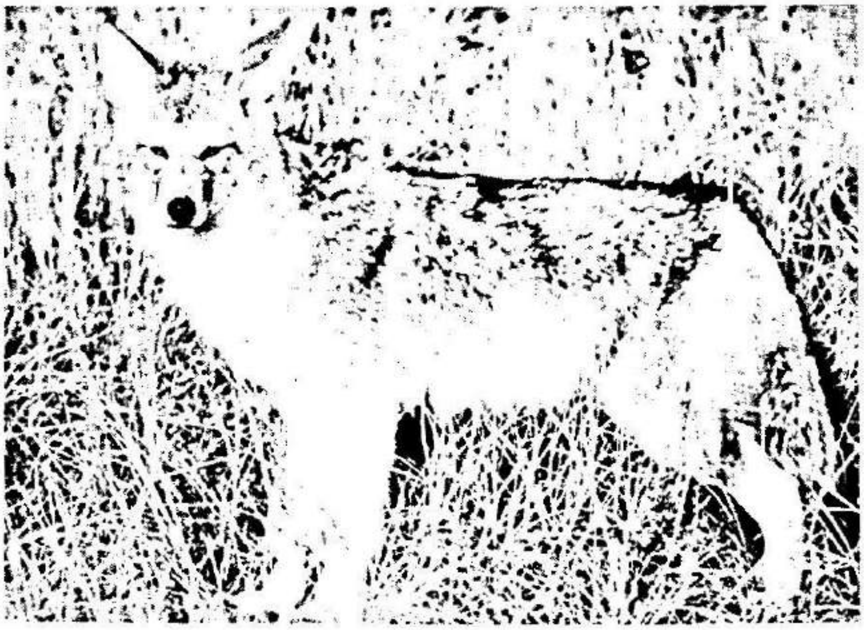
THE EFFECTS OF CONTROL

ON

COYOTE POPULATIONS



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THE EFFECTS OF CONTROL ON COYOTE POPULATIONS: A SIMULATION MODEL[1,2]

Guy E. Connolly, Staff Research Associate, Division of Wildlife and Fisheres Biology, University of California, Davis[3]

William M. Longhurst, Wildlife Biologist, Division of Wildlife and Fisheries Biology, University of California, Davis

ABSTRACT: According to a model developed to simulate coyote population dynamics, the primary effect of killing coyotes is to reduce the density of the population thereby stimulating density-dependent changes in birth and natural mortality rates.

Tests of varying levels of control kills showed that a coyote population can maintain itself and even increase its numbers except at the very highest levels of control. If 75 percent of the coyotes are killed each year, the population can be exterminated in slightly over 50 years.

Birth control combined with killing coyotes directly reduced both the breeding and maximum populations more than when either method was used separately. However, birth control is not yet feasible for field operations.

In this model, coyote populations reduced by intensive control recovered to precontrol densities within three to five years after control was terminated. Under current conditions, considering the restrictions placed upon control methods, coyote densities probably cannot be significantly reduced except in limited geographical areas.

The yearling pregnancy rate and the mean litter size are probably the best criteria for indicating the level of control, although the proportion of yearlings in the breeding population, the proportion of pups in the control kill, and the ratio between the control kill and breeding population also vary with the intensity of control.

Coyote control data from Mendocino County, California, were compared with the model output. The existing county control program does not appear

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[1]Submitted for Publication April 30, 1975.

[2]A contribution from Western Regional Research Project W-123, Evaluating Management of Predators in Relation to Domestic Animals.

[3]Present address: U. S. Fish and Wildlife Service, Twin Falls, Idaho

to affect overall coyote numbers but locally it may be stimulating the rate of reproduction.

INTRODUCTION

Killing coyotes, primarily because they prey on livestock, has been widely practiced in the western United States for many years. Tremendous sums have been spent on trapping, poison bait programs, shooting, den hunting, the Humane Coyote Getter, and M-44 devices (Cain, et al. 1972). Control objectives have apparently shifted from extermination (Adams, 1930), to population reduction ("prophylactic control"), to selective removal of problem animals (Cain, et al., 1972). In addition to the federal control program carried out by the U.S. Fish and Wildlife Service and its cooperators, fur trappers and sport hunters take many coyotes. In California alone sport hunters are estimated to take over 80,000 coyotes annually (Swick, 1974). However, coyote numbers seem to be increasing over much of the West (U.S. Congress, 1973; page 58) in spite of all these efforts.

Considering this history it is logical to wonder what the effect of control actually is on coyote populations. Cain, et al. (1972) questioned whether control activities influenced overall coyote densities in some states even when 1080 (sodium monofluoroacetate) poison stations were commonly used. Young and Jackson (1951; page 156) have described the effectiveness of trapping and poisoning "like digging a hole in the ocean." Detailed study of this matter has been surprisingly limited in relation to the magnitude of the control effort.

This paper describes the development and use of a simple simulation model to examine the probable effects of control on coyote populations.

DESCRIPTION OF THE SIMULATION MODEL

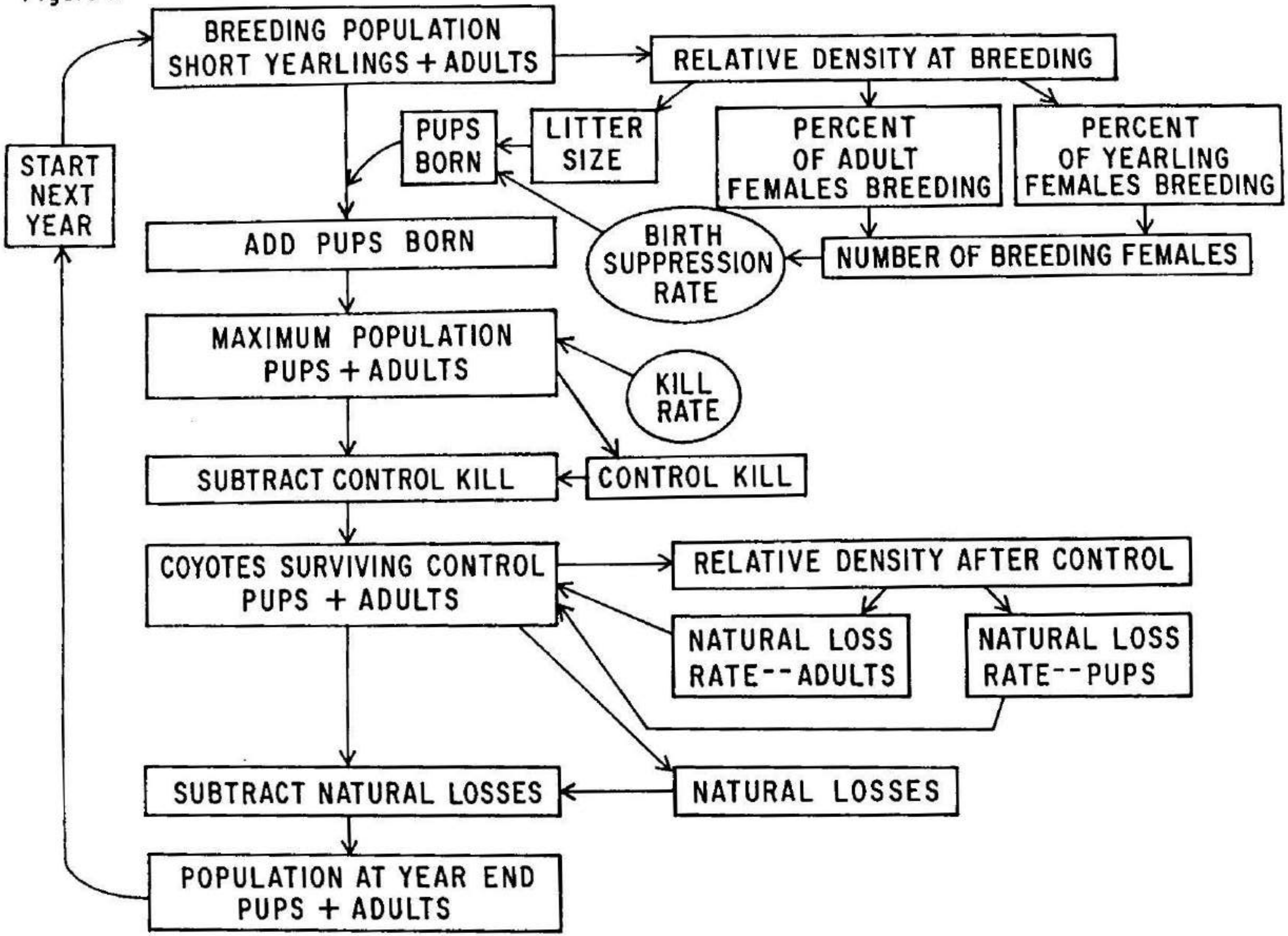
In this model the population consists of a seasonally variable number of coyotes. Natural coyote populations are of the "birth-pulse" type, with births occurring at one season while deaths occur the year round (Gier, 1968; Knowlton, 1972). Numbers are lowest after the breeding season (just before the birth pulse) and highest just after the birth pulse. We have simulated the annual population cycle in three steps: births, control mortality, and natural mortality which includes all other types of mortality. In effect, the take of coyotes by sport hunters and fur trappers is additive to the number of coyotes killed by federal, state, county agencies or private individuals to alleviate livestock depredations. For purposes of this model all of these forms of coyote removal are lumped together under control mortality. It should be realized, however, that sport hunting and fur trapping are non-selective in their removal of coyotes from the population whereas coyote killing to alleviate livestock losses tends to be focused on localized problem areas and on individual "killer" coyotes. The coyotes remaining at the end of the year constitute the breeding population for the next year. These events are related schematically in figure 1.

Our simulated population differs from actual populations in several respects. For example, we describe the minimum population (just before whelping) as the breeding population. Actually the population at breeding might be substantially higher than the minimum population, depending on natural and control loss during gestation. In this model, breeding is significant only in terms of the numbers of pups born, and this is a function of the minimum population.

As noted above, we have simulated the annual coyote population cycle in three steps: births, control mortality, and other "natural" mortality. Though in reality all forms of mortality may occur throughout the year, considerable abstraction from this pattern was needed in the model to keep the calculations within reasonable limits. In each year the control kill numbers are taken from the maximum population. Natural losses are then calculated for the animals surviving control. The justification for this is that intensive control, in the form of den hunting, often is applied to the maximum population. If pups are not killed in their dens, survival is thought be be high until fall (Knowlton 1972). In the model, both control and natural losses are calculated once each year. The whelping season also is compressed into a single calculation each year, even though in nature it may last several weeks.

In our model two forms of human intervention ("control") in the coyote population are considered: coyotes may be killed or females may be prevented from having pups through the use of chemosterilants. Either or both forms of intervention may be applied in any combination of rates. In the absence of "control," the model simulates the dynamics of a population that is affected only by natural losses. The control kill and birth suppression

Figure I. DIAGRAM OF COYOTE POPULATION DYNAMICS MODEL



rates are specified arbitrarily by the investigators at the beginning of each run (or at the beginning of each year if desired). Reproductive and natural loss rates are generated within the model and are variable with coyote density, as described in detail later.

This coyote model may be called an "if-then" simulator. That is, if a specified set of initial conditions is true, then over time a certain set of results will follow. If a specified control level is pursued over time the population will eventually stabilize at a level different than that when no control is practiced. Various population parameters can then be compared with similar values from an uncontrolled population to infer the effect of that level of control on the coyote population. The concepts of this model are generally similar to those employed by us in a deer simulation model (Anderson, et al., 1974).

This model is an abstract representation of a complex biosystem. Like any other model it is a simplification of real phenomena and requires certain assumptions. Some of these assumptions are implicit in figure 1. Others follow:

(1) In the absence of control, the population is stable, both in numbers and age structure. The population occupies an area of unspecified size which has sufficient resources to sustain a breeding population of just 100 coyotes each year. For simplicity the carrying capacity of this area for coyotes is assumed to be constant year after year. In reality, the carrying capacity varies with climate, food supplies and other factors beyond the scope of this model.

(2) In the model the population contains two age classes: pups (from birth to 12 months of age), and adults (over 12 months old). As the whelping season approaches, the pups of the previous year are called yearlings to distinguish them from the newborn pups.

(3) Adult recruitment is limited to pups which survive their first year. Immigration and emigration either do not occur or occur at equivalent rates.

(4) Birth and death rates are constant for adult coyotes of all ages.

(5) The sex ratio of both pups and adults is 50:50.

(6) There is no sex-specific mortality; i.e., natural and control losses consist of equal numbers of males and females, both among pups and adults.

(7) Control loss rates apply to the maximum population. Natural loss rates apply to the coyotes surviving control.

(8) Each run begins with 100 coyotes at breeding time, 60 adults and 40 yearlings. (The reason for this age composition is given in the description of the natural mortality functions.)

The coyote population model diagrammed in figure 1 represents a set of variables related to one another by simple functions and difference equations. The variables and their interrelationships are listed in table 1. For details of programming and calculations see Appendix.

BIRTH AND NATURAL LOSS FUNCTIONS

We believe that birth rates are higher and natural loss rates lower in an intensively controlled coyote population than in an uncontrolled population. We agree with the concept that intensive population reduction alleviates the constraints that ordinarily limit numbers in an uncontrolled population. In our view these constraints (density-dependent variables) consist most importantly of intraspecific competition for limited resources, primarily food. Likewise competition for other habitat resources, such as favored denning sites, may increase with density and serve to limit reproductive success. Social stress in relation to density may also have a bearing in this regard as would transmission of diseases and parasites. Whatever the specific natural limiting factors are, it is known that both pregnancy rates (Gier, 1968) and litter size (Knowlton, 1972) vary with control intensity and environmental conditions. While environmental conditions for coyotes may be influenced by weather or land use practices, intensive control also appears to enhance environmental conditions for the surviving coyotes. As explained by Henderson (1972). . . "reducing the numbers of predators makes it easier for the remaining predators to survive the winter and come through in better shape."

While it is accepted that control can induce increased birth and natural survival rates in coyote populations, the magnitude of these effects at various control intensities has not been fully determined. However, in this model it was necessary to mathematically define these functional relationships. Since it would have been impossible to identify and separately quantify each environmental factor affecting births and natural losses, the relative density was used as a proxy variable encompassing all the density dependent effects. The relative density is simply the number of coyotes in the population expressed as a fraction of the number which would have been present in the absence of control. When no control is practiced the relative density is one, and birth and natural loss rates are unchanged. As the population is reduced by control, the relative density is also reduced, causing corresponding changes in the birth and natural loss rates which are functionally related to relative density.

Five parameters in this model vary with relative density: the pregnancy rates for adult (Ba) and yearling (By) female coyotes, the average litter size (L), and natural mortality rates for adults (Na) and pups (Np). Detailed descriptions of the functions follow:

<u>Adult pregnancy rate (Ba)</u>

It has been shown that 60 to 90 percent of the adult female coyotes produce litters (Gier, 1968; Knowlton, 1972). For this model all coyotes older than yearlings (12 months of age when pups are born) are considered to be adults. We assume that, in the average year, 70 percent of the adult females produce litters in an uncontrolled population (relative density = 1), and that this pregnancy rate increases to 90 percent as the population is reduced by control to half the precontrol density (fig. 2). We take 90 percent as the biological limit for this parameter, so the adult pregnancy rate remains at 90 percent for all relative densities below 0.5. The adult pregnancy rate function from $D_1 = 1.0$ to $D_1 = 0.5$ is described by the equation:

$$Ba = 1.1 - 0.4 D_1$$

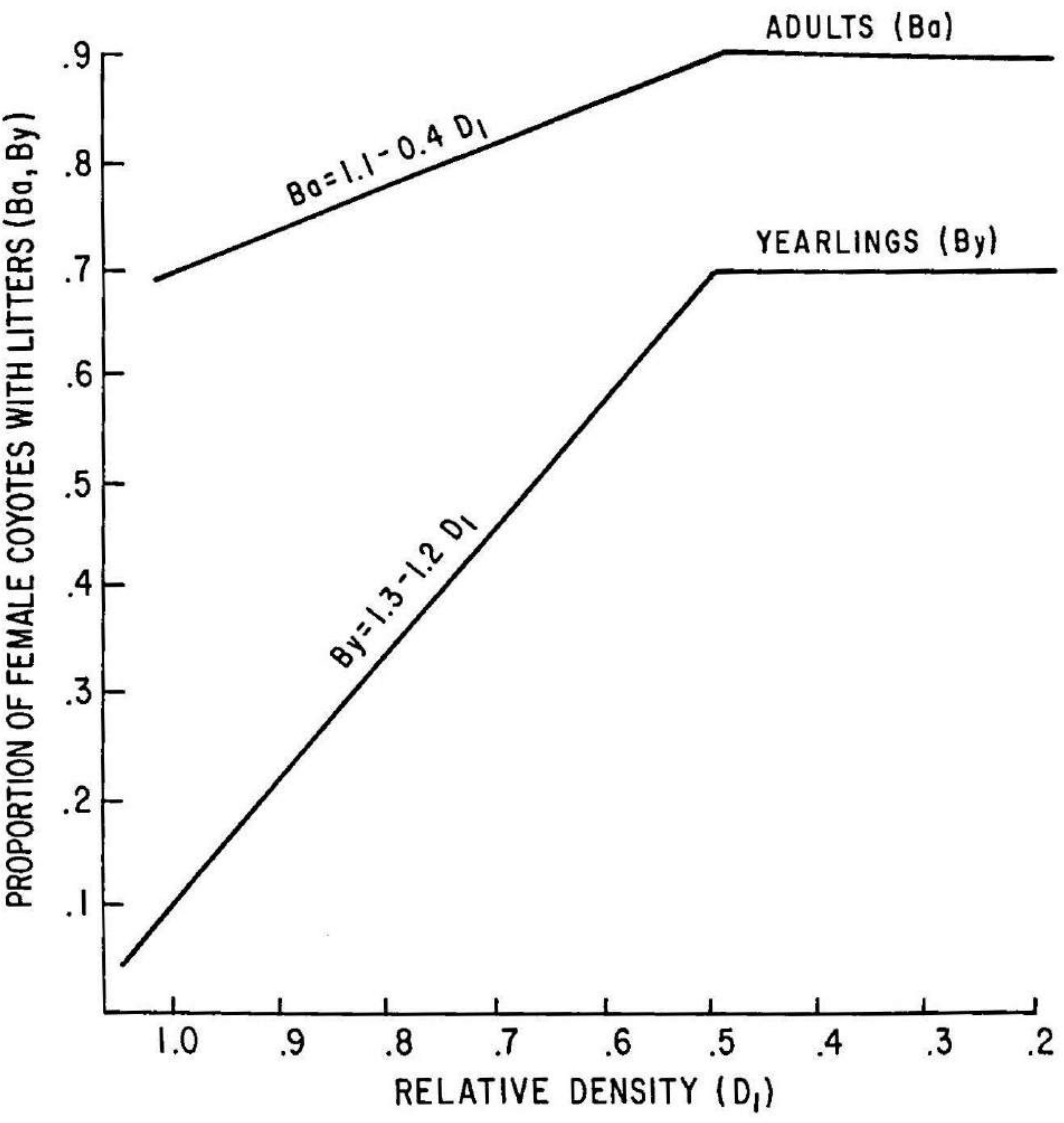
which was calculated by least squares regression techniques.

<u>Yearling pregnancy rate (By)</u>

The fraction of yearling female coyotes bearing litters may range from 0 to 70 percent (Gier, 1968). Breeding yearlings are those which bear pups at about 12 months of age. We suggest that in an uncontrolled population

Figure 2.

PROPORTIONS OF FEMALE COYOTES BREEDING IN RELATION TO DENSITY



($D_1 = 1.0$), 10 percent of the yearlings breed, and that this rate increases to 70 percent as the population is reduced by control to half the precontrol density (fig. 2). With 70 percent set as the biological limit for this parameter, the yearling pregnancy rate remains at 70 percent for all relative densities below 0.5. The relationship from $D_1 = 1.0$ to $D_1 = 0.5$ is described by the equation

$$By = 1.3 - 1.2\ D_1$$

which was calculated by least squares regression procedures.

Litter size (L)

Published estimates of average litter size range from 2.8 to 8.9 pups per litter (Knowlton, 1972). However, litters of 12 or more pups are not uncommon. Wade (1975) records 16 litters containing 154 pups taken by Benton Whitman in Yakima and Columbia counties, Washington, in 1955, for an average of 9.6 per litter.

We propose an average litter size of 4.5 in an uncontrolled population ($D_1 = 1.0$), increasing to 9 pups per litter as the population is reduced to half the precontrol density (Figure 3). With 9 set as the maximum for this parameter, the litter size remains at this level for all relative densities below 0.5. The relationship from $D_1 = 1.0$ to $D_1 = 0.5$ is given by the equation $L = 13.5 - 9\ (D_1)$, which was also calculated by least squares procedures.

Relative density (D_1, D_2)

In this model the birth functions are based on relative density at breeding (D_1). This relates breeding success to the density dependent constraints operative at the time of breeding. Because the breeding portion of the uncontrolled population always contains 100 coyotes, the denominator for calculating D_1 is always 100 (table 1).

For mortality calculations, a different reference point was needed for relative density. Both pups and adults die, but only the animals surviving control are susceptible to natural mortality. The relative density after control (D_2) is based on the numbers of animals susceptible to natural mortality. As this value is 203.5 coyotes each year in the uncontrolled population, the denominator for calculating D_2 is always 203.5 (table 1).

Adult natural mortality (Na)

Knowlton (1972) estimated that in the absence of control the annual mortality rate was about 40 percent. We feel that this rate will decline

Figure 3.

COYOTE LITTER SIZE RELATED TO COYOTE DENSITY

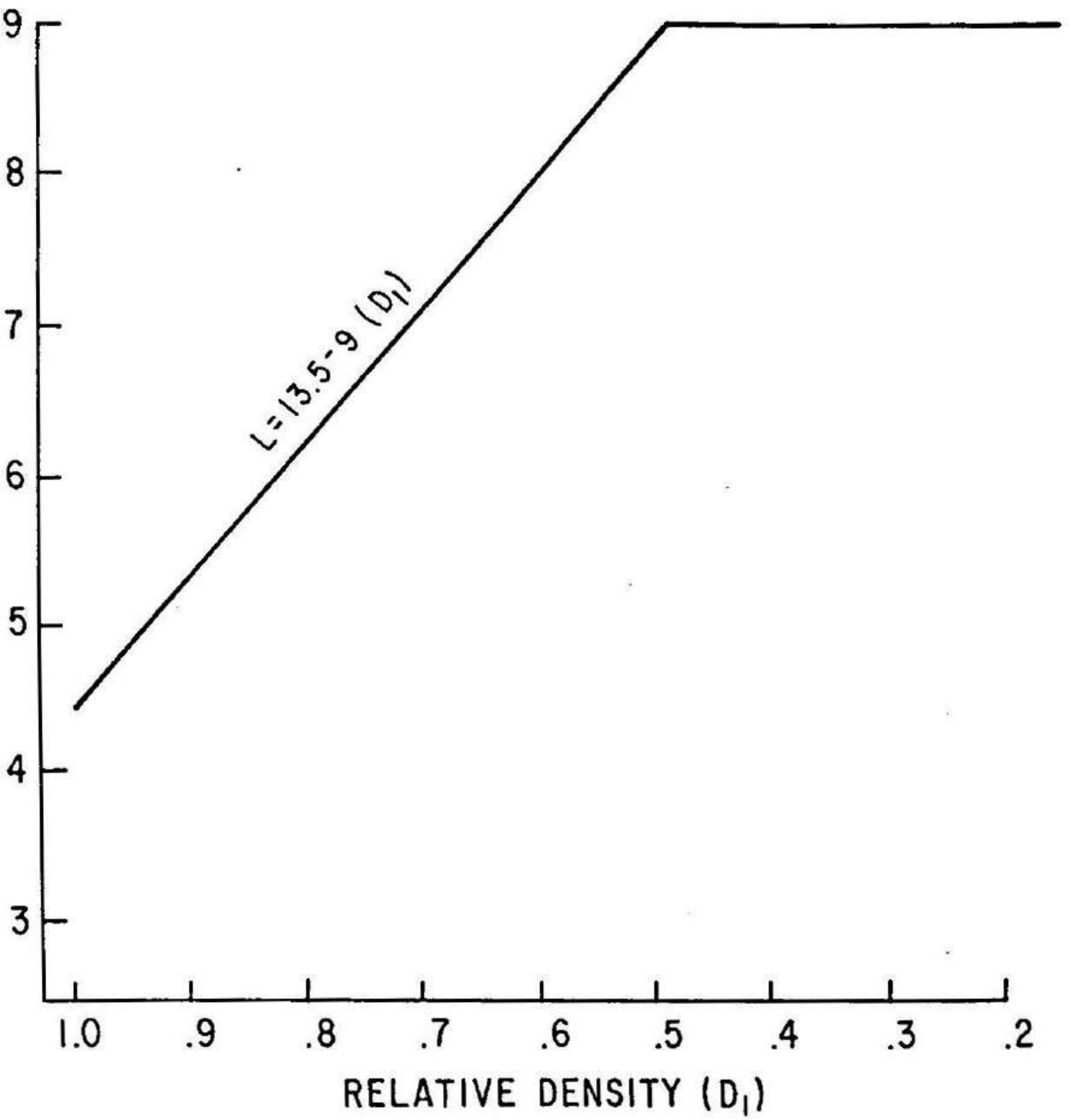


Table 1. Variables for the coyote population dynamics model.

Variable	Symbol	Relation to other variables
Yearling coyotes at breeding	Cy	$Cy(t) = P(t - 1) - Pk(t - 1) - Pn(t - 1)$
Adult coyotes at breeding	Ca	$Ca(t) = Cb(t - 1) - Ak(t - 1) - An(t - 1)$
Minimum (breeding) population	Cb	$Cb = Cy + Ca$
Relative density at breeding	D_1*	$D_1 = Cb/100$
Proportion of yearling females with litters	By†	$By = fD_1$
Proportion of adult females with litters	Ba†	$Ba = fD_1$
Breeding females (number with litters)	F1$^{\phi}$	$F1 = 0.5(1 - S)(ByCy + BaCa)$
Proportion of breeding females suppressed	S	Specified by investigator
Litter size	L†	$L = fD_1$
Pups born	P	$P = L(F1)$
Proportion of pups produced by yearling females	Py	$Py = (0.5L)(1 - S)(ByCy)/P$
Maximum population	Cm	$Cm = Cb + P$
Proportion of coyotes killed in control	K	Specified by investigator
Pups killed by control	Pk	$Pk = P(K)$
Adults killed by control	Ak	$Ak = Cb(K)$
Total control kill	Kt	$Kt = Pk + Ak$
Proportion of pups in control kill	Kr	$Kr = Pk/Kt$
Control kill as proportion of breeding population	Kb	$Kb = Kt/Cb$

*D_1 expresses the breeding population as a fraction of the breeding population in the absence of control.

†These values increase as D_1 decreases. The functions are described in Figures 2 and 3.

$^{\phi}$Assumes a 50:50 sex ratio at breeding.

Table 1. (continued)

Variable	Symbol	Relation to other variables
Relative density after control	D_2[Ψ]	$D_2 = (Cm - Kt)/203.5$
Proportion of pups dying of natural causes	Np[§]	$Np = fD_2$
Proportion of adults dying of natural causes	Na[§]	$Na = fD_2$
Pups dying of natural causes	Pn	$Pn = Np(P - Pk)$
Adults dying of natural causes	An	$An = Na(Cb - Ak)$
Total natural mortality	Nt	$Nt = Pn + An$
Pups at year end	$Cy(t + 1)$	$Cy(t + 1) = P(t) - Pk(t) - Pn(t)$
Adults at year end	$Ca(t + 1)$	$Ca(t + 1) = Cb(t) - Ak(t) - An(t)$
Total year end population	$Cb(t + 1)$	$Cb(t + 1) = Cm(t) - Kt(t) - Nt(t)$

[Ψ] D_2 expresses the population surviving control (Also = population susceptible to natural losses) as a fraction of the maximum population in the absence of control.

[§] These values decrease as D_2 decreases. The functions are described in Figure 4.

as the population is reduced by control but it will never be lower than 10 percent. For the purpose of this model we set the adult natural mortality rate at 40 percent in the uncontrolled population ($D_2 = 1.0$), declining toward 10 percent as D_2 approaches 0 (fig. 4). The relationship $Na = 0.1 + 0.3\ (D_2)$ was calculated using least squares regression techniques.

Pup natural mortality (Np)

For the uncontrolled coyote population ($D_2 = 1.0$), this rate was calculated from the assumptions and rates for other parameters given previously. It is apparent that in a stable population with no control, the pup natural mortality rate can be calculated from the number of pups born and the number of pups surviving to one year of age:

Table 2. Example of simulated dynamics of a population of 100 coyotes as affected by control (D_2) over an 11 year period.*

Annual Values of Variables

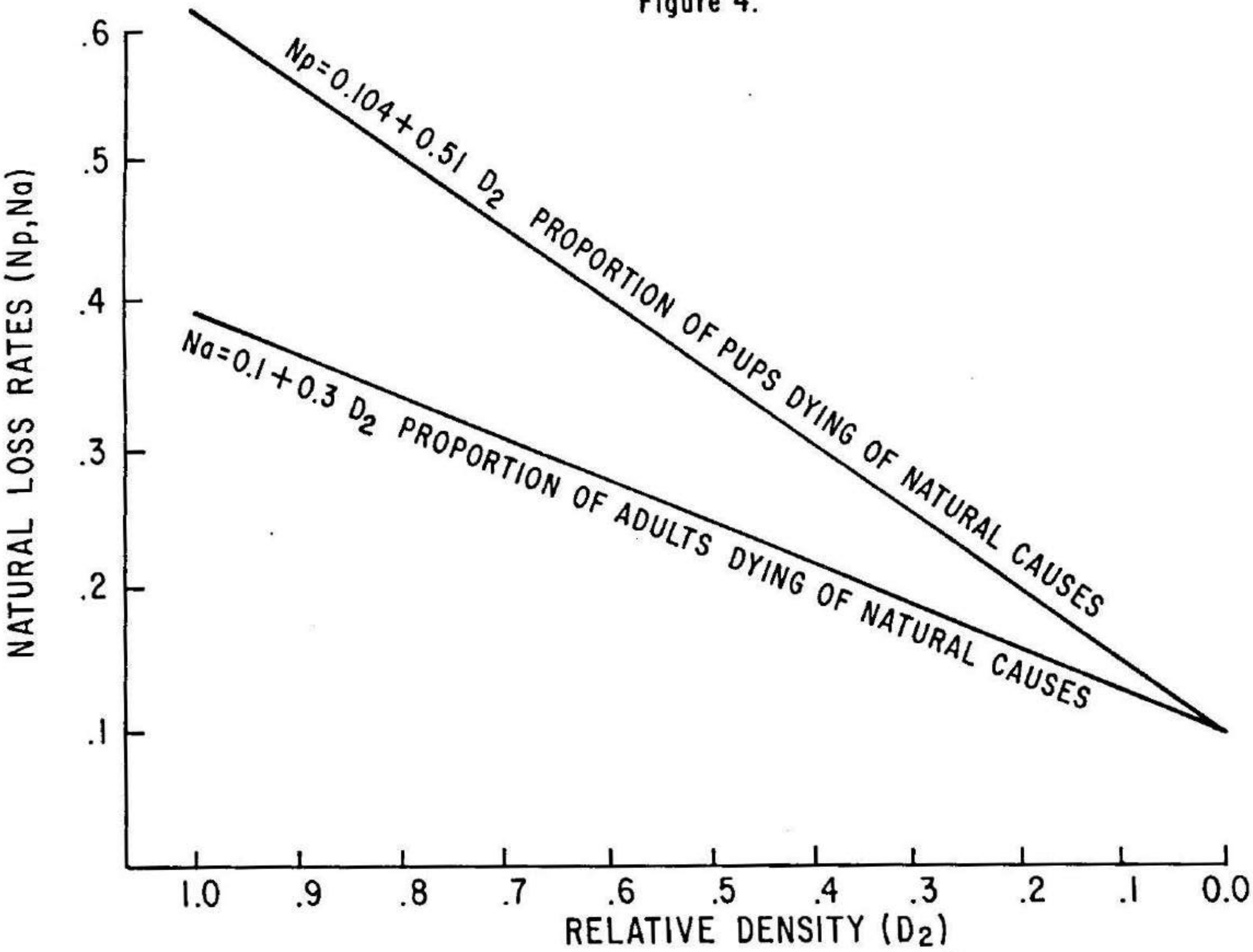
Variables[†]	YEARS 1	2	3	4	5	6	7	8	9	10	11
Cy	40.00	33.00	49.00	43.00	46.00	45.00	46.00	45.00	45.00	45.00	45.00
Ca	60.00	38.00	26.00	28.00	26.00	27.00	26.00	27.00	27.00	27.00	27.00
Cb	100.00	71.00	75.00	71.00	73.00	72.00	72.00	72.00	72.00	72.00	72.00
By	0.10	0.45	0.40	0.45	0.43	0.44	0.43	0.44	0.44	0.44	0.44
Ba	0.70	0.82	0.80	0.82	0.81	0.81	0.81	0.81	0.81	0.81	0.81
Fl	23.00	23.00	20.00	21.00	21.00	21.00	21.00	21.00	21.00	21.00	21.00
L	4.50	7.10	6.80	7.10	7.00	7.00	7.00	7.00	7.00	7.00	7.00
P	104.00	163.00	136.00	150.00	143.00	146.00	145.00	145.00	145.00	145.00	145.00
Cm	204.00	234.00	211.00	221.00	216.00	218.00	217.00	218.00	217.00	217.00	217.00
Pk	52.00	81.00	68.00	75.00	72.00	73.00	72.00	73.00	73.00	73.00	73.00
Ak	50.00	35.00	37.00	35.00	36.00	36.00	36.00	36.00	36.00	36.00	36.00
Np	0.36	0.40	0.37	0.38	0.37	0.38	0.38	0.38	0.38	0.38	0.38
Pn	19.00	32.00	25.00	28.00	27.00	28.00	27.00	27.00	27.00	27.00	27.00
Na	0.25	0.27	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26	0.26
An	12.00	10.00	10.00	9.00	9.00	9.00	9.00	9.00	9.00	9.00	9.00

*In this run 50 percent of the pups and 50 percent of the adults were killed each year.

[†]For explanation of symbols see table 1.

COYOTE NATURAL MORTALITY RATES RELATED TO DENSITY

Figure 4.



$$Np = (P - Cy)/P \quad \text{(Symbols defined in table 1.)}$$

As previously stated, this model assumes a breeding population of 100 coyotes each year in the absence of control (assumptions 1 and 8*). If the adults are replaced solely by pups surviving to be yearlings (assumption 3), and the adult mortality rate is 40 percent (Knowlton, 1972), then short yearlings must comprise 40 percent of the breeding population. Therefore, $Cy = 40$.

The number of pups born depends on the number of breeding females and the average litter size ($P = L \times Fl$, table 1). In a breeding population of 60 adults and 40 yearlings with a 50:50 sex ratio (assumptions 8 and 5), there are 30 adult females and 20 yearling females. If 70 percent of the adult females and 10 percent of the yearlings produce litters, as estimated in figure 2 ($D_1 = 1.0$), the uncontrolled population contains 23 breeding females. If the litter size is 4.5 (fig. 3, $D_1 = 1.0$), the number of pups born (P) is 103.5. From these estimates, in the uncontrolled population $Np = (103.5 - 40)/103.5 = 0.614$.

This estimate differs from the value of 0.67 proposed by Knowlton (1972) primarily because we used separate pregnancy rates for yearling and adult females, while Knowlton used one value for all females.

As in the case of adult natural mortality, we feel the natural loss rate of pups will decline as the population is reduced by control but will never be under 10 percent. For the pup natural mortality function (fig. 4) we set the value in the uncontrolled population ($D_2 = 1.0$) at 0.614, as calculated above, declining toward 10 percent as D_2 approaches 0. The resulting function is described by the equation $Np = 0.104 + 0.51 (D_2)$ as calculated by least squares regression techniques.

<u>Discussion of birth and death functions</u>

The functions shown in figures 2 to 4 are the most important variables in this model. We reemphasize that the form of these functions is largely speculative, although each is based on the best available data. During the formulation and validation phases of model development, the functions were changed several times. It became apparent that minor changes would not alter our conclusions significantly. Although additional research is

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*Refer to numbered assumptions on page 5.

needed to define the functions more precisely, the model is so constructed that improved or refined functions can be substituted for the present ones.

CONTROL KILL RATES

Coyote pups are thought to be less wary than adults and therefore more likely to be taken by trappers. With this in mind, our model allowed pups and adults to be killed at different rates. Theoretically, pups and adults could be killed at any combination of rates. To limit the number of combinations simulated, we sought to take pups and adults in the proportions actually expected in operational control programs. Wade (personal communication)* indicated that as the intensity of control increases, the proportion of pups in the total control kill also increases. Considering all methods of direct control efforts, pups would be expected to comprise little more than half of the kill at low control levels. Under the most intensive control as many as 80 percent of the coyotes taken might be pups. We found that by taking the same percentages of pups and adults present in the population, the composition of the control kill changed as expected when the intensity of control was increased. This is attributed to the increase in the birth rate as the intensity of control increased. After it became apparent that different kill rates for pups and adults would not be needed, the program was simplified to apply a single kill rate to both pups and adults.

EFFECTS OF CONTROL ON THE SIMULATED COYOTE POPULATION

Figure 1 shows the two kinds of human intervention or "control" that may be applied to coyote populations -- birth control or direct killing. We have tested the impacts of both kinds of control, both singly and in combination.

The general response of our simulated coyote population to control is illustrated in table 2. Each run began with a previously uncontrolled population of 100 coyotes at breeding. As control was applied in the first year coyote numbers were reduced, causing compensatory changes in birth and natural loss rates in subsequent years. If the control kill was held year after year at a constant percentage of the population, as shown in table 2, the population stabilized within a few years at a lower density than was the case in the absence of control. This occurred regardless of which form

*D. A. Wade, Extension Wildlife Specialist, Animal Damage Control, University of California, Davis.

of control was practiced. If the kill or birth control rate changed from year to year the population did not stabilize, but fluctuated in response to the variable control in effect. If the level of control exceeded the capacity of the population for compensations in birth and natural loss rates, the population did not stabilize but declined toward zero.

Under field conditions it is rare for exactly the same rate of control to be achieved from year to year; the population therefore, does not stabilize. Likewise the carrying capacity of the coyote habitat may change from one year to the next, and this also prevents stabilization of numbers.

The effects of killing coyotes on the population were studied by a series of runs ranging from no control to 75 percent annual control kill (table 3). The values shown are at stability, when the previously uncontrolled population had fully responded to the control level under test. (See years 9 to 11 in table 2, for example.) In table 3 each value representing a specific number of coyotes was rounded to the nearest whole number. For this reason, some of the numbers do not cross check.

As shown in table 3, killing coyotes affects every variable of the coyote population. Some parameters were affected more than others. As the percentage of coyotes killed annually increased, the breeding population (Cb) decreased, while the maximum population (Cm) increased slightly due to increased numbers of pups (P) born. As the control kill (Kt) increased natural losses (Nt) decreased. The effects of population reduction on the proportion of females breeding (By,Ba), litter size (L), and natural loss rates (Np,Na) were forecast in figures 2 to 4, but are reiterated so that results can be analyzed.

One variable which changed only slightly with control intensity was the number of breeding females (Fl). This resulted from increased proportions of females breeding (By,Ba) as the breeding population (Cb) was reduced. Knowlton (1972) pointed out that the greatest adjustments in productivity of local coyote populations may result from variations in the percentage of yearlings becoming sexually mature. In our model this is simulated by the proportion of yearling females with litters (By). However, the relative frequency of yearlings in the breeding population (Cy/Cb) also increases with control intensity. The net contribution of yearling females to reproduction is given by Py, the proportion of pups produced by

Table 3. Simulation of effects on a coyote population of killing various numbers of pups and adults.

Variables*	PERCENTAGES OF PUPS AND ADULTS KILLED ANNUALLY (K)								
	0	10	20	30	40	50	60	70	75†
	Annual values at population stability								
Cy	40.00	42.00	44.00	45.00	46.00	45.00	43.00	34.00	2.00
Cb	100.00	97.00	93.00	87.00	80.00	72.00	62.00	45.00	3.00
By	0.10	0.14	0.19	0.26	0.34	0.44	0.56	0.70^{ϕ}	0.70^{ϕ}
Ba	0.70	0.71	0.73	0.75	0.78	0.81	0.85	0.90^{ϕ}	0.90^{ϕ}
Fl	23.00	22.00	22.00	21.00	21.00	21.00	20.00	17.00	1.00
L	4.50	4.80	5.20	5.70	6.30	7.00	7.90	9.00^{ϕ}	9.00^{ϕ}
P	104.00	107.00	114.00	122.00	133.00	145.00	159.00	152.00	10.00
Py	0.09	0.13	0.19	0.28	0.37	0.48	0.60	0.71	0.76
Cm	204.00	204.00	206.00	209.00	213.00	217.00	221.00	197.00	14.00
Kt	0.00	20.00	41.00	63.00	85.00	109.00	132.00	138.00	10.00
Kr	0.00	0.52	0.55	0.58	0.62	0.67	0.72	0.77	0.80
Kb	0.00	0.21	0.44	0.72	1.10	1.50	2.10	3.10	3.30
Np	0.61	0.56	0.52	0.47	0.42	0.38	0.33	0.25	0.11
Na	0.40	0.37	0.34	0.32	0.29	0.26	0.23	0.19	0.11
Nt	104.00	87.00	72.00	59.00	48.00	36.00	27.00	15.00	0.00

*For explanation of symbols see table 1.

†Population did not stabilize. Values shown are for year 50.

$^{\phi}$Values generated in model exceeded set limits and therefore were replaced by specified maximum values.

yearling females. This value ranged from less than 10 percent in the uncontrolled population to almost 75 percent before an extinction level of control was reached. For this reason we concur with Knowlton (1972) that the greatest potential for increased reproduction lies with the yearling age class.

Several authors have described the seeming futility of attempting to reduce coyote numbers by killing coyotes (Young and Jackson, 1951; Cain, et al., 1972; Henderson, 1972). In table 3 perhaps the best indication of this is Kb, which expresses the annual control kill as a fraction of the breeding population. A value of 1.0 for this parameter means that the annual control kill equals the breeding population. Note that a kill of about three coyotes fpr every animal at breeding would be needed to hold the breeding population (Cb) below 50 percent of the pre-control level. Even if this figure is not precise it is apparent that a very high kill rate is needed to eliminate coyotes.

Our model suggests that coyotes through compensatory reproduction can withstand an annual control level of 70 percent, but not 75 percent. However, even at the 75 percent control level, the population persisted more than 50 years. We must point out that to achieve these results, 75 percent of the coyotes must be removed in each and every year. When 75 percent were taken in four of every five years, with no control in the fifth year, the breeding population (Cb) fluctuated between 28 and 76 coyotes with an average of 42 and the control kill (Kt) averaged 102 animals per year.

EFFECTS OF BIRTH SUPPRESSION ON THE COYOTE POPULATION

Limiting coyote numbers by inhibiting reproduction with antifertility agents rather than killing them directly is an attractive idea, at least in theory. As pointed out by Balser (1964, page 356), "It may be more practical to prevent animals from being born than to reduce their numbers after they are partially or fully grown and established in a secure environment." Suppressing reproduction might also prevent the comensating increase in reproduction associated with killing coyotes. Most importantly, antifertility agents might be more acceptable to the public than large scale coyote killing programs, especially if people were adequately informed on the biological facts about coyote populations.

If an ideal birth control (chemosterilant) chemical or combination of chemicals could be developed, one dosage would sterilize either males or females for life. However, the chemosterilants tested to date are effective only on females during a short period in the breeding cycle and they must receive dosages each year. Likewise we did not concern ourselves with the problems of bait distribution or Environmental Protection Agency registration of the chemicals.

In this model we have examined the effects of birth suppression in a series of runs in which from 0 to 95 percent of the normally breeding females were prevented from having litters (table 4). No other form of control was practiced. All values representing coyote numbers were rounded to the nearest whole number. For this reason some of the numbers in table 4 may not cross check.

The effects of birth suppression on the coyote population differed in several respects from the effects of killing coyotes. As the intensity of birth suppression increased, the breeding population (Cb) declined slightly (up to S = 0.6), but the number of pups born (P) dropped nearly 50 percent (table 4). These results contrasted sharply with the effects of increasing the control kill (table 3), which caused a marked decline in the breeding population (Cb) but an increase in the number of pups born (P). The net effects of these differences were that the maximum coyote population (Cm) declined with increased birth suppression (table 4) but increased with the control kill (up to K = 60 percent, table 3).

We believe the key to the different population responses to these two kinds of control is the reproductive potential of young females. As shown in table 3, the proportion of yearlings (Cy) in the breeding population (Cb) increased with the control kill. The percentage of females with litters also increased, with the potential of yearlings (By) greater than that of adults (Ba). The composite effect of these variations is that the proportion of pups produced by yearling females (Py) increased with the control kill.

Turning again to the results of birth suppression (table 4), we see that Py is virtually constant at all levels of suppression. Not only does the proportion of yearlings in the breeding population (Cy/Cb) decline as S increases, but the increase in the proportion of yearlings breeding (By) is

Table 4. Simulation of effects of birth suppression by chemosterilants on a coyote population.

Variables*	PERCENTAGE OF BREEDING FEMALES SUPPRESSED ANNUALLY (S)					
	0	20	40	60	80	95†
	----------Annual values at population stability----------					
Cy	40.00	37.00	34.00	29.00	21.00	5.00
Cb	100.00	99.00	97.00	92.00	79.00	32.00
By	0.10	0.11	0.14	0.20	0.36	0.70ϕ
Ba	0.70	0.70	0.71	0.73	0.79	0.90ϕ
Fl	23.00	19.00	15.00	10.00	5.00	1.00
L	4.50	4.50	4.80	5.30	6.40	9.00ϕ
P	104.00	87.00	71.00	54.00	34.00	6.00
Py	0.09	0.08	0.10	0.11	0.14	0.13
Cm	204.00	186.00	168.00	146.00	113.00	39.00
Kt	0.00	0.00	0.00	0.00	0.00	0.00
Np	0.61	0.57	0.53	0.47	0.39	0.20
Na	0.40	0.37	0.35	0.32	0.27	0.16
Nt	104.00	86.00	71.00	54.00	34.00	6.00

*For explanation of symbols see table 1.

†Population declined slowly after year 20 but appeared stable by year 50. Values shown are for year 50.

ϕValues generated in model exceeded and therefore were replaced by specified maximum values.

limited because the breeding population remains near pre-control levels. Birth suppression thus provides a "double-barrelled" effect, directly limiting the maximum population (Cm) by restricting the number of pups born (P), and indirectly preventing increased breeding by young females by restricting the relative numbers (Cy/Cb) and breeding success (Cy) of yearlings.

Livestock losses to coyotes are said to be particularly serious during spring and summer because of the food requirements of the pups (Wade, 1973). In this connection the birth suppression approach is particularly attractive because it reduces the number of pups born and presumably the depredations associated with the feeding of pups. In contrast, increased killing of coyotes might actually increase depredations near den sites, as the number of breeding females (Fl) remains nearly constant while the litter size (L) increases with the control kill (table 3). The critical relationship may be the level of competition for available food resources in relation to coyote density.

Since birth suppression offers real advantages over more traditional means of coyote control, it is unfortunate that this approach has not yet been perfected to the point of field application. While initial trials were promising (Balser 1964), later tests were less successful (Linhart, et al., 1968). The main constraints appeared to be consumption of baits by nontarget animals, many coyotes are not exposed to baits, and the drug used, diethylstilbestrol, is only effective in the female coyote for a limited period. There may be hope for future developments, but at present birth control is not a viable alternative to existing control methods.

THE EFFECTS OF INTEGRATED CONTROL (BIRTH SUPPRESSION + KILLING) ON THE COYOTE POPULATION

It seems unlikely that birth control will supplant conventional methods of coyote control, at least in the near future, and even with an effective birth suppression program it is likely that some coyotes would still have to be killed in chronic depredation areas. Therefore, we have tested the effects of killing and birth control combined (table 5). The two kinds of control might be applied in any combination of rates, but in table 5 the alternatives are limited to equal percentage rates for both kinds of control within each run. As in previous tables the values representing numbers of coyotes were rounded to the nearest whole number.

In general, the results of integrated control are intermediate between those obtained with either birth control or killing applied separately. Integated control (table 5) reduced the breeding coyote population (Cb) more effectively than when either control method was applied separately (tables 3 and 4). However, the consequences of reducing the breeding population include increased productivity of yearling females (By) and increased litter size (L), which lead to more pups born (P) under integrated control (table 5) than would be the case with birth control only (table 4). There appears to be a trade-off relationship between the breeding population (Cb) and number of pups born (P), in that it is hard to minimize both parameters simultaneously. The breeding population can be reduced by a heavy control kill, but at the cost of increased reproduction and increased maximum population. Conversely, the number of pups produced (P) can be reduced most by birth control in a breeding population kept as large as possible. Of the strategies tested so far in our model, the best prospect for reducing both breeding and maximum populations would be integrated control at the highest practicable rate.

RECOVERY OF COYOTE POPULATIONS FROM CONTROL

One aspect of coyote population dynamics which has received little study is the capacity of a heavily controlled population to increase after control is terminated. This was simulated for two different levels of control -- 50 percent and 75 percent annual control kill for 20 years -- followed by as many years without control as were required for the population to recover to the precontrol level. The response of the breeding population (Cb) to these treatments is shown in figure 5.

The population from which 50 percent of the coyotes were removed annually stabilized after 6 years with a breeding population (Cb) of 72 coyotes each year. Other parameters of this controlled population at stability are given in table 3 (K = 50 percent). After control was terminated the population recovered to its precontrol level in 3 years (fig. 5). By the beginning of the fourth year after control was stopped, the numbers of yearlings and adults in the breeding population were similar to those in the pre-control population.

Table 5. Simulation of effects of integrated control (birth suppression + killing) on a coyote population.

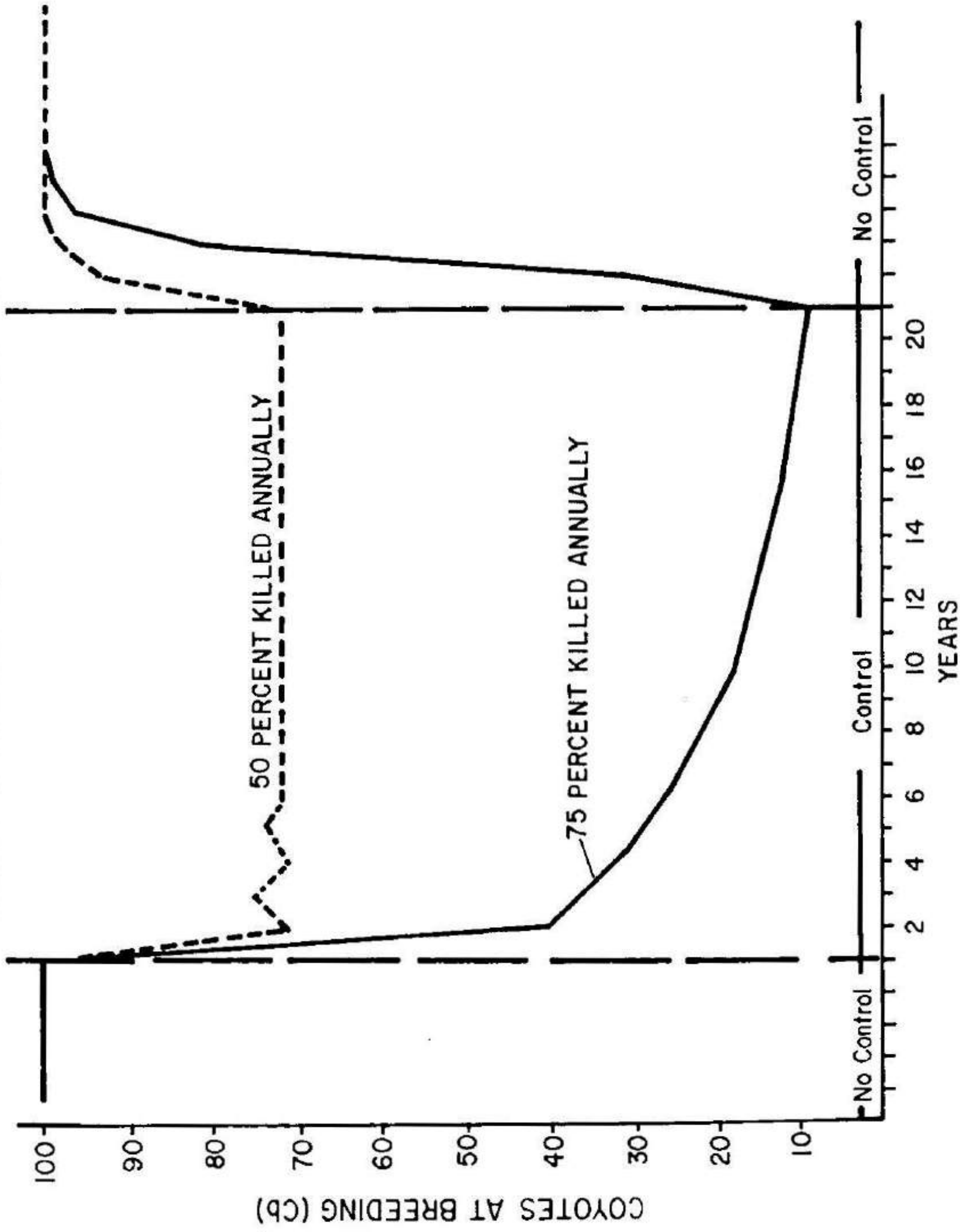
	PERCENTAGES OF BREEDING FEMALES SUPPRESSED AND COYOTES KILLED ANNUALLY (S=K)						
Variables*	0	10	20	30	40	50	60[†]
	Values at population stability						
Cy	40.00	41.00	41.00	40.00	37.00	31.00	6.00
Cb	100.00	96.00	89.00	80.00	68.00	52.00	10.00
By	0.10	0.15	0.23	0.34	0.48	0.67	0.70[ϕ]
Ba	0.70	0.72	0.74	0.78	0.83	0.89	0.90[ϕ]
Fl	23.00	21.00	18.00	16.00	13.00	10.00	2.00
L	4.50	4.80	5.40	6.30	7.40	8.80	9.00
P	104.00	100.00	99.00	98.00	96.00	87.00	13.00
Py	0.09	0.13	0.21	0.31	0.42	0.53	0.53
Cm	204.00	196.00	188.00	179.00	164.00	140.00	23.00
Kt	0.00	20.00	38.00	53.00	65.00	70.00	14.00
Kr	0.00	0.50	0.53	0.55	0.58	0.63	0.57
Kb	0.00	0.21	0.42	0.66	0.95	1.30	1.50
Np	0.61	0.55	0.48	0.42	0.35	0.28	0.13
Na	0.40	0.36	0.32	0.28	0.25	0.20	0.11
Nt	104.00	80.00	61.00	45.00	30.00	17.00	1.00

*For explanation of symbols see table 1.

[†] Population failed to stabilize. Values shown are for year 10.

[ϕ] Values generated in model exceeded and therefore were replaced by specified maximum values as shown.

Figure 5.
COYOTE POPULATION RESPONSES TO CONTROL



Previously we noted that coyotes would be exterminated if 75 percent were killed each year (table 3). After 20 years at this level of control the breeding population was reduced to nine coyotes (fig. 5). However, in our model the response to cessation of control was rapid. The breeding population regained the precontrol density by the end of the fifth year after control was terminated. If this projected recovery rate is accurate, there is no need for concern that the coyote may become a rare or endangered species.

THE FEASIBILITY OF REDUCING COYOTE NUMBERS BY CONTROL

We have shown that coyotes could conceivably be exterminated if sufficient numbers are killed for a sufficient number of years. However, there is a great difference between killing coyotes in a computer and killing them in the field.

In field operations the effort needed to take each coyote increases with the intensity of control as a result of reduced density. Field operations usually cannot be planned to obtain specified percentage kill rates, but only to apply control within the limits of available funds and manpower. Fortunately (or unfortunately, depending upon one's point of view) it is usually beyond the range of economic feasibility to apply enough control to exterminate the coyote. Because of limited resources, predator control agencies generally concentrate their efforts in areas where depredations on livestock are most severe. This "hot-spot" control pattern leaves most of the coyotes subject to light control, so that surplus animals are available to repopulate the areas where control is heavy.

Animal control specialists generally agree that poisons were the most effective means of reducing coyote populations. Prior to the presidential ban (President's Executive Order Number 11643 of February 8, 1972), about 80 percent of all predatory animals killed in federal control programs were taken with toxicants (Bureau of Sport Fisheries and Wildlife, 1973). Cain, et al. (1972, page 42) reported that the use of 1080 may have caused coyote populations to decline in seven western states. The Cain committee also concluded that generalized coyote population control may be the most effective approach to reducing livestock losses. Whatever teh desirability of such control, we do not believe substantial coyote reductions can usually be effected over broad areas without the use of toxicants. As shown in tables 3 to 5, coyotes will persist except with the most intensive control.

The techniques presently used for coyote control include trapping, the "M-44" cyanide ejector device in some areas, shooting both on the ground and from aircraft, and den hunting. The relative effectiveness of these methods may differ with the intensity of control. Efforts to reduce the population by trapping or aerial shooting just before breeding would probably decline in effectiveness proportional to the decline in the breeding population (Cb) as control levels increase (table 3). However, the number of females with litters (Fl), and presumably the number of dens, declines only slightly with increasing control (table 3). Therefore, it appears that den hunting should remain quite effective even at high rates of control. Aerial shooting has proven very effective in areas of sparse cover but cannot be relied upon in brushy or timbered areas.

As mentioned earlier, the take of coyotes in many areas by sport hunting may greatly exceed the number removed through deliberate control programs. Likewise, in some places bounties are still being paid as an incentive to kill coyotes. Considering the strong compensatory reproductive response of coyote populations to reduction, if control, sport, and bounty hunting collectively do not reduce numbers annually on a continuing basis by at least 75 percent, no sustained decline in the population can be achieved. Therefore, to summarize, in most situations, killing coyotes at rates below 75 percent may merely stimulate reproduction and aggravate the problem by increasing the seasonal population pressure on the food supply. With such increased competition for food, it is reasonable to expect coyotes to turn more to alternative food sources such as livestock. From this standpoint chemosterilants may be especially useful if they can be applied effectively, since they do not tend to cause increased food competition.

INDICATORS OF CONTROL INTENSITY

Since reliable estimates of coyote numbers are notoriously difficult to obtain, the information needed to plan intelligent predator management programs is not usually available. In most areas we simply do not know how the control kill relates to the size of the population, or even whether coyote numbers are increasing or decreasing. However, there are several statistics measurable from the control kill which can serve as indices to the level of control actually being achieved. Perhaps the most useful of these are measures of reproductive success.

Our work suggests that the proportion of yearlings in the breeding population (Cy/Cb), the proportion of females with litters (Cy,Ba), the litter size (L), the proportion of pups in the control kill (Kr), and the ratio between the control kill and breeding population (Kb) all vary with the intensity of control (table 3). Several of these rates can be determined by examination of the carcasses of coyotes killed in control programs, and of the results compared with table 3 or other estimates to infer the actual control level. Probably the most indicative data would be the yearling pregnancy rate (By) and the litter size (L). All of these measures vary with environmental conditions as well as control intensity. To separate these influences would require sampling of uncontrolled coyote populations to establish baseline data for comparison with the controlled populations. Annual samples of coyotes for a period of years would also be desirable to estimate the range of variability associated with year to year changes in environmental conditions.

Predator control administrators frequently cite the number of animals killed as a measure of control effectiveness. While this statistic is often the only one available, it has little meaning unless it can be related to the number of coyotes remaining in the population. Whenever an estimate of the breeding population (Cb) is available, the control kill (Kt) may be expressed as a fraction of the breeding population to obtain a better index of control effectiveness. As noted earlier (table 3) this ratio (Kb) should exceed 3.0 if control is maintaining the population below half of its normal (uncontrolled) density.

COYOTE CONTROL IN MENDOCINO COUNTY, CALIFORNIA

This section describes actual coyote control as practiced in Mendocino County and relates this control program to our model. Mendocino County was chosen as an example because of our experience on coyote studies at the University of California, Hopland Field Station within this county.

Mendocino County contains 3,500 square miles of rugged forest and range lands in north coastal California. Dense redwood and Douglas fir forests cover much of the coastal half of the county. The eastern half is a mosaic of grassland, oak woodland, hardwood, chaparral, and coniferous forest types. The grassy openings grazed by livestock are typically close to woods or chapparal thickets, which provide good escape cover for coyotes. Vehicle access in many areas is restricted by the steep terrain and dense vegetation. Approximately 20 percent of the county is public land (National Forest or National Resource Land) where little livestock grazing or predator control is practiced.

About half of Mendocino County is grazed by livestock, and coyotes occur on virtually all of the livestock ranges. Coyotes have preyed on livestock, particularly hseep, in this part of the state since the early days of European settlement. A predatory animal control program has been carried out under county auspices for the past 30 years and the area has been divided into six districts with a full-time hunter trapper working each district. The trappers are supervised by the Director of Animal Control. Most of the coyotes are taken by steel traps and den hunting, but some calling employing sirens or commercial predator calls is done as well. M-44 devices were also used until banned by the executive order in 1972. No other toxicants have been used recently. Aerial hunting is not practical in this area because of the dense vegetation and steep terrain.

In 1973-74 the Mendocino County Animal Control Department made an estimate of the numbers of coyotes in the county (Vann, personal communication).* Each trapper district was evaluated by sections, with the trappers giving their best estimate of the coyote population in each section. Areas not being trapped were inspected by the Director and the numbers of coyotes were estimated from scat counts, tracks, sightings, and den numbers. The estimates for all areas were summarized for a total breeding population of about 4,135 coyotes for the entire county.

When this estimate was made it was thought to be conservative. Director M. Vann now believes (March, 1975) that the previous estimate should be revised upwards by several hundred. Approximately 50 percent of the county, including all areas east of highway US 101, is heavily populated by coyotes and an additional 30 percent is lightly populated. While it is difficult to verify Vann's estimate of coyote numbers in the county, we believe it

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*M. Vann, Director of Animal Control, Mendocino County.

is reasonable and we had independently estimated the breeding population at about 4,000 animals before learning of Vann's work.

Vann reported that although coyotes may be found throughout the livestock ranges of Mendocino County, not all of the county is subject to intensive control. Occasional den hunting or calling is done in many areas, but only about 25 percent of the county is worked intensively. The areas of greatest coyote density, particularly public lands, receive little or no control.

Widespread, intensive predator control is not possible in this county because of limited funds and public opposition to control in excess of proven needs. Therefore, the control strategy is to concentrate on areas where livestock losses to predators are most serious. These often are ranches adjacent to wild lands too steep or too brushy to support livestock. Such wild lands apparently serve as "coyote reservoirs," providing a ready source of animals to replace those taken by trappers from the livestock ranges nearby. Under these circumstances, the trappers take as many coyotes as possible from the immediate problem areas. They also work the "refuge" areas, particularly by den hunting, in an attempt to minimize the numbers of coyotes available to repopulate the problem areas.

The number of coyotes taken by Mendocino County trappers is quite constant from year to year. During the five year period 1970 to 1974 an average of 334 coyotes was taken each year. The yearly totals ranged from 303 to 363 during this period. In addition to the coyotes removed by county trappers, perhaps 50 per year are taken by deer hunters, sport hunters, and callers. Few, if any, are taken for fur. Comparing the coyote control program in Mendocino County to the output (table 3) of our theoretical model, it is evident that the overall control kill is quite low. Taking the estimated breeding population (Cb) of 4135 coyotes and the estimated control kill (Kt) of 384 per year (334 by trappers and 50 by sport hunters) as explained above, the control kill amounts to 9 percent of the breeding population. This kill ratio (Kb) is low in relation to the values for Kb in table 3, suggesting that the actual kill rate (K) in Mendocino County is about 5 percent of the maximum population.

In addition to the kill ratio (Kb), we also determined the average coyote litter size in the county from trappers' reports indicating the numbers of unborn pups in pregnant females. Twenty-nine litters were reported from 1968 through March 1975. The fetal counts ranged from two to 11 with an average of 5.4 pups per females. Thirteen of the 29 litters contained five pups each. Referring again to table 3, an average litter size (L) of 5.4 would be expected when approximately 25 percent of the coyotes are killed each year. This is a substantially higher control rate than that indicated by the kill ratio (Kb) as determined above. However, the litter size estimate (L) is biased toward that portion of the county where control is intensive, while the kill ratio (Kb) represents the entire county. This illustrates the difficulty of applying a simple model assuming a uniform control rate to field conditions where the actual control rate varies locally. Nevertheless this comparison agrees with our concept of the "hot spot" pattern of control effectiveness and suggests that effects are most evident in the immediate areas of intensive control. We conclude that coyote control as practiced in Mendocino County has little impact on overall coyote numbers.

We have no recommendations to improve the effectiveness of predator control in Mendocino County for reducing livestock losses. Such recommendations would depend on cost effectiveness data beyond the scope of this study. If, as we believe, the existing program removes predators from problem areas without significantly influencing overall coyote numbers, it may be considered to serve the interests of both ranchers and preservationists. However, there is room for improvement in the collection of data from the animals taken in control.

As noted earlier, a number of statistics measurable from the control kill can serve as indices to the level of control being achieved. These include the proportion of yearlings in the breeding population (Cy/Cb in tables 1, 3), the proportion of females with litters (By, Ba), the litter size (L), the proportion of pups in the control kill (Kr), and the ratio between the control kill and breeding population (Kb). With the exception of the kill ratio (Kb) and litter size (L), as discussed above, little information of this kind exists in Mendocino County.

This information could be determined if the age, reproductive status, and litter size were recorded for each coyote taken by control officers.

To determine the age would require one canine tooth from each coyote for laboratory counts of cementum layers (Linhart and Knowlton, 1967). This would not be necessary for animals which were obviously juvenile. Uterine examinations for reproduction data can readily be done in the field. Regardless of the time of year, the presence of placental scars will reveal that pups were born in the previous breeding season. The number of scars indicates the number of pups produced (Gier, 1968).

EFFECTS OF COYOTE CONTROL ON NONTARGET SPECIES

Several of the effective coyote killing techniques in present use are not completely selective for coyotes. The catch of foxes, raccoons, skunks, and other nontarget animals in coyote traps is grounds for much opposition to predator control (U.S. Congress, 1973; pages 320-342). While we did not include these nontarget animals in our model, we wish to point out that the principles of population dynamics demonstrated for coyotes apply to other animal species as well. It is likely that most, if not all, populations of nontarget animals possess the ability to compensate for man-caused mortality by increased birth and reduced natural loss rates, just as coyotes do. Also the natural losses in the populations of these nontarget species should be similar to those of coyotes so that population turnover is high and the effects of removing a few additional animals inadvertently would be insignificant and difficult to even detect.

If this is true, predator control programs are not likely to eradicate or even seriously affect the nontarget species. As a matter of record, governmental animal control programs have not significantly threatened the future of a single animal species, endangered or not (U.S. Congress, 1973; pages 380-382). None of this is to excuse the indiscriminant destruction of wildlife, but only to point out that the incidental catch of nontarget animals in predator control programs is not, of itself, grounds for terminating predator control in areas of proven need.

CONCLUSION

This report discusses the level of control needed for eradication of coyote populations and the feasibility of achieving such control. We emphatically DO NOT recommend eradication as the preferred coyote management strategy. Eradication is the limit of control intensity at the opposite end of the scale from no control. Both limits are important reference points to to compare with intermediate levels of control. Our aim in this paper is to evaluate the effects of various management strategies and to elucidate their consequences.

Killing coyotes unselectively with the techniques presently available, is not a very feasible means of reducing populations over broad geographical areas. This report suggests that other means should be found to reduce coyote depredations, and that better understanding of coyote population dynamics is required.

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APPENDIX

PROGRAMMING AND CALCULATIONS

The relationships shown in figure 1 and table 1 of the main text of this paper were programmed for solution on a Wang Model 360 electronic calculator with Model CP-1 card programming attachment. In its final version the program contained 152 steps. The sequence of calculations was as follows:

1. Store initial values for Cy, Ca, Cb, and K (refer to table 1 for explanation of symbols). In each run the initial values for Cy, Ca, and Cb were 40, 60, and 100, respectively.
2. Insert program card 1.
3. Calculate and store D_1.
4. Calculate By.
5. Apply By to Cy to determine the number of yearling females with litters.
6. Calculate Ba.
7. Apply Ba to Ca to determine the number of adult females with litters.
8. Sum numbers of yearling and adult females with litters to determine Fl.

8a. In runs where part of the breeding females are subjected to chemosterilization, apply S to Fl to determine the value of Fl after birth suppression.

9. Calculate L.
10. Calculate P.
11. Calculate Cm.
12. Remove program card 1; insert card 2.
13. Calculate Pk and subtract it from P.
14. Calculate Ak and subtract it from Cb.
15. Calculate and store D_2.
16. Calculate Np.
17. Apply Np to (P - Pk) to determine Pn.
18. Subtract Pn from (P - Pk) to determine Cy for the next year.
19. Calculate Na.
20. Apply Na to (Cb - Ak) to determine An.
21. Subtract An from (Cb - Ak) to determine Ca for the next year.

22. Add Cy and Ca (from steps 18 and 21) to determine Cb for the next year.

23. Remove program card 2.

Steps 2-23 constitute one annual cycle in the coyote model. To begin the next year the user returns to step 2. As calculated in steps 18, 21, and 22, the initial values for Cy, Ca, and Cb for the next year are in storage. Two program cards were required to accommodate the entire model. Card 1 covered reproduction and card 2 the mortality phase of the model.

Throughout this model the calculations were sequential and endogenous; i.e., each step proceeded from values calculated and stored previously. The only exceptions to this were as follows:

A. To begin a run four initial values were stored (step 1).

B. STOP commands were used throughout the program to permit monitoring the calculations. Whenever $D_1 < 0.5$ the calculated values of By, Ba, and L (steps 4, 6, and 9) exceeded the specified maxima (figs. 2 and 3). In such cases each excessive value was replaced by the specified maximum before the calculations were continued.

C. Step 8a was used only in runs where part of the females were prevented from breeding. This step was performed manually because the limited storage capacity of the Wang 360 prevented storing the value of S.

The Wang 360 calculator used in this study features visual display of results. No output is printed. In using this model it was necessary to copy the output as displayed (see table 2, for example). In practice it was found that the calculations were made as fast as the operator could change cards and copy the results. This procedure was slower than it would have been on a high speed computer, but was much more efficient in the formulation, validation, and programming stages.

The output from this model (table 2) does not include all the variables shown in table 1. However, the variables not explicit in the model can readily be calculated from the output. In early stages of model development all the variables in table 1 were included as output but it soon became apparent that it would be more efficient to limit the program to essentials, calculating the other variables from the output after the model reached stability.