3) Where populations are regulated primarily through density-dependent processes, exploitation rates (up to the optimum) will tend to increase productivity and reduce natural mortality of the remaining individuals.
- 4) Exploitation rates can reach a point at which extinction of the population will occur if continued.
- 5) Somewhere between no exploitation and excessive exploitation there lies a level at which the maximum sustained (equilibrium) yield can be obtained.
- 6) The maximum exploitation rate is at least partially a function of the biotic potential or production rate of the species.
- 7) The age composition and the number of animals remaining after exploitation are key factors in the dynamics of exploited animal populations.

These principles are not universal but seem to represent the general pattern. Important exceptions occur and the theory is not complete. The theory as summarized above implicitly deals only with populations in either carefully controlled situations or populations existing in simple and nearly constant environments.

Objectives and hypotheses to be tested

This research is concerned with the extension of the theory of optimal exploitation (i.e., an animal population existing in a randomly varying, serially correlated environment) and the testing of several hypotheses. This fairly general conceptualization encompasses a number of important special cases as simplifications (e.g., animal populations in uncorrelated or unchanging environments).

Sequences of related decisions (strategies) must be considered for an understanding of a general theory of optimal exploitation. Strategies in this complex case must cope with the randomly varying environmental conditions and the complex ways that population dynamics are related to environmental variables. Exploitation strategies, in this context, must recognize the uncertainty regarding the stochastic and time-dependent nature of physical factors in the environment, and the effects of a particular harvest decision on the animal population. Regarding animal populations exploited by man, decisions concern the optimal number of animals to harvest or the optimal harvest rate, while the objec-

tive is optimal sustained exploitation. This research is designed to examine three major questions:

- 1) Can optimal exploitation strategies be derived for animal populations in stochastic, serially correlated environments? This deals with the question of the very existence of meaningful exploitation strategies in stochastic environments.
- 2) Annual survival rates are affected by the harvest rate in many exploited animal populations. Would optimal exploitation strategies be altered in form if the effect of exploitation was compensatory? This is a hypothesis that harvest mortality replaces natural mortality up to some threshold level.
- 3) Many animal populations are under the influence of both intrinsic population forces and physical components in the environment. What is the relative importance of these variables on the number of young produced and the optimal level of exploitation?

Experimental animal

The Mallard (*Anas platyrhynchos*) was selected for an analysis of optimal exploitation strategies and as a basis for examining the questions above. The Mallard is well-suited as an example of an animal population existing in a stochastic, serially correlated environment, and much is known concerning its life history and ecology in North America. The Mallard is the most abundant duck in North America and its basic field biology is reasonably well-understood (Dzubin 1969, Smith 1971, Stoudt 1971, Dzubin and Gollop 1972). The size of the adult breeding population has averaged ≈ 11 million birds over the past 18 yr and the fall population size has averaged over 20 million birds and has been as large as 35 million (Anon. 1970).

The breeding range of the Mallard includes nearly all of the northern states in the United States and nearly all of Canada. Prairie and parkland areas of the Dakotas and Minnesota and the southern portions of Alberta, Saskatchewan, and Manitoba represent the primary breeding range. As the Pleistocene glaciers receded from this area, millions of small depressions, or potholes, were left in the land across nearly 1.3 million km². Water accumulates in these basins and provides nesting and brood-rearing sites for Mallards and other waterfowl. Gollop (1965) estimated nearly 10 million basins capable of holding water exist in southern Canada alone. Reproductive success is highly dependent upon the number of basins filled with water during the nesting and brood-rearing period (Crissey 1969).

Mallards are migratory and substantial mixing of

the various population segments occurs on the wintering grounds. Mallards are hunted for sport during fall and winter months. The average annual harvest in North America has been approximately 4–6 million.

The Mallard has been the subject of extensive data-collecting programs in North America over the past two decades (Crissey 1963, 1970). About 3 million Mallards have been banded and nearly 0.4 million of these have been recovered. Estimates of survival and harvest rates can be made from an analysis of these data. Several extensive surveys conducted annually in the United States and Canada have provided estimates of the sizes of breeding populations (R. Pospahala, *unpubl. data*) and the size, age, and sex composition of the harvest (Martin and Carney 1976). Previous research on the Mallard and a review of data-collecting programs were recently summarized by Anderson and Henny (1972).

The enormous quantity of data available on the Mallard reflects the economic and social values of the species to man. These data provide a nearly unique opportunity to study population phenomena in an exploited animal population. The purpose of this paper is not to attempt the solution of specific practical problems arising from the sport hunting of Mallards, but rather, to explore the theory of optimal exploitation of animal populations in stochastic environments.

METHODS

I constructed a mathematical model to represent the dynamics of the Mallard population and the most important environmental variables. Using the theory of dynamic programming (Bellman 1957, Bellman and Dreyfus 1962, Nemhauser 1967), a general mathematical method of sequential optimization, I developed optimal exploitation strategies. Dynamic programming is a quantitative approach for finding optimal strategies, not merely the best parameter values for a given strategy. It does not predetermine the form of the strategy (White 1969:89).

Dynamic programming is the only method adequate to cope realistically with what is known concerning the ecology and exploitation of the Mallard. It is well-suited to models involving stochastic components, nonlinearities, and piece-wise functions. Direct feedback control is an integral component of the solution. Furthermore, the technique can be employed with a wide variety of constraints or boundary conditions. As Slobodkin and Richman (1956:209) noted, "Extra-biological factors often influence exploitation procedures. These may include such things as the aesthetic or political opinions of the consuming public. . . ." Most important is the fact that dynamic programming can be applied to

stochastic models where uncertainty and unpredictability are important components of the system under study. The population model representing the ecology of the Mallard was complex; analytical solutions were infeasible and numerical solutions were obtained using a large digital computer. A computer algorithm was written in FORTRAN IV following Nemhauser (1967:69–70, 155) for multistate variable, stochastic dynamic programming models.

RESULTS

Model construction

The mathematical model I constructed allowed an examination of optimal strategies beginning with a simple, conceptual model of annual population change. This approach allowed a convenient synthesis of the available literature, estimates of various population parameters, the relationships among important variables, and hypotheses concerning the effect of exploitation on survival. The size of the population in year $t + 1$ was defined to be the number of surviving adults in year t plus the number of surviving young in year t . This was expressed as

$$N_{t+1} = N_t \phi_t^a + Y_t \phi_t^y, \quad (1)$$

where: N_t = the size of the adult breeding population in year t (on 15 May). All birds are assumed to be sexually mature at this time.

Y_t = the number of young produced in year t . This represents only birds capable of flight, i.e., the late summer population. A 1:1 sex ratio is assumed.

ϕ_t^a = survival rates of adults (a) in year t . This represents an annual rate.

ϕ_t^y = survival rate of young (y) in year t . This represents survival from approximately 15 September through the following 15 May.

This model satisfies the fundamental point made by Watt (1955:287) regarding realistic models of exploited populations: ". . . It (the model) must utilize the absolute numbers of the population left behind. Admittedly, this is difficult information to obtain, but what is biologically important to the future history of any population is not what is taken away from it but what remains." Before the population model can be useful, we must define ϕ_t^a , ϕ_t^y , and Y_t in terms of other relevant variables. This subject is examined in the following sections. Additional details are given in Anderson (1974).

Production of young. Since 1955, estimates of the number of Mallard young have varied from 5.9



FIG. 1. Aerial view of mallard breeding habitat near Redvers, Saskatchewan. As many as 3.5 million small pond basins have contained water in good years on the central breeding grounds in southcentral Canada. (Photo by W. F. Crissey).

million (1961) to 22.1 million (1957). Production of young appears to be closely related to two primary factors: the size of the breeding population and the number of water areas on the central breeding grounds (Crissey 1969). The number of ponds is an excellent index to environmental conditions influencing production. Ponds represent breeding and nesting sites, feeding areas and brood-rearing areas for Mallards (Fig. 1). A description of the relationship between these variables was developed by Hammack and Brown (1974) as an extension of Beverton and Holt's (1957:49) equation. Allowing the production of mallards to be dependent upon the size of the breeding population and environmental conditions, the following relationship was hypothesized:

$$Y_t = (1/aP_t^b + c/N_t)^{-1}, \quad (2)$$

where: P_t = number of ponds present on the central breeding grounds in year t .

a , b and c are constants in the model.

This model allows a realistic consideration of important environmental variables which limit production of young (Klomp 1972). This is important because environmental conditions on the central breeding grounds have fluctuated widely.

I used data collected since 1955 on annual breeding population size, production, and the number of ponds to estimate parameters of the model and examine its applicability. Parameter estimation was accomplished using a nonlinear least squares algorithm (Dixon 1970). Results are summarized as follows:

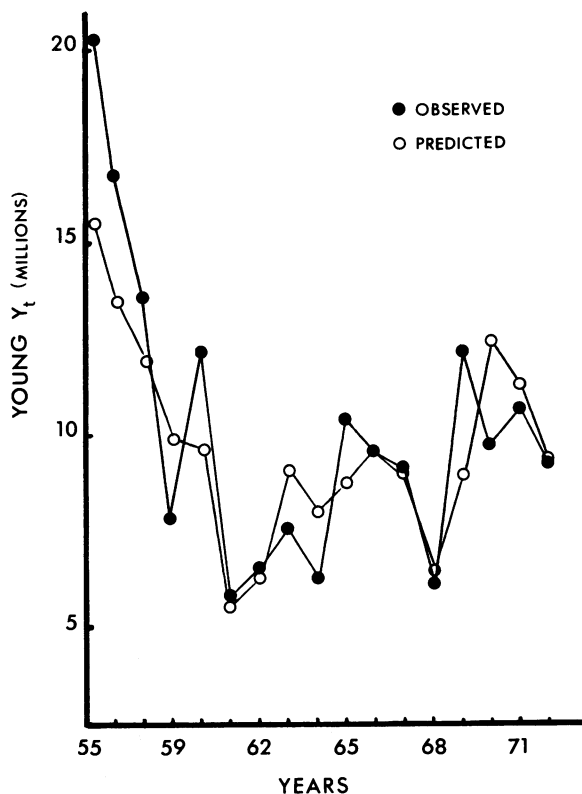


FIG. 2. Observed and predicted values of the production of young mallards. Predicted values were derived from the production model. The data appear to fit the model quite well.

$$Y_t = (1/12.48 P_t^{0.851} + 0.519/N_t)^{-1} \quad (3)$$

$$t_a = 3.4^{**} \quad R = 0.83^{**}$$

$$t_c = 2.6^* \quad R^2 = 0.69^{**},$$

where: * = 0.05 and ** = 0.01 significance level.

This model accounts for a large proportion (69%) of the variance in the annual number of young produced (Fig. 2). In addition, each of the three parameters of the model are statistically significant from zero, although b is not significantly different from one. It appears that the form of the model and the parameter estimates are adequate.

Environmental variables. The number of ponds present in a given year on the central breeding areas in southern Canada represent a measure of the important environmental variables in a particular year because ponds represent essential habitats for breeding Mallards and their young. The number of ponds on the central breeding areas in midsummer (July) has varied from 0.6 (1961) to 3.5 (1955) (Henny et al. 1972). Information on the size or perimeter of ponds is not available.

An analysis of information since 1955 on the annual number of midsummer ponds and annual

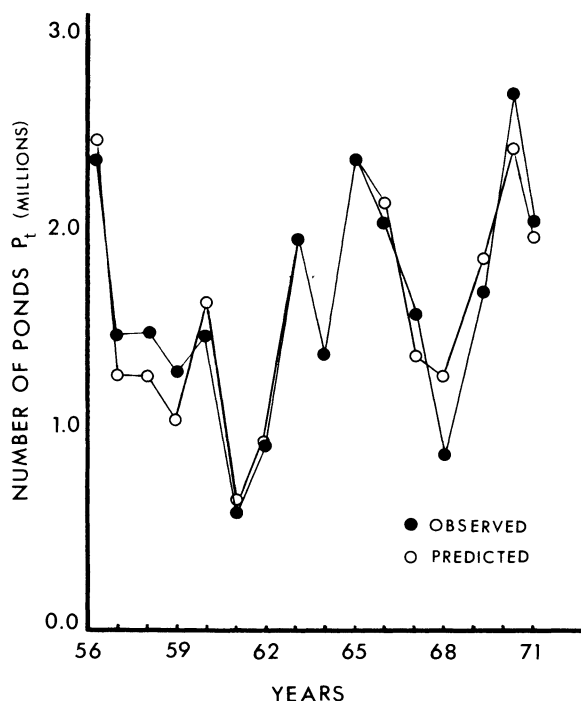


FIG. 3. Observed and predicted values of the number of ponds on the central breeding grounds. Predicted values were derived from the pond model. An excellent fit is indicated.

precipitation records suggested the following relationship:

$$P_{t+1} = -2.76 + 0.391 P_t + 0.233 R_t$$

t values	4.5**	8.5**	(4)
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$$R = 0.93^{**} \quad R^2 = 0.87^{**} \quad F_{2,12} = 41.3^{**},$$

where: R_t = precipitation (in inches) during the annual interval t to $t + 1$ (1 August through the following 31 July).

This expression represents the hypothesis that the number of ponds in year t is a function of the number of ponds the previous year and the amount of precipitation received during the 12-mo interval. This model describes a high proportion (87%) of the annual variation in pond numbers and appears quite satisfactory for our purposes (Fig. 3). The number of ponds in year t and the amount of precipitation were both highly significant. Precipitation is relatively more important than pond numbers the previous year in its effect on pond numbers (standard partial regression coefficients of 0.88 and 0.46, respectively). I concluded the model and parameter estimates were satisfactory.

Precipitation. Since 1937, average annual precipitation on the central breeding area has varied

from as low as 31.2 cm (1960) to as high as 53.6 cm (1954). Analyses of these data indicated that the annual precipitation series can be well described as a normally distributed random variable ($\chi^2 = 1.0$, 5 df), with a mean and variance of 41.81 cm and 11.20 cm, respectively (Pospahala et al. 1974). Thomas (1965) found similar patterns in Canadian precipitation and suggested a form of the gamma distribution if significant positive skewness was observed in the data.

Nonparametric tests (Dixon and Massey 1969: 343–354) failed to reject the hypothesis that the annual precipitation data were independent and random ($z = 0.28$ and 0.15). I conclude that annual precipitation on the central breeding areas of the Mallard can be described (approximately) as an independent, normally distributed random variable.

Size of the fall population. The size of the fall population is composed of adult ducks that survived the summer period and their (flying) young

$$F_t = \phi^s N_t + Y_t, \quad (5)$$

where: F_t = the size of the fall population on 15 September in year t

ϕ^s = survival rate of adult ducks during the 15 May–15 September period. This is considered to be a constant of 0.92.

Survival rates. Survival rates in a given year were assumed to be a function of the size of the fall population and the number of animals harvested. I define

$$\phi_t = f(D_t, F_t)$$

$$H_t = D_t / F_t,$$

where: ϕ_t = survival rate in year t (age- and sex-specific),

H_t = exploitation (harvest) rate in year t ,

D_t = number of ducks harvested in year t .

Estimates of survival and harvest rates were developed from an analysis of banding data using the maximum likelihood methods of Seber (1970) and Robson and Brownie (1973). A band reporting rate of 0.4 was assumed to estimate harvest rates. Annual estimates of survival and harvest rates were made for each age and sex class for all geographic areas throughout North America represented by banded samples.

It seemed reasonable to hypothesize that total survival decreased as the rate of exploitation increased (Wagner 1969:270). The following relationship was chosen to represent this hypothesis:

$$\phi_t = 1 - a \exp b H_t, \quad (6)$$

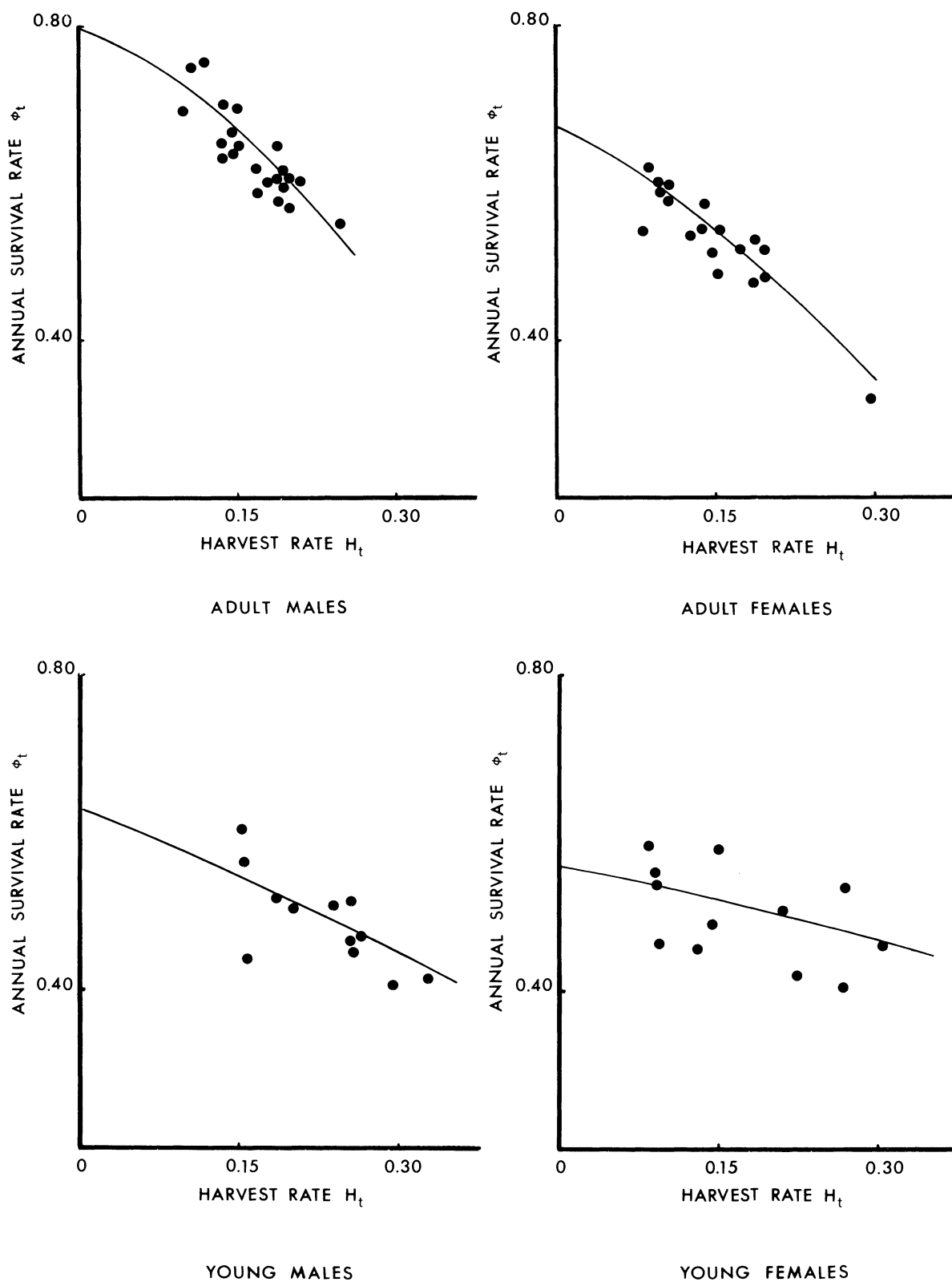


FIG. 4. Age- and sex-specific survival functions estimated from banding data. Points on each graph represent time averages of survival and harvest rates for various geographic areas in North America.

where: ϕ_t = survival rate in year t ,
 a and b are constants for a specific age
 and sex class; vectors of dimension 4.

This relationship suggests that the average survival rate in unexploited populations (i.e., $H_t = 0$) will fluctuate around the value $(1 - a)$.

Estimates of the parameters a and b were made for each age and sex class using a nonlinear least squares algorithm (Dixon 1970) and are summarized below and in Fig. 4:

$$\text{Adults } \phi_t^a = 1 - 0.37 \exp 2.78 H_t \quad (\text{average of } \delta \delta \text{ and } \varnothing \varnothing) \quad (7)$$

$$\text{Young } \phi_t^y = 1 - 0.49 \exp 0.90 H_t \quad (\text{average of } \delta \delta \text{ and } \varnothing \varnothing) \quad (8)$$

Age-sex class	t-value (b)	Correlation coefficient	Coefficient of determination	Degrees of freedom
Adult $\delta \delta$	6.8**	0.85**	0.73	20
Adult $\varnothing \varnothing$	9.3**	0.90**	0.80	16
Young $\delta \delta$	3.7**	0.77**	0.58	11
Young $\varnothing \varnothing$	1.4	0.46	0.21	11

The models for adults seem quite adequate and seem to indicate a significant decrease in annual survival as exploitation rates increase. In general, adult males survive at a higher average rate than adult females, but sustain a substantially higher exploitation rate. Adult Mallards generally survive better than their young. In contrast to adult males, young females appear to sustain a very substantial nonhunting mortality and may be less affected by exploitation.

The survival functions, which were estimated from banding data, involve several limitations. The harvest rate, H_t , derived from banding data, was taken as an estimate of D_t/F_t . The sampling errors associated with the estimates of ϕ_t and H_t are inversely correlated and, at least partially, account for the relationships we observe (Fig. 4). For this reason an alternative hypothesis of the effect of exploitation rate on annual survival was developed and is examined in a following section.

Optimal exploitation strategies

The mathematical model developed in the previous section was used to derive optimal strategies using dynamic programming and to provide a basis for hypothesis-testing. The term strategy is used here in reference to stochastic situations; whereas the term policy refers to deterministic processes (Kaufman 1967:104).

The size of the breeding population in year $t + 1$ was expressed as a function of (1) the size of the breeding population in year t , N_t , (2) the state of the environment (ponds on the central breeding

grounds) in year t , P_t , and (3) the level of exploitation in year t , D_t .

Here we will define N_t and P_t as state variables as they describe the state of the population and the environment in a given year. The level of exploitation in a given year is a variable under man's control and is the result of a decision each year, D_t . With this as background, a central question can be posed. What sequence of decisions D_t , $t = 1, 2, 3, \dots, T$, concerning the level of exploitation will allow the expected sustained yield to be a maximum? This is a question of decision making or strategy formulation in the face of uncertainty.

Before going further, it may be appropriate to define the desirable properties of an optimal exploitation strategy. An ideal strategy would

- 1) be globally optimal with respect to the objective of maximum sustained yield;
- 2) realistically reflect the uncertainty with respect to the stochastic and serially correlated nature of the environment;
- 3) allow for frequent differences in the observed size of the population and the state of the environment in year $t + 1$ compared to what was expected (predicted) in year $t + 1$;³
- 4) allow optimal decisions to be based on the observed state of the system in year t , regardless of what was expected; i.e.,³

$$D_t^o = f(N_t, P_t);$$

- 5) be ergodic in the sense that it would be independent of the time period considered, i.e.,

$$D_t^o = D^o = f(N, P); \text{ and}$$

- 6) be able to deal realistically with constraints, e.g., the undesirability of closing the resource to exploitation for, say, n years.

Dynamic programming can be viewed as a method for solving decision models with the following structure:

³ Points 3 and 4 are closely related and are made more clear by the following example: Consider a florist who expects to sell 200 potted plants next month (June). He, therefore, orders 200 plants to arrive before 1 June. In fact, he sells but 30 plants during June (far from the expected value). If he still expects to sell 200 plants the following month (July), he would be foolish to order 200 more plants to arrive before 1 July. The point is the florist should be able to observe the state of his inventory each month and base his decision on the number of plants to order on the actual number of plants he has not the expected number. This is a key point and an essential aspect of sequential or time-dependent stochastic decision processes.

- 1) The decision variables and associated constraints are grouped according to stages, and the stages are considered sequentially.
- 2) Relevant information concerning the state of the system is contained in the state vector.
- 3) The current decision, given the present state of the system, has a stochastically predictable influence on the state of the system at the next stage.
- 4) Optimality of the current decision is judged in terms of its influence on the present stage and all subsequent stages.

The general theory is based on the Markov Property and the Principle of Optimality. The Markov Property defines events at time $t + 1$ to be (stochastically) dependent only on events at time t .⁴ The Principle of Optimality is stated, "An optimal policy has the property that whatever the initial state and initial decision are, the remaining decisions must constitute an optimal policy with regard to the state resulting from the first decision" (Bellman 1957:83). These points are discussed in detail by Howard (1960), Aris (1964), Roberts (1964), Kaufman (1967), Kaufman and Cruon (1967), and other references cited in the Methods section of this paper.

Dynamic programming model. The population dynamics of the Mallard were conceptualized in terms of annual time periods, 15 May to the following 15 May. These annual periods were defined as stages and numbered backwards with $n = 1$ for time T , and $n = L$ for time 1. The subscript n then merely refers to the stage number. The subscripts n and t are made clear by the following:

Time: $1, 2, \dots, t, t + 1, t + 2, \dots, T$
 Stage index: $L, \dots, n + 2, n + 1, n, \dots, 2, 1$.

The state variables, N_n and P_n , are related by the following stage transformation equations (from Eq. 1 through 8):

State variable 1

$$N_{n+1} = N_n [1 - 0.27 \exp 2.08(D_n/F_n)] + [1 - 0.40 \exp 0.67(D_n/F_n)] \quad (9)$$

State variable 2

$$P_{n+1} = -2.76 + 0.39 P_n + 0.233 R_n \quad (10)$$

where: $Y_n = [1/(12.48 P_n^{0.851}) + 0.519/N_n]^{-1}$
 $F_n = 0.92 N_n + Y_n$

⁴ Howard's (1960) example is particularly descriptive of the Markov Property. Consider a frog jumping from lily pad to lily pad. The frog's jump to the next lily pad is dependent on the lily pad he is presently sitting on (and the angle and length of the jump), not on his previous whereabouts.

R_n = independent normal variable (16.46, 4.41).

For convenience, denote \mathbf{X}_n as a 2-dimensional state vector containing N_n and P_n . Also, define W as a vector-valued function which transforms the state vector over time, i.e., $\mathbf{X}_{n+1} = W(\mathbf{X}_n)$.

The objective of maximum sustained yield must be quantified if we expect to study decision strategies with this as an objective. First, the return at stage n , r_n , is simply the number of animals harvested at stage n ; $r_n = D_n$. In addition, D_n is a function of \mathbf{X}_n , and r_n is known only probabilistically. Therefore, we define a function for the expected return resulting from a decision made in stage n ,

$$\bar{r}_n = \sum_{k_n} p_n(k_n) \cdot r_n(\mathbf{X}_n, D_n, k_n). \quad (11)$$

The last term on the right specifies that the return (number of animals harvested at stage n) resulting from a particular decision in stage n is a function of the state of the system \mathbf{X}_n , the decision D_n , and the random variable k_n . The expected return \bar{r}_n is determined by merely weighting each return by its frequency of occurrence, $p_n(k_n)$, the probability distribution of the random variable k_n . Luce and Raiffa (1957) and Chernoff and Moses (1959) provide a rigorous justification for this procedure. The random variable k_n represents the fact that the specific result of a particular decision is known only probabilistically. A symmetric density was assumed for k_n using $D_n(\mathbf{X}_n)$ as the mean, with probability 0.6. Values 10% above and below the mean were allowed, each with probability 0.2.

Finally, the optimal expected return (as a function of the state vector) is defined as the objective of maximum yield,

$$\bar{f}_n(\mathbf{X}_n) = \max \bar{r}_n \text{ (over all } D_n < 2.0 \text{ million in increments of 0.02 million).} \quad (12)$$

Nemhauser (1967:25) points out that in ordinary optimization problems, the optimal return is usually a number. However, here the optimal expected return, $\bar{f}_n(\mathbf{X}_n)$, is a function—a sequence of numbers, one for each value of the state variables, \mathbf{X}_n . The determination of $\bar{f}_n(\mathbf{X}_n)$ is a nonlinear optimization problem for each value of the state variables for each stage, $n = 1, 2, \dots, L$. Stochastic components enter the dynamic programming model at each stage in two distinct places, the return function and the state variable for environmental conditions. The expectation for the return function was computed using Eq. 11. The state variable for environmental conditions is a function of annual precipitation, modeled as an independent, normally distributed random variable. It was not necessary to compute expectations

of the function in this case because the stage transformation is a linear function, i.e.,

$$\begin{aligned} E(P_{n+1}) &= E[a + bP_n + cR_n] \\ &= a + bP_n + cE(R_n) \\ &= a + bP_n + c\bar{R}_n. \end{aligned}$$

A multistage system consists of a series of stages joined so that the output of one stage becomes the input for the next stage. Nemhauser (1967:155) provides the fundamental recursion equations for the optimal expected return,

$$\bar{f}_n(\mathbf{X}_n) = \max_{D_n} \sum_{k_n} p_n(k_n) \cdot Q_n(\mathbf{X}_n, D_n, k_n) \quad 1 \leq n \leq L, \quad (13)$$

where:

$$\begin{aligned} Q_n(\mathbf{X}_n, D_n, k_n) &= \bar{r}_n(\mathbf{X}_n, D_n, k_n) \\ &\quad + \bar{f}_{n-1}[W(\mathbf{X}_n, D_n, k_n)] \quad 2 < n < L \end{aligned}$$

$$Q_1(\mathbf{X}_1, D_1, k_1) = r_1(\mathbf{X}_1, D_1, k_1).$$

Dynamic programming provides an algorithm for finding $\bar{f}_L(\mathbf{X}_L)$ and the associated optimal decision sequence $D_L^o, D_{L-1}^o, \dots, D_n^o, \dots, D_1^o$ (or, equivalently, $D_1^o, D_2^o, \dots, D_t^o, \dots, D_T^o$). The extension of an L -stage system to an infinite one is important in the concept of maximum sustained exploitation. It would be inappropriate to consider exploitation strategies that are dependent on the time period considered. Rather, interest lies in exploitation strategies that are independent of L , the length of time considered.

In general, the optimal return function $\bar{f}_n(\mathbf{X}_n)$ depends on the stage n and the state \mathbf{X} of the system (as the notation implies). When there are a large number of stages remaining and there is regularity in the stage returns and the stage transformation, we might expect that the optimal decisions become independent of the stage index. This is precisely true only for ergodic processes. Specifically, we set L to be large enough so that the solutions become independent of stage number and optimal decision functions at each stage become stable. This allows optimal decisions to be a function of only the state vector, $D^o(\mathbf{X})$. Maximum sustained yield is measured as $\bar{f}_L(\mathbf{X}_L)$, where L is sufficiently large. It is the expected, long-term return resulting from the sequence of optimal decisions, which are functions of the state of the system. This is the most simple maximum sustained yield objective.

The optimal decision strategy resulting from the dynamic programming formalism is itself stochastic, except for the first optimal decision, $D_1^o(\mathbf{X}_1)$ (Nemhauser 1967:156). The remaining optimal decisions cannot be expressed deterministically until the sto-

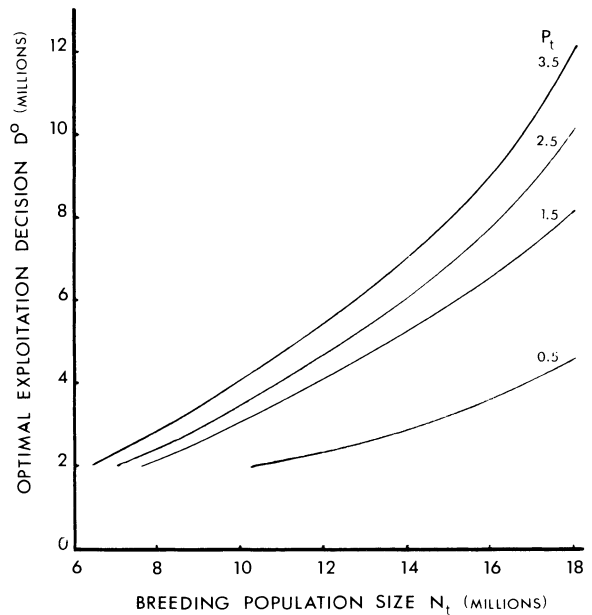


FIG. 5. Optimal exploitation decisions as a function of the state variables: the size of the breeding population, N_t ; and the number of ponds on the central breeding grounds, P_t .

chastic elements that precede them have been revealed. At each stage an optimal decision can be made only after observing the state variables. This is merely a property of stochastic processes and not a deficiency of dynamic programming.

Strategy formulation. Using the population model and the optimization method of dynamic programming we can examine the first question proposed in this research: Can optimal exploitation strategies be derived for animal populations in stochastic,

TABLE 1. The optimal decision matrix, $D^o(\mathbf{X})$, under the hypothesis that exploitation is largely an additive force of mortality. (All figures in millions)

	Ponds (P_t)						
	0.5	1.0	1.5	2.0	2.5	3.0	3.5
Breeding population size (N_t)							
6	2.0	2.0	2.0	2.0	2.0	2.0	2.0
7	2.0	2.0	2.0	2.0	2.1	2.2	2.3
8	2.0	2.1	2.2	2.3	2.4	2.6	2.8
9	2.0	2.4	2.6	2.8	2.9	3.2	3.4
10	2.0	2.7	3.1	3.3	3.5	3.8	4.1
11	2.2	3.1	3.6	3.9	4.1	4.5	4.8
12	2.4	3.4	4.1	4.4	4.7	5.1	5.5
13	2.6	3.9	4.7	5.1	5.4	5.6	6.2
14	2.9	4.2	5.3	5.8	6.1	6.6	7.0
15	3.2	4.8	5.9	6.5	7.0	7.5	8.0
16	3.6	5.3	6.6	7.3	7.8	8.5	9.0
17	4.0	5.7	7.3	8.0	8.8	9.7	10.4
18	4.5	6.5	8.1	9.1	10.0	10.8	11.9

serially correlated environments? Ergodic optimal exploitation strategies exist for Mallards (Fig. 5 and Table 1). The optimal decision functions stabilized at $L = 10$ for all values of the state vector. I estimated the average annual expected yield, $\bar{f}_L(\mathbf{X}_L)/L$, to be 6.2 million. The relationship between the optimal exploitation decision and breeding population size is convex (Fig. 5) while the relationship with the environmental variable is nearly linear or slightly concave.

The exploitation strategy is easy to employ: assume that in year t we observe 12.0 million breeding Mallards and 2.5 million ponds on the breeding grounds. From the optimal decision matrix (Table 1) the optimal level of exploitation is 4.7 million. Under this decision, we expect 13.8 million breeding Mallards and 2.0 million ponds in year $t + 1$ (from Eq. 9 and 10). In year $t + 1$ we must again observe the state of the breeding population and the environment. In general, our expectations or predictions will not materialize exactly. There will be differences between what we expected compared to what was actually observed the following year. For example, we might actually observe 10.0 million breeding Mallards and 1.5 million ponds, rather than the 13.8 and 2.0 million we expected. The optimal exploitation strategy, developed from the theory of dynamic programming, allows for these differences. From the Principle of Optimality, we see that the remaining decisions constitute an optimal strategy with regard to the observed state variables resulting from the previous decision. This indicates that our optimal exploitation level in year $t + 1$ should be based on the actual size of the breeding population and the actual number of ponds in year $t + 1$ (11.0 and 1.5 million, respectively) and not on what was expected. Therefore, we enter the decision matrix (Table 1) using $N_t = 11.0$ and $P_t = 1.5$ and find that the optimal decision is 3.6 million for year $t + 1$.

Optimal exploitation level can also be based on the estimated size of the fall population. The relationship between the size of the fall population and the optimal decision is convex (Fig. 6). The relationship between these two variables is nearly the same regardless of the environmental conditions. Although this appears to be an alternative, it is merely another way to represent the fact that the optimal decision is a function of the state variables N_t and P_t , since

$$\begin{aligned} F_t &= f(N_t, Y_t) \\ \text{and } Y_t &= f'(N_t, P_t) \\ \text{then } F_t &= f''(N_t, P_t), \text{ the state variables.} \end{aligned}$$

Optimal rate of exploitation is higher when the

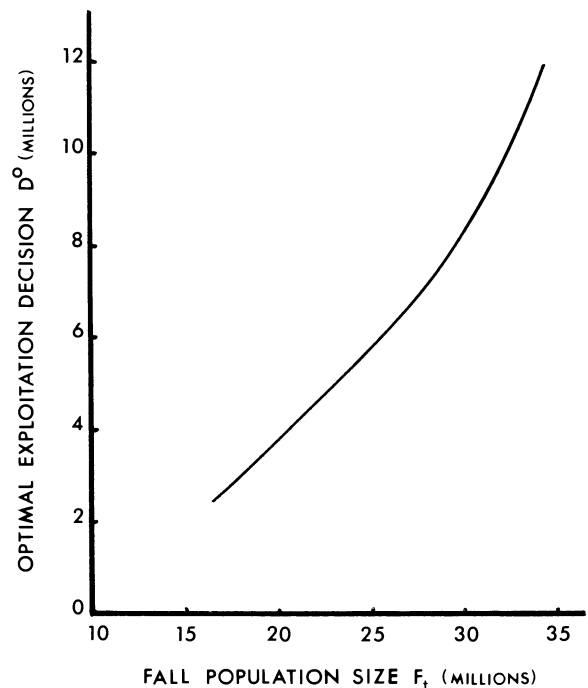


FIG. 6. The optimal exploitation decision as a function of the size of the fall population size.

size of the fall population is large. The expected size of the breeding population in year $t + 1$, given that the optimal exploitation strategy was followed in year t , is slightly larger if environmental conditions in year t were good than if they were average or poor. Conversely, if environmental conditions in year t are poor, the optimal strategy will tend to return relatively fewer breeding birds to the breeding grounds in year $t + 1$. This tendency results from the serially correlated environment and is an attempt to avoid overcrowding and suboptimal production rates because production is partially density-dependent.

Hypothesis testing

Effect of compensatory mortality on optimal exploitation strategies. Below a certain level of exploitation, Mallard populations may be resilient, with survival rates increasing to compensate for the individuals removed. The annual survival rate of young and adult Mallards is hypothesized to be unaffected by exploitation up to a point: an exploitation rate of 0.25 in the case studied. The implication is that the population is limited by factors other than hunting. Below a certain level, exploitation does not decrease the annual survival rate, i.e., the forces of hunting and natural mortality are compensatory. Beyond this level, exploitation has a marked effect on annual survival. Under a hypothesis of com-

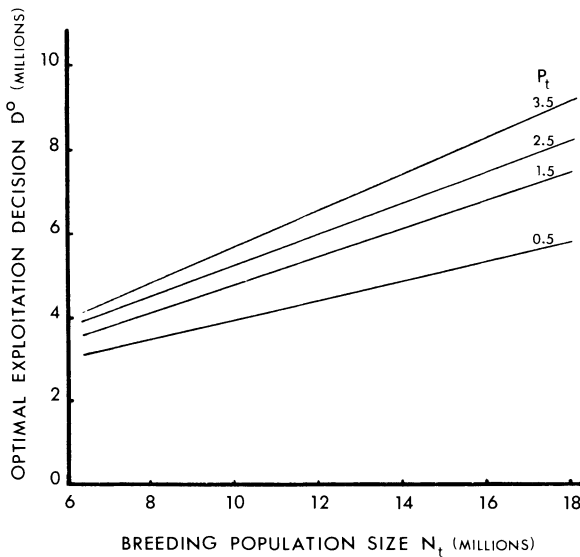


FIG. 7. The optimal exploitation decision as a function of the size of the breeding population under an hypothesis of compensatory mortality.

compensatory mortality, natural mortality, V_t , is related to hunting mortality, H_t , as

$$V_t = a - bH_t \quad \text{for } H_t \text{ less than a critical level; } 0.25 \text{ in the example}$$

$a = 0.57$ (adults) or 0.50 (young) in the example, and

$b = 1.0$ if the two forces of mortality are perfectly compensatory.

I shall not argue whether Mallard populations respond to exploitation in this manner; I merely want to examine the effect of such an hypothesis on exploitation strategies.

The population model employed in the previous section (Eq. 9 and 10) was modified to incorporate a compensatory mortality process. Survival rates for adults and young were taken to be 0.57 and 0.50, respectively, for exploitation rates up to 0.25. Beyond an exploitation rate of 0.25 annual survival rates were taken to decrease as a result of exploitation pressure:

$$\begin{aligned} \phi_t^a &= 0.57 - 1.2(H_t - 0.25) \\ \phi_t^y &= 0.50 - 1.0(H_t - 0.25) \end{aligned} \quad \text{for } H_t > 0.25. \quad (14)$$

Other aspects of the model were unchanged. New optimal exploitation strategies were derived using dynamic programming and several findings contrast with the earlier results.

The average annual expected yield, $\bar{f}_L(\mathbf{X}_L)/L$, was estimated to be 6.46 million. The specific values of the optimal decision function are given in Table 2. The relationship between the optimal exploitation decision and the breeding population size is approxi-

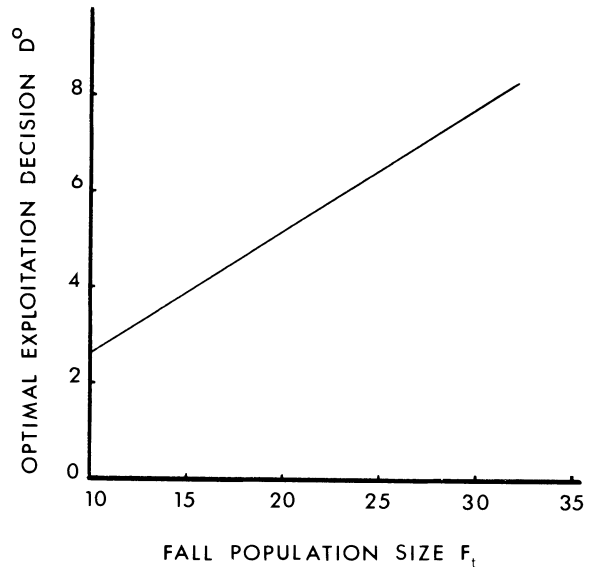


FIG. 8. The optimal exploitation decision as a function of the size of the fall population under an hypothesis of compensatory mortality.

mately linear (Fig. 7) as is the relationship with the environmental conditions. The optimal exploitation decision is approximately linearly related to the size of the fall population (Fig. 8), and the size of the breeding population in year $t + 1$ is linearly related to the optimal exploitation decision in year t .

The optimal level of exploitation in a given year is that which makes the exploitation rate equal to 0.25; therefore, the annual survival rates for adults and young equal to 0.57 and 0.50, respectively. In other words, the optimal strategy is to exploit the population to the point where hunting and non-

TABLE 2. The optimal decision matrix, $D^\circ(\mathbf{X})$, under an hypothesis of compensatory mortality. (All figures in millions)

	Ponds (P_t)						
	0.5	1.0	1.5	2.0	2.5	3.0	3.5
Breeding population size (N_t)							
6	3.0	3.4	3.6	3.7	3.8	3.9	4.0
7	3.2	3.5	3.8	3.9	4.0	4.1	4.2
8	3.4	3.8	4.1	4.3	4.5	4.7	4.8
9	3.7	4.0	4.2	4.5	4.8	5.1	5.3
10	3.9	4.4	4.8	5.0	5.2	5.4	5.6
11	4.2	4.7	5.1	5.4	5.6	5.9	6.1
12	4.4	4.9	5.4	5.7	6.0	6.3	6.5
13	4.6	5.3	5.9	6.3	6.4	6.7	7.0
14	4.8	5.5	6.1	6.4	6.7	7.1	7.4
15	5.1	5.8	6.4	6.8	7.1	7.5	7.8
16	5.3	6.1	6.8	7.2	7.5	8.0	8.3
17	5.6	6.4	7.2	7.5	7.8	8.3	8.7
18	5.8	6.7	7.5	7.9	8.2	8.7	9.2

hunting mortality are not compensatory. The optimal harvest is then the point at which hunting becomes important as an additional component of mortality, 0.25 in the example.

Relative importance of the state variables. Many animal populations are under the influence of both intrinsic population forces and physical components in the environment. What is the relative importance of these variables on the optimal level of exploitation? To answer this question for Mallards, we can estimate the partial differentials of the optimal decision function with respect to the size of the breeding population and the number of ponds; $\frac{\Delta D^o}{\Delta N}\bigg|_{\bar{P}}$ and $\frac{\Delta D^o}{\Delta P}\bigg|_{\bar{N}}$. The notation $\frac{\Delta D^o}{\Delta N}\bigg|_{\bar{P}}$ represents the change in the optimal exploitation decision, ΔD^o , as the result of a change in the size of the breeding population, ΔN ; evaluated at the average number of ponds, \bar{P} . The differentials ΔN and ΔP were standardized in terms of their respective means and standard deviations because they are measured on different scales. Therefore,

$$\left. \begin{array}{l} \Delta N = 2 \text{ SD} = 6.4 \\ \Delta P = 2 \text{ SD} = 1.4 \end{array} \right\} \text{one standard unit.}$$

Under the assumption that mortality as a result of exploitation is additive to other forms of mortality, $\frac{\Delta D^o}{\Delta N}\bigg|_{\bar{P}}$ and $\frac{\Delta D^o}{\Delta P}\bigg|_{\bar{N}}$ equal approximately 3.2 and 1.1, respectively. I conclude that a (standardized) change in the size of the breeding population is more important in the optimal exploitation decision than is a (standardized) change in the environmental conditions.

Under the assumption that mortality forces are compensatory, the partial differentials $\frac{\Delta D^o}{\Delta N}\bigg|_{\bar{P}}$ and $\frac{\Delta D^o}{\Delta P}\bigg|_{\bar{N}}$ equal 2.2 and 1.1, respectively. Again, it appears that breeding population size is the more important variable in the exploitation process. Environmental conditions on the breeding grounds are important in the exploitation process but probably not as important as the size of the breeding population.

It is also of interest to examine the relationship of the state variables to the number of young produced in year t . We have already established that the size of the breeding population and the environmental conditions are highly significant in the production of young Mallards. Now we will examine the relative importance of these two variables. We will study the effect of a change in one of the state variables on the number of young produced while holding the other state variable at its mean value. Partial differentials of the number of young were computed with respect to the size of the breeding

population and the number of ponds. The differentials ΔN and ΔP were standardized as before. These statistics indicated that the two state variables were approximately equal in relative importance in the production of young. Specifically, $\frac{\Delta Y}{\Delta N}\bigg|_{\bar{P}} = 3.1$ and $\frac{\Delta Y}{\Delta P}\bigg|_{\bar{N}} = 3.6$. This is an interesting result and indicates the importance of environmental variables to the study of Mallard population dynamics.

DISCUSSION

An essential point in population ecology is how a population responds to predation or exploitation (Wagner 1969, Huffaker 1970). Mech (1966:167), studying moose and wolves on Isle Royale in Lake Superior, noted, "The important question is whether wolves merely substitute for other factors or whether they kill more animals than other factors would."

The alternatives are illustrated by two extremes: mortality because of exploitation (or an additional predator) may be largely additive to other mortality forces, or compensatory, at least to some threshold level. This question is unresolved for almost all exploited populations, including the Mallard.

Exploitation of adult deer and marine mammals may be primarily an additive form of mortality (Eberhardt 1960, Gulland 1970). Fisheries biology is based on the concept that total mortality increases with increased fishing pressure (Gulland 1971). Exploitation of waterfowl populations may also represent an additive form of mortality (Hickey 1955, Moisan et al. 1967, Geis et al. 1971), and Geis (1963) presents several reasons why this may be the case in migratory waterfowl as opposed to non-migratory species.

In contrast, pheasants, quail, and rabbits may be examples where exploitation mortality is largely compensatory with other forms of mortality (Errington 1935, 1945, 1956, Wagner 1969). Predators (human and nonhuman) merely remove surplus animals, ones that would succumb even in the absence of natural enemies or exploitation. Death of one individual improves another's chance of survival. If a prey population is resource-limited, e.g., food, predators may merely remove animals that would otherwise die (Lack 1954:157). Indeed, by removing part of the prey population in fall and early winter, predators (or exploitation) might reduce the extent of competition for resources of the prey and, therefore increase survival of the prey.

Laboratory studies of lower forms of animals suggest that mortality as the result of exploitation (usually simple removal) is highly compensatory, both birth and death rates being "resilient" (Nicholson 1954, Slobodkin and Richman 1956, Silliman and Gutsell 1958). In general, the evidence for

compensatory forces of mortality seems more convincing and is perhaps the more general alternative. The research reported here on the Mallard did not attempt to resolve this question. The analysis of banding data on the relationship between annual survival and harvest rate suggest an inverse function (Fig. 4). A hypothesis of compensatory mortality was formulated because: (1) sampling errors of estimates of survival and exploitation rates are inversely correlated, (2) results of several carefully controlled laboratory experiments on other animals indicated compensatory forces of mortality, and (3) generally inconclusive literature on the specific effect of exploitation on survival rates.

Major results

The existence of optimal exploitation strategies was shown under rather general conditions. This appears to be an important result. Exploitation strategies were based on seemingly unrestrictive and general assumptions regarding the dynamics of the population and the environment, and their interaction. Birth rates were shown to be dependent on population density and environmental conditions. Death rates were functions of exploitation rates under two general hypotheses, parameters of the models were usually both age- and sex-specific, and the environment was described as stochastic and serially correlated (Markovian). Optimal exploitation strategies for more simple (or less well-studied) population processes may be examined as special cases of the general approach suggested here. Optimal exploitation strategies were found to exist and to be easy to understand and employ. Direct feedback control is an integral component of the decision-making process.

The relationship between the optimal exploitation strategy and the breeding population size was convex under the hypothesis that hunting is an additive form of mortality and essentially linear under the hypothesis that hunting and nonhunting mortality are compensatory. When the breeding population is small, the optimal level of exploitation is higher, if exploitation is a compensatory form of mortality rather than an additive form of mortality. Conversely, if the breeding population is large, the optimal level of exploitation is higher if exploitation is an additive force of mortality rather than compensatory. The expected yield was similar under the two hypotheses.

Exploitation of animal populations in stochastic environments can seemingly be based on two concepts: (1) an average "optimal" level of exploitation, D^* , used each year; or (2) an optimal strategy based on the observed state of the population and environment (\mathbf{X}_t) each year. Both possibilities are examined.

The use of an average value each year has two disadvantages. First, it is inefficient and therefore hardly optimal as a strategy. In most years, the population would be either underharvested or overharvested. Second, a positive probability exists that a sequence of poor years could seriously jeopardize the population if it continued to be exploited at the average level. Watt (1968:406) noted that some strategies (Watt termed them policies) are optimal if used only once or a small number of times but may be grossly suboptimal if used repeatedly (Swartzman and Van Dyne 1972).

Optimal strategies depend on the situation encountered, but the situation encountered depends on the previous exploitation decision (Watt 1968). For these reasons, it seems necessary to base exploitation decisions in year t on the observed population and the environment in year t . This is clearly the result indicated from the solution of the dynamic programming model.

We can speculate on how the results of this study add to the principles summarized in the Introduction of this paper. One new principle is suggested: the optimal level of exploitation in year t must be based on the observed state variables in year t unless the dynamics of the population, the state of the environment, and the result of the exploitation decisions are completely deterministic.

Relative importance of extrinsic and intrinsic factors has been the subject of much ecological research (Watson 1969). In this study, these factors were examined in relation to the number of young Mallards produced. This was convenient because the state vector contained extrinsic and intrinsic variables. Mallard production appears to be regulated by both density-dependent and environmental components. Analysis indicated that the two components were nearly equal in importance.

In contrast, the size of the breeding population is more important in the exploitation process. A (standardized) change in the size of the breeding population is more important in the optimal exploitation decision than is a (standardized) change in the environmental conditions. Although population growth is primarily influenced by environmental conditions on the central breeding grounds, harvest is more dependent on the standing crop, the size of the breeding population.

If the population was not exploited, its size would probably fluctuate more widely ($\sigma^2[N_t]$ would be larger) than if the population was optimally exploited. Optimal exploitation tends to keep the population from very high or very low levels.

The functional form of the optimal exploitation strategy derived in this study was robust with respect to small changes in production rate. Because specific

values in the optimal decision sequence depend on the production rate, the form of the decision sequence appears to change little. In general, however, I suggest that not only the optimal level of exploitation, but also the form of the exploitation strategy is partially dependent on the production rate of the animal. The relative importance of the breeding population size in the exploitation process may decrease as fecundity increases.

Population model

Mathematical models have been used frequently in ecology since the beginning of the century. Models have been used in ecology primarily for descriptive or predictive purposes (Jaquette 1970). Until the second half of the century, models in ecology were deterministic; recently, stochastic models have become increasingly more common. Only in the last two or three decades have population models directly incorporated environmental components. Control models, particularly stochastic control models such as those examined in this study, are new in ecology. Formulation of the exploitation problem is extremely general. Concepts of state vectors and stage transformation functions are completely general. Populations may be modeled deterministically or stochastically. The dynamic programming formulation is the most general available for optimization problems and is particularly attractive for exploitation studies.

The specific models employed in this research are relatively general and can be expected to be useful, with different parameter estimates, for several other species of ducks in North America. With some modification or simplification, the model might be adequate for studying other exploited bird or small mammal populations. This is possible because birth and death rates are general functions of population and environmental factors. A very general description of the environment and its effect on the population is possible.

Further generality can easily be allowed in the dynamic programming formalism. Additional age classes can be studied by increasing the number of elements in the state vector. More important is the possibility of including additional information on important environmental variables. These variables would also appear as state variables and their dynamics must be defined by stage transformation equations. No restrictions are imposed on the type of model used to describe (or hypothesize) the way in which variables change from one time period to the next. The objective or return function can also be generalized. For example, the probability of the population decreasing below a certain level could be incorporated into the objective of maximum sus-

tained yield to allow a more conservative strategy. For example, the simple return function

$$r_n = D_n - \alpha[\text{prob}(N_n < a)] \quad \text{where } \alpha > 0$$

represents a maximum sustained yield objective whereby strategies are more conservative as α increases. This paper has treated the case where $c = 0$, i.e., no penalty associated with the risk of causing the population to decrease below some level, a . Extra-biological factors can be incorporated into the objective function, as above, or through constraints imposed on the range of D_n . For example, in this study, $D_n < 2.0$ million birds were excluded due partially to political realities.

Limitations. The model developed for these investigations is merely an approximate description of the population dynamics of the Mallard. There were some difficulties in quantifying the problem: determining which variables were most relevant, hypothesizing relationships among variables, and estimating parameters. Although the quantitative approach has its limitations, there are also advantages, e.g., subjective judgement is reduced and the powers of logical analysis are extended.

The computational effort required to obtain numerical solutions to the dynamic programming model was substantial (90 min on an IBM 360/65®). If the model were to become more complex, particularly if additional state variables were formulated, computational requirements would increase very rapidly. Two changes in the computer algorithm would reduce the computational aspect considerably: (1) a Fibonacci search procedure to find $D^o(\mathbf{X}_n)$, and (2) storage of numerical values of the transformation function $\mathbf{X}_{n+1} = W(\mathbf{X}_n)$ rather than computing them repeatedly at each stage. These changes might reduce the computing time by 60%–80% and would be imperative if additional state variables were to be added.

The most important limitation of the research may be that I was unable to consider other exploited waterfowl species directly. Several congeners have life histories, ranges, and general ecology similar to those of the Mallard. These species, as well as species of waterfowl in other genera, are also exploited by man. The feasibility of developing realistic, species-specific exploitation strategies recognizing the complex and unknown interactions among species seems remote.

Practical use. If optimal exploitation strategies were to be employed in the practical management of the sport hunting of Mallard ducks, it would be appropriate to reexamine the model in its entirety at perhaps 4–6 yr intervals. This would allow reassessment of the assumptions and the consideration of changing conditions. Improved parameter esti-

mates would be possible because additional data would be available for analysis. The addition of new variables and relationships could be incorporated if necessary. Of course, it would be necessary to conclusively resolve whether hunting mortality is partially additive or compensatory to some point.

ACKNOWLEDGMENTS

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