A MODEL FOR MANAGEMENT PREDICTIONS OF TERRITORIAL BIRD POPULATIONS[1]

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ABSTRACT

A model was developed to compare alternative management schemes that can be employed to regulate the population level of birds having a territorial or resource limited breeding organization. The alternatives of habitat modification, removal of birds, and sterilization were compared. The model is based on the dynamics of the female segment of the population, but provision is made in the case of sterilization for predicting the effects of treatment either of females only or of both sexes.

Territoriality has received considerable attention as a possible population regulatory mechanism in certain species of animals, particularly birds (Nice, 1944; Tinbergen, 1957; Wynn-Edwards, 1962, and Brown, 1969a). A territorial limitation on the number of males breeding would have significant genetic consequences, but would not influence the reproductive capacity of the population as long as a sufficient number of males are available to fertilize the females in the population. In monogamous species, territoriality of males may have a limiting effect on the number of females which reproduce, but in polygynous species such territoriality will not limit reproduction (Brown, 1969a, p. 304), and territorial behavior of the females or environmental limitation on nest sites is necessary for this mechanism to operate.

The Population Growth Equations. At population densities below the level of complete utilization of territorial space or nest sites the equation

$$N_t = \lambda N_{t-1} \tag{1}$$

where N_t = number of animals at time t, and λ = finite rate of increase, can be subdivided into the adult survival and the recruitment.

Let q = the probability of dying of breeding females ($0<q<1$) and

b = the recruitment (the number of one year old females alive per breeding female the previous season)

so

$$\lambda = 1 - q + b. \tag{1a}$$

Equation (1) can be written as

$$N_t = (1-q+b)N_{t-1}. \tag{2}$$

For seasonally breeding vertebrates which do not breed in their natal season, it is convenient to express the time interval in years and consider recruitment to result from the previous year's reproduction. Because the recruitment is expressed as the number of one year old females alive per breeding female the previous season, this procedure eliminates the need to estimate juvenile mortality rates.

When the population density is such that all the available female territories or nest sites are used, the equation must reflect the recruitment per territory or per breeding female and the survival of the nonbreeding females.

Let q' = the probability of dying of nonbreeding females, and

M = the maximum number of females that can breed under the existing environmental or behavioral limitations.

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When $N_t > M$, the growth of the population can be described by

$$N_t = (1-q+b)M + (1-q')(N_{t-1} - M). \tag{3}$$

Let us define the equilibrium level as the number of birds that are present when the population stabilizes. We can calculate the equilibrium level of the females in the population from equation (3). In any year y after equilibrium

$$N_y - N_{y-1} = M(b-q) - q'(N_{y-1} - M) = 0, \tag{3a}$$

so

$$N_y = M + \frac{(b-q)M}{q'}. \tag{4}$$

If $q = q'$, equation (4) becomes

$$N_y = \frac{bM}{q} \tag{5}$$

The assumptions implicit in this model are:

1. Behavioral or environmental factors limit the number of females in the population which reproduce.
2. Animals do not breed in their natal season.
3. All animals are capable of breeding when one year old.
4. Other density dependent factors are neglibile, however, animals excluded from breeding may be subject to a higher (or lower) mortality rate than breeding animals.
5. Potential fecundity is independent of age after maturity.
6. There is no immigration into or emigration from the population.

The growth curve for a species with a breeding and nonbreeding annual survival probability of 50% and an annual recruitment of 0.8 females per breeding female is illustrated in figure 1. From this basic model, equations 2 and 3, predictions can be made for the effects of a management program on a territorial or nest-site-limited species.

Habitat Modification. The response of a population to habitat destruction or construction can readily be predicted from equations 2 and 3. Figure 2 illustrates the population change of an equilibrium population in response to partial destruction of the previously available habitat and to construction of new habitat so that the number of available nest sites or territories is one-half or twice the previously available habitat. These predictions are obtained by substituting the new value of M into the equations and solving the equations for subsequent years until equilibrium is again attained. It can readily be seen that the equilibrium level changes in direct proportion to the amount of suitable habitat available.

Removal of Animals. A constant removal effort over a period of years will remove approximately the same proportion of animals each year rather than the same number. It will also increase the recruitment per bird in the population if the removal is such that the population does not decline below the level $N_t > M$. A higher proportion of the animals will be breeding, because the number of animals attaining territories or nest sites remains constant. The recruitment per breeding bird will decline only in proportion to the level of removal.

To predict the response to a management program involving the removal of a specified proportion of the population each year the probabilities in equations 2 and 3 can be adjusted to include the mortality due to management efforts.

Let q_m = proportion of animals removed by management scheme, and
q_a = probability of dying including both management and natural mortality.

Since a bird can be removed from the population either by natural mortality or management induced mortality, the adjusted probability of dying for breeding females is

$$q_a = q_m + (1 - q_m)q. \tag{6}$$

This adjustment to the probability of dying is applied to both the breeding and non-breeding segments of the population. If young animals are subject to removal by the management scheme before the breeding season following their natal year, the recruitment per breeding female must also be adjusted.

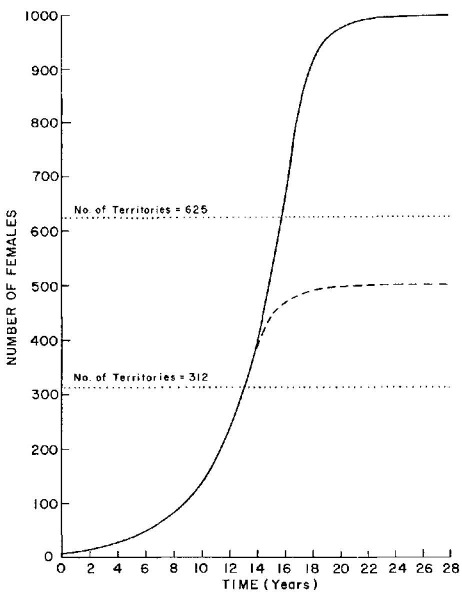

FIGURE 1

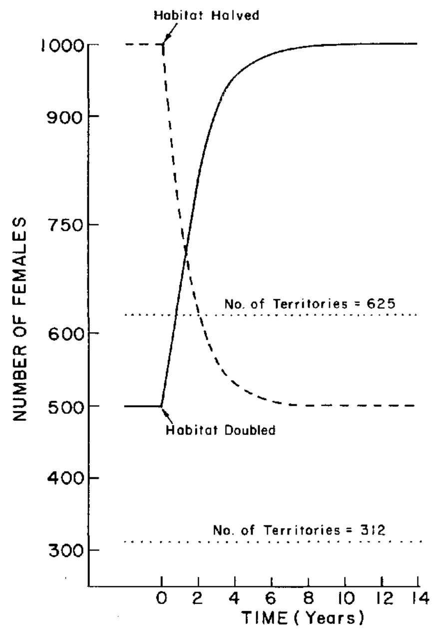

FIGURE 2

FIGURE 1. Population growth curve from equations (2) and (3) with a probability of dying of 0.5 of breeding and non-breeding animals and an annual recruitment of 0.8 females per breeding female.

FIGURE 2. Effect of modification of habitat level on a territorial population with a probability of dying of 0.5 for breeding and non-breeding animals and an annual recruitment rate of 0.8 females per breeding female.

Let b_a = adjusted recruitment rate,

then

$$b_a = b(1 - q_m). \tag{7}$$

A management scheme involving removal will only result in a new equilibrium level if, from equation 4,

$$\frac{b_a - q_a}{q'_a} > 1. \tag{7a}$$

If the above relationship holds, a new equilibrium will be attained at $N_y > M$. If the relationship does not hold, N_t will become $< M$ at some point in the management program and equation 2 will then predict the decline of the population to extinction unless the management scheme is modified. The response of a hypothetical population to a management program involving removal of a constant proportion of animals is illustrated in figure 3.

Temporary Sterilization or Fertility Reduction. If we assume that the treated animals compete normally with non-treated animals, the response of the population to a management program utilizing temporary sterilization of a proportion of the females or reduction in fertility, can be predicted by adjusting the recruitment in equations 2 and 3.

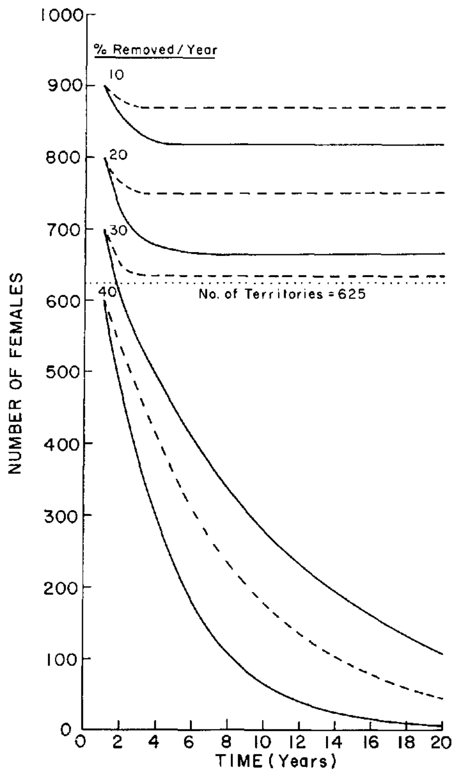

FIGURE 3

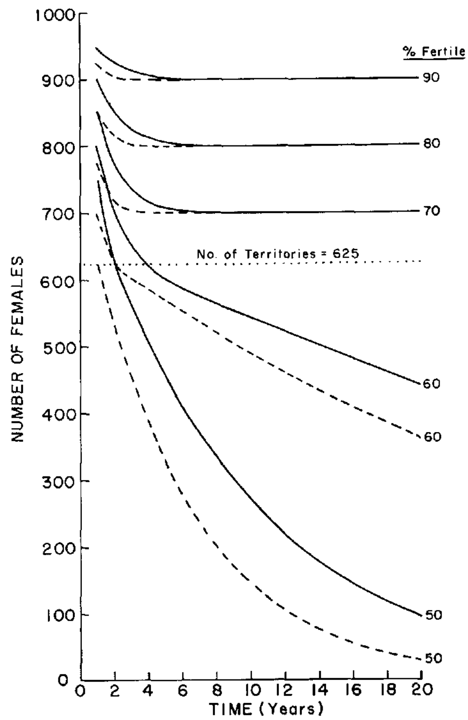

FIGURE 4

FIGURE 3. Effect of removal on a territorial population. Initial probability of dying is 0.5 (solid line) or 0.75 (broken line) and the annual recruitment rate is 0.8 females per breeding females (solid line) or 1.2 females per breeding female (broken line).

FIGURE 4. Effect of temporary fertility reduction on a territorial population. Initial probability of dying is 0.5 (solid line) or 0.75 (broken line) and the annual recruitment rate is 0.8 females per breeding females (solid line) or 1.2 females per breeding female (broken line).

Let f_f = proportion of females fecund or proportional fertility after treatment, and

b_a = adjusted recruitment rate

$$b_a = bf_f.$$

Figure 4 illustrates the predicted response of a hypothetical population to management schemes involving temporary reduction of fertility in a long-term treatment program. The assumption is made that the treated animals behave normally and compete equally with non-treated animals for territories and/or nest sites. A new equilibrium level is predicted by equation 4 when

$$\frac{b_a - q}{q'} > 1.$$

Permanent Steriland-Breeding Segment Only. The response of a population to treatment of the breeding segment so that a proportion of the treated females become permanently sterile is more complex in that the effect of the treatments is cumulative.

Let f = the proportion of females that are fertile after treatment. Subscripts of N indicate years of treatment $(0<f<1)$, then

$$N_1 = (1-q')(N_o - M) + (1+bf-q)M, \tag{8}$$

$$N_t = (1-q')(N_{t-1} - M) + qM \sum_{i=1}^{t-1} (1-bf^i-q)(1-q)^{i-1} + (1+bf^t-q)(1-q)^{t-1}M \quad \text{for } t \geq 2. \tag{9}$$

Since this management scheme is acting through modification of the recruitment, we shall examine the change in recruitment to the population before considering the equilibrium level of the population.

Let A_t = recruitment to the population in year t of treatment, then

$A_1 = bfM,$

$$A_t = \sum_{i=1}^{t-1} bf^iMq(1-q)^{i-1} + bf^tM(1-q)^{t-1}, \text{ for } t \geq 2. \tag{10}$$

Let y be any year after equilibrium is reached as t becomes large then,

$$bf^tM(1-q)^{t-1} \to 0,\ 0<f<1,\ 0<p<1,$$

$$A_y \sim bfMq \sum_{i=0}^{y-2} f^i(1-q)^i \to \frac{bfmq}{1-f+fq}. \tag{11}$$

This expression contains M and is only valid for treatment levels in which $N_y \geq M$. Treatment schemes in which N_t becomes $<M$, if continued, result in the population becoming extinct.

Let C = recruitment per breeding female at N_y after treatment $(N_y > M)$.

$$C = \frac{A_y}{M}$$

$$C \sim \frac{bfq}{1-f+fq}. \tag{12}$$

If $q = q'$, we can estimate the new equilibrium level of the population from equation 5 by substituting C for b.

$$N_y = \frac{CM}{q}. \tag{13}$$

If $q \neq q'$, we can use equation 4.

$$N_y = \frac{M(C-q)}{q'} + M \tag{14}$$

As t becomes large,

$$(1+bf^t-q)(1-q)^{t-1}M \rightarrow 0$$

so from equation 9,

$$N_y \sim (1-q')(N_{y-1}-M)+qM\sum_{i=1}^{y-1}(1-q)^i+qMbf\sum_{i=0}^{y-1}f^i(1-q)^i$$

$$N_y \sim (1-q')(N_{y-1}-M)+M(1-q)+M\left(\frac{bfq}{1-f+fq}\right).$$

Substituting C from equation 12,

$$N_y \sim (1-q+C)M+(1-q')(N_{y-1}-M). \tag{15}$$

Equation 15 is the same as equation 3 except that the initial birth rate, b, has been replaced by the new equilibrium birth rate, C. This provides a check on the manipulations. Equations 13 and 14 can be derived directly from equation 15 by the procedure used to derive equations 4 and 5 from equation 3.

Equation 9 allows us to estimate N_t only when $N_t \geq M$. If N_t becomes less than M, we must consider N_{t-1} as the number of breeding females. If $N_t < M$, there is no excess of non-breeding females. Since we cannot have a negative excess,

$$(N_{t-1}-M)(1-q')=0.$$

The population history when $N_t < M$ consists of treatments when $N_t > M$ and $N_t < M$. Let x = the number of seasons since N_t became $< M$,

$$N_t=(1-q)N_{t-1}+A_t, \tag{16}$$

$$A_t=qM\sum_{i=x}^{t-1}bf^{i-k}(1-q)^i+bf^t(1-q)^{t-1}M + \sum_{i=1}^{x}A_{t-1}bf^i(1-q)^{i-1}. \tag{17}$$

When $C < q$ the population will not reach equilibrium until $N=0$ unless the treatment scheme is modified so that the birth rate per breeding females is again larger or equal to the death rate. Equations 16 and 17 allow us to predict the population levels at various lengths of treatment after reduction of the population below the level at which all females are breeding. Figure 5 illustrates the response of a hypothetical population to the management scheme involving permanent sterilization of a proportion of the breeding females.

Treatment of All Females with a Permanent Sterilant. A management scheme in which all the females in a population (both breeding and non-breeding) are equally vulnerable to treatment presents additional difficulties in response estimation because some individuals are vulnerable to treatment before entering the breeding segment of the population.

Of the cohort of animals resulting from reproduction during a given season, some animals enter the breeding segment of the population in the first season following their natal season and the remainder do not enter the breeding segment until the following season. We are assuming that older females have priority in obtaining territories and/or nest sites and that all females in their second and subsequent breeding season obtain territories and/or nest sites. The above conditions probably apply to certain passerine birds such as the Red-winged Blackbird (*Agelaius phoeniceus*).

Let P_t = the number of first season animals breeding, and
Q_t = the number of first season animals not breeding.

The recruitment can be expressed as

$$A_t=P_t+Q_t. \tag{18}$$

The number of animals in the population expressed in terms of recruitment to the breeding population of second season animals and recruitment to the total population of first season when $N_t > M$, can be expressed as:

$$N_t = M(1-q) + Q_{t-1}(1-q') + A_t \tag{19}$$

Expressed in terms of the number in each age class in terms of the age at first breeding this equation becomes:

$$N_t = M(1-q)^t + \sum_{i=1}^{t} P_{t-i+1}(1-q)^{i-1} + (1-q')\sum_{i=0}^{t-1} Q_{t-i-1}(1-q)^i + Q_t \tag{20}$$

Since equations 19, and 20 do not contain an expression for the birth rate or effect of the treatment upon the birth rate, we shall examine the change in the recruit-

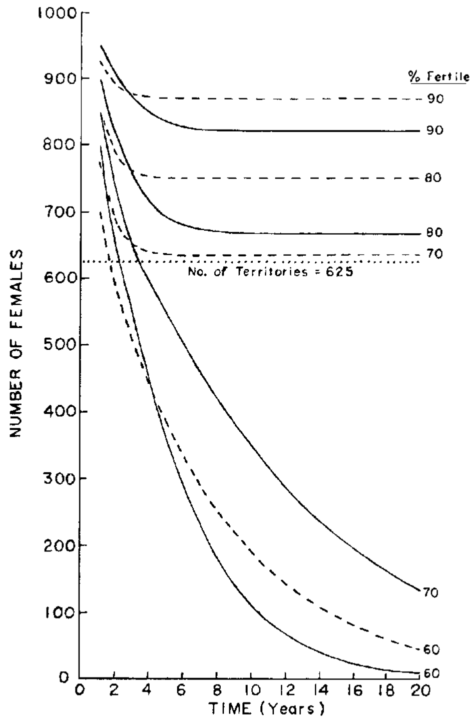

FIGURE 5

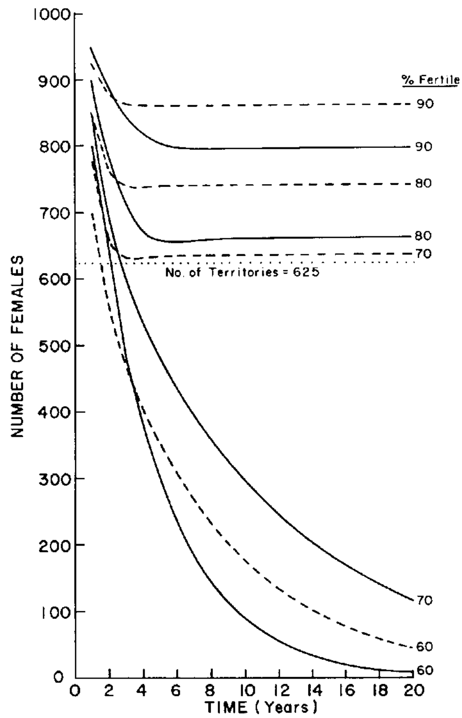

FIGURE 6

FIGURE 5. Effect of permanent fertility reduction (treatment of breeding females only) on a territorial population. Initial probability of dying is 0.5 (solid line) or 0.75 (broken line) and the annual recruitment rate is 0.8 females per breeding females (solid line) or 1.2 females per breeding female (broken line).

FIGURE 6. Effect of permanent fertility reduction (treatment of all females) on a territorial population. Initial probability of dying is 0.5 (solid line) or 0.75 (broken line) and the annual recruitment rate is 0.8 females per breeding females (solid line) or 1.2 females per breeding female (broken line).

ment (A_t) during a continuing management program at the same treatment level. Then $A_1 = Mbf$, and

$$A_t = Mbf^t(1-q)^{t-1} + \sum_{i=1}^{t-1} P_{t-i}bf^i(1-q)^{i-1} + (1-q')\sum_{i=2}^{t} Q_{t-i}bf^i(1-q)^{i-2} \quad \text{for } t \geq 2 \tag{21}$$

If the new equilibrium birth rate after extended treatment is larger than the death rate, the population will reach a new equilibrium level at $N_y > M$. As t becomes large, $\mathrm{Mbf^t(1-q)^{t-1}} \to 0$ then,

$$\text{(21a)} \qquad \mathrm{A_t \to \sum_{i=1}^{t-1} P_{t-i} bf^i (1-q)^{i-1} + (1-q') \sum_{i=2}^{t} Q_{t-i} bf^i (1-q)^{i-2}}$$

At equilibrium, N_y is a constant $> M$, so from equation 19, we get

$$\text{(22)} \qquad \mathrm{N_y = M(1-q) + Q_{y-1}(1-q') + P_y + Q_y,}$$

since $\mathrm{M = M(1-q) + Q_{y-1}(1-q') + P_y}$, and

$$\text{(23)} \qquad \mathrm{N_y = M + Q_y,}$$

Both N_y and M are constants at this time, so Q_y must also be a constant at the new equilibrium level. $\mathrm{N_y = M(1-q) + (N_y - M)(1-q') + A_y}$ and

$$\text{(24)} \qquad \mathrm{A_y = P_y + Q_y,}$$

so both A_y and P_y must also be constant at equilibrium.

We can describe the recruitment at the new equilibrium level by rewriting equation 21a as:

$$\text{(25)} \qquad \mathrm{A_y \sim P_y bf \sum_{i=0}^{t-2} f^i (1-q)^i + (1-q') Q_y bf^2 \sum_{i=0}^{t-2} f^i (1-q)^i.}$$

Since t is large

$$\text{(26)} \qquad \mathrm{A_y \sim \frac{P_y bf}{1-f+fq} + \frac{Q_y bf^2 (1-q')}{1-f+fq},}$$

so from equation 24,

$$\text{(27)} \qquad \mathrm{P_y + Q_y \sim \frac{P_y bf}{1-f+fq} + \frac{Q_y bf^2 (1-q')}{1-f+fq}.}$$

At equilibrium $N_y > M$ and $Q_y = Q_{y-1}$, so from equation 22

$$\text{(28)} \qquad \mathrm{P_y = Mq - Q_y(1-q').}$$

An approximation of the value of P_y and Q_y can not be obtained by solving equations 27, and 28 simultaneously. If $Q_y > 0$, $N_y > M$, the equilibrium level of a management program can be predicted by equation 23.

If in any season in the treatment program the number of females becomes less than or equal to the number of breeding sites available ($N_y \leq M$), all the first year females will breed so that the equation must be modified. Continued treatment at the same level will eventually result in the population becoming extinct.

Let $\mathrm{A_b}$ = recruitment from females recruited prior to $\mathrm{N_t < M}$ and
$\mathrm{A_a}$ = recruitment from females recruited after $\mathrm{N_t < M}$,

$$\text{(29)} \qquad \mathrm{A_b = Mbf^t(1-q)^{t-1} + \sum_{i=x}^{t-1} P_{t-i} bf^{i+1} (1-q)^i + (1-q') \sum_{i=x}^{t-1} Q_{t-i} (1-q)^{i-1}}$$

From equation 21 the recruitment from females recruited prior to the year when N_t became less than M can be expressed. Since when $N_t \leq M$, all the females will reproduce in the first season, the recruitment resulting from females recruited in the year $\mathrm{N_t}$ became less than M or later is,

$$\text{(30)} \qquad \mathrm{A_a = \sum_{i=1}^{x} A_{t-i} bf^i (1-q)^{i-1}}$$

For t after the year when $N_t < M$, we can therefore express the total recruitment in any season by the relationship,

$$A_t = A_b + A_a,$$

or

$$(31)\quad A_t = Mbf^t(1-q)^{t-1} + \sum_{i=x}^{t-1} P_{t-i}bf_{i+1}(1-q)^i + (1-q')\sum_{i=x}^{t-1} Q_{t-i}bf^{i+1}(1-q)^{i-1} + \sum_{i=1}^{x} A_{t-i}bf^i(1-q)^{i-1}$$

The decrease in the population can be predicted from equations 31 and 16 after the population is reduced below the level at which all females are breeding. Figure 6 illustrates the response of a hypothetical population to this type of management program.

Comparison of Management Schemes Involving Sterilization. The decision to employ a management program utilizing sterilization necessitates the availability of an appropriate agent for the target species and the development of suitable application techniques for the population. The choice between a temporary or permanent agent may depend entirely upon the properties of the available agents.

If a permanent sterilization program is chosen, the choice between treating only breeding animals or treating the entire population may depend upon the accessibility of the animals at different times of the year. For example, if the target species is migratory the accessibility on the breeding areas in summer may be different from the accessibility in the wintering areas. Association of the target species with non-target species may also vary between seasons and possible side effects on other species may be the deciding factor. The model presented predicts only small differences in the realized equilibrium levels between the schemes of treating only the breeding segment or treating the whole population (figures 5 and 6) so the choice can be based on the above considerations alone. It should be noted that the model predicts that the equilibrium levels resulting from the removal of birds and from permanent sterilization will be similar. Removal will, however, provide a greater initial response of the population (figure 3).

The prediction for temporary sterilization is a smaller response to the same treatment effort (proportion of birds sterilized) than for permanent sterilization (figure 4). A temporary sterilization program, however, has the advantage of producing a long-term response independent of the values of the probabilities of dying and recruitment rate per breeding female (figure 4). As long as the population is not reduced below the level at which the available breeding habitat is fully utilized ($N_t > M$) the proportional reduction of the equilibrium population level is the same as the proportional reduction in fertility. The initial response, however, depends upon the probabilities of dying and the recruitment rate per breeding female.

Treatment of both Sexes. In a monogamous species, the result of treating both sexes can be predicted by multiplying the respective fertilities of the sexes after treatment and using this value for the value of f in the appropriate equations (*i.e.*, equations 9, 11, 12, 21, and 31),

$$f = f_m f_f,$$

where f_m = proportion of males fertile after treatment and f_f = proportion of females fertile after treatment. An assumption here is that the probabilities of dying are independent of sex and that the sexes are equally represented in the recruitment.

For polygynous species in which the assumptions for the equations representing the female segment of the population are also valid for the male segment, the equilibrium level for treatment of both sexes can be estimated by considering the treatment for each sex separately and combining the results as follows:

A. Estimate A_y for treatment of each sex separately using the fertility of the sex considered and the female parameters for the other variables.

B. Calculate C for treatment of each sex separately,

Let

A_{yf} = recruitment of females if only females are treated and

A_{ym} = recruitment of females if only males are treated,

then

$$C_f = \frac{A_{yf}}{M},$$

and

$$C_m = \frac{A_{ym}}{M}.$$

C. Calculate the adjusted recruitment,

$$C_a = \frac{C_f C_m}{b} \tag{32}$$

Substitution of equation 32 into equation 4 using the parameters for the females segment of the population will give an estimate for the equilibrium level of the population under the projected treatment scheme if, $\frac{C_a - q'}{q'} > 1$.

The prediction of yearly changes in a polygynous population with permanent treatment of both sexes, in which the probabilities of dying of males and females may or may not differ, can be accomplished in a similar manner if both sexes meet the assumptions specified for the model. This can be accomplished by considering the treatment of males and females separately for each year and determining an adjusted recruitment to the population.

Let A_{ta} = adjusted recruitment of females at time t,

A_o = recruitment of females per breeding female to equilibrium non-treated population,

A_{tf} = recruitment per female if only females treated, and

A_{tm} = recruitment per female if only males treated,

then

$$A_{ta} = \frac{A_{tm} A_{tf}}{A_o}. \tag{33}$$

Substituting the adjusted recruitment value from equation 33 into the following equation will allow prediction of the change in the number of females in any year t when both sexes are treated and $N_t > M$:

$$N_t = M(1-q) + (N_{t-1} - M)(1-q') + A_{ta}. \tag{33a}$$

If $N_t \leq M$ predictions of the population decline can be made by substitution for A_{ta} for A_t in equation 16.

Combination of Approaches. The parameters of recruitment, probability of dying, and habitat availability can be manipulated independently or simultaneously in a management scheme. The treatment can be applied yearly in the same proportion or varied to attain the desired population response. A constant treatment by habitat manipulation implies destruction or construction to a level which is a constant proportion of the original habit and maintenance at that level. From a practical viewpoint, it is often difficult to reduce fertility or apply removal so that $b_a = q_a$. Therefore maintenance of the population at a level $N_t <$ initial M is best accomplished by habitat modification. The difficulty of increasing recruitment or decreasing the probabilities of dying also indicate habitat modification as the choice in a management scheme aimed at increasing a population above the non-treatment level.

Buffer Habitats. Several species of passerines are able to use marginal habitat for breeding at population levels above the number at which all the territories in the optimal habitat are utilized. Brown (1969a, b) discuss the consequences of this utilization in terms of recruitment to the population. A non-breeding excess does not exist for these species until the population level is greater than the total number of territories available in all habitats that are suitable for breeding.

Let z = the number of habitats utilized

M_i = the number of territories available of quality i,

b_i = recruitment (the number of one year old females alive per breeding female the previous year) by habitat quality,

q_i = the probability of dying of breeding females ($0 < q_i < 1$) by habitat quality,

where i = the order of desirability of habitat (*i.e.*, 1 = most desirable, 2 = second most desirable, *etc.*).

An equation for the growth of a population from a level below full utilization of the optimal habitat to equilibrium can be derived where z = the number of habitats utilized, including the habitat utilized by non-breeding surplus if existing:

$$N_t = N_{t-1}(1 + b_1 - q_1) \qquad , z = 1$$
$$N_t = M_1(1 + b_1 - q_1) + (1 + b_2 - q_2)(N_{t-1} - M_1) \qquad , z = 2$$
$$N_t = M_1(1 + b_1 - q_1) + M_2(1 + b_2 - q_2) + (1 + b_3 - q_3)(N_{t-1} - M_1 - M_2) \qquad , z = 3$$

so,

$$N_t + \sum_{i=1}^{z-1} M_i(1 + b_i - q_i) + (1 + b_z - q_z)(N_{t-1} - \sum_{i=1}^{z-1} M_i). \tag{34}$$

Since teritorial size frequently differs with habitat suitability the values assigned to M_i must be obtained from the relative numbers of birds in the respective habitats when filled. The least desirable occupied habitat is designated M_z and considered to be unfilled.

During the growth of a population, the value of (z-1) increases as habitats are filled and the birds begin to utilize the next most suitable habitat. The value of z used in the summation of equation 34 therefore also increases since it represents the number of habitats utilized.

Let $N_t = N_{t+1} = N_y$ at equilibrium, then from equation 34

$$N_y - (1 + b_z - q_z)(N_y + \sum_{i=1}^{z-1} M_i) = \sum_{i=1}^{z-1} M_i(1 + b_i - q_i)$$

$$N_y q_z - N_y b_z = \sum_{i=1}^{z-1} M_i(b_i - q_i) - \sum_{i=1}^{z-1} M_i(b_z - q_z)$$

$$N_y = \frac{\sum_{i=1}^{z-1} M_i(b_i - q_i) - \sum_{i=1}^{z-1} M_i(b_z - q_z)}{q_z - b_z}$$

$$N_y = \frac{\sum_{i=1}^{z-1} M_i(b_i - q_i)}{q_z - b_z} + \sum_{i=1}^{z-1} M_i.$$

Since

$$\sum_{i=1}^{z-i} M_i < N_y \leq \sum_{i=1}^{z} M_i,$$

then

$$(35) \qquad \frac{\sum_{i=1}^{z-1} M_i(b_i - q_i)}{q_z - b_z} > 0.$$

The number of habitats (z) utilized at equilibrium can therefore be determined by solving equation 35 for successive values of z. The highest value of z which still gives a positive result is the number of habitats utilized at equilibrium under the specified recruitments, probabilities of dying, and habitat capacities.

The response of the population to a management program can be obtained from equation 34 for populations utilizing breeding habitats of differing euqlity in the same manner as from equations 2 and 3 for populations utilizing only one breeding habitat. Similarily a prediction of new equilibrium level, resulting from a continuing management program, can be obtained from equation 35. If N_t becomes $< M_1$ as a result of a management program, continued treatment at the same level will result in eventual extinction of the population.

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Having the proceedings of the 1973 symposium on Cedar Bog in published form is a valuable contribution to the literature concerning this unique Ohio natural asset, a remnant northern bog. The papers, or summaries, cover: preglacial and glacial geology; hydrology; climatology; vegetation, including papers on the history of botanical studies, disjunct species, fungi, algae, lichens, slime molds, and meadow succession adjacent to the bog; animal life, including papers on fishes, orthoptera, lepidoptera, terrestrial mollusca, and the eastern massasauga rattlesnake. Several parts of the publication which were not presented as one of the 17 papers in the formal symposium provide added usefulness: a deserved dedication, with portrait, to Dr. Edward S. Thomas; a preface setting forth the purpose of the symposium and the ecological importance of the Bog; a fascinating personal account by Dr. Thomas of how Cedar Bog was acquired by the State of Ohio; a reprinting of Alfred Dachnowski's 1910 classic paper from the *Ohio Naturalist*, "A cedar bog in central Ohio;" an extract from the U.S.D.A. Soil Survey of Champaign County about the "Soils of the Cedar Bog area" with an outline of distribution of soil types on an aerial photograph of the Bog area; and "A Cedar Bog bibliography" of 147 entries. Accompanied with this publication, one could walk the boardwalk in the Bog with increased enlightenment and added admiration for those who had the foresight to have preserved this special Ohio bog.

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