

Simulations of Demographic Compensation in Coyote Populations

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SIMULATIONS OF DEMOGRAPHIC COMPENSATION IN COYOTE POPULATIONS¹

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Questions associated with demographic patterns of coyotes (*Canis latrans*) are inherent in the controversy surrounding predator control programs for this species. A considerable capacity for variation is indicated in the wide range of demographic-parameter estimates from numerous re-

gional studies. Despite intensive long-term control measures, coyote numbers do not appear to be reduced and the species has extended its range (Mech 1978). Density-dependent variation in natality and survival, in response to exploitation, must be considered as a strong compensatory component of population regulation in coyotes.

Compensatory mortality (increased survival) and natality (e.g., increased litter size, proportion of females breeding, reproductive lifespan, decreased age at 1st breeding) have been observed in exploited species (Mosby 1969, Campbell et al. 1973,

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Table 1. Projected rates of increase with 27 combinations representing high, low, and midpoint values in 3 demographic parameters for coyote populations.

Proportion females breeding (%)	Survival (%)	Finite rate of increase (λ)		
		4.30 ^a	5.95 ^a	7.60 ^a
36	71.9	1.83	2.25	2.68
36	44.9	1.14	1.41	1.67
36	18.0	0.45	0.56	0.67
63	71.9	2.66	3.41	4.16
63	44.9	1.66	2.13	2.60
63	18.0	0.66	0.85	0.67
90	71.9	3.50	4.56	5.63
90	44.9	2.18	2.85	3.52
90	18.0	0.87	1.14	1.41

^a Mean litter size.

Murton et al. 1974, Anderson and Burnham 1976, Roseberry 1979) and implicated in some coyote studies (Knowlton 1972, Connolly and Longhurst 1975). Because published analyses of compensation often suffer from a posteriori consideration, lack of control populations for adequate independent comparisons, and invalid use of correlation and regression methods, compensatory phenomena remain poorly identified and rarely understood. An alternative approach is establishment of theoretical attribute boundaries based upon knowledge of the species (Conley 1983) and complemented by simulation modeling that generates a continuum of combinations useful in formulating subsequent research and management strategy. This method was used by Connolly and Longhurst (1975) through simulations that addressed projected population densities in response to hunting and birth suppression regimes. The objective of this study is to provide an overview of the potential for demographic response in coyotes based on estimates of vital statistics from real coyote populations subjected to varying levels of exploitation. We used a similar approach in deriving rates of increase with emphasis on compensatory aspects of coyote demographics.

METHODS

Several features of coyote natural history are important to this analysis. The mating system is primarily monogamous and adults are iteroparous. Both sexes exhibit a limited winter fertility period and multiple young are produced in the spring. Coyotes have an average life span of 3–8 years (Wormer 1964), although reports of older coyotes are common (Young and Jackson 1951, Gier 1968, Clark 1972, Knowlton 1972, Nellis and Keith 1976). The size of social groups varies from seasonally paired adults to relatively stable groups as large as 7 (Lehner 1976). Coyote “families” consist of the mated male and female plus pups of the year.

Data regarding litter size, proportion of females breeding, and mortality rates for coyotes were obtained from the literature (Hamlet 1938; Rogers 1965; Gier 1968; Linhart et al. 1968; Clark 1972; Knowlton 1972; E. K. Boggess, unpubl. rep., Iowa Conserv. Comm. Fed. Aid Proj. W-115-R-12, 1975; Nellis 1975; Knudsen 1976; Nellis and Keith 1976; Fowler 1979; Mitchell 1979). For each of these 3 population attributes, a high, a low, and a midpoint were determined resulting in 27 combinations (Table 1).

Population simulations were conducted using a computer model described by Conley (1978) and used in studies of several other species (e.g., Lenarz and Conley 1980, 1982; Watts and Conley 1981). Only the female portion of the population was modeled under the assumptions that male–female survival is equal and the sex ratio at birth is 1:1. There is no published evidence for extreme sex ratio skewness that could inhibit reproductive patterns; thus, the validity of these assumptions, although perhaps not true, does not affect the intent of this discussion.

Average litter sizes (Table 1) corre-

spend, if reduced by one-half under the assumption of a 1:1 sex ratio at birth, to age-specific fertility— $F(x)$, the expected number of daughter offspring produced by an age x to $x + 1$ female that produced offspring (Conley 1978). Mortality was converted to age-specific survival— $p(x)$, the probability of survival from age x to $x + 1$ —by assuming constancy across ages in the published data. This assumption is necessary because of the complete absence of relevant data. Thus, we obtained survival functions from available mortality data and combined available data on litter sizes and proportion of breeding females into an expected production of female offspring per female of ages x to $x + 1$. The derived data on survival and natality focus the simulations that are designed to bracket existing information.

RESULTS AND DISCUSSION

As proportion of females breeding and survival values increase, other things being equal, finite rates of increase (λ) will also increase (Table 1). Because λ represents per capita replacement (time scale is t to $t + 1 = x$ to $x + 1$), $\lambda < 1$ indicates a declining population, $\lambda > 1$ indicates an increasing population, and $\lambda = 1$ represents a stationary population.

The resulting projections exhibited a preponderance of increasing populations; 6 (22.2%) of the hypothetical populations declined and 21 (77.8%) increased. Increases in λ with increased survival, litter size, or proportion breeding may be intuitively expected from a knowledge of the generating functions; however, examination of parameter combinations reveals some important implications. At the lower range of average litter size (4.3), "control" measures would have to reduce survival below 39.1% to achieve a decreasing population even if only 36% of the females were breeding (Table 2). At the

Table 2. Survival values at $\lambda = 1$ for each combination of litter size and proportion of females breeding.^a

Proportion females breeding (%)	Mean litter size	Survival (%)
36	4.30	39.1
36	5.95	31.8
36	7.60	26.8
63	4.30	27.0
63	5.95	21.1
63	7.60	17.3
90	4.30	20.5
90	5.95	15.7
90	7.60	12.8

^a Interpolated from Table 1 by calculating percent survival with $\lambda = 1$ as a function of average survival and λ 's for each level of proportion breeding and litter size.

upper litter size (7.6), effective control with 36% of the females breeding would require reduction of survival to below 26.8%. With 90% of the females breeding, survival must be below 12.8% to achieve $\lambda < 1$. The survival values (Table 2) yield populations with $\lambda = 1$ and even lower survival would be required to achieve population reduction. Statistical demonstration of decreasing populations is difficult for marginal reductions because density estimates for coyote populations often exhibit high variances. Control programs inflicting <50% mortality could not be expected to produce declining populations using any of the combinations of litter size and percent breeding (Table 2). These approaches assume no survival compensation beyond the chosen $p(x)$ value. If the documented mortality (from which our survival values were derived) created a compensatory response resulting in increased survival of those remaining, then the $p(x)$ estimates (Table 2) would be conservative. Conversely, if the extremes of all values were considered, a rapidly increasing population would be projected ($\lambda = 5.63$).

Besides litter size and survival, population responses could be expressed as im-

migration, decreased age at 1st breeding, or increased reproductive lifespan; attributes for which we have no data. Possible environmental influences, such as food or habitat, are included to the extent that they are reflected in the demographic attributes we considered. However, modeling represents a practical management approach that identifies system attributes exhibiting highest values as expected response indicators. This series of simulations emphasizes the possible importance of compensation in the population dynamics of exploited coyotes. One implication of these results is that control measures emphasizing mortality effects may be self-defeating (Knowlton 1972, Connolly and Longhurst 1975).

Analysis of an unexploited coyote population appears necessary. The extent to which coyote populations compensate for increased exploitation appears to be considerable. This compensation, combined with the coyote's general ecological adaptability, may explain its continuing demographic success.

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MARTEN HABITAT PREFERENCES IN THE NORTHERN SIERRA NEVADA

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Escalating harvest of remnant old-growth forests in the Pacific Northwest has precipitated concern for marten (*Martes americana*) as an old-growth dependent species (Meslow et al. 1981). Although recent studies have increased our understanding of marten habitat requirements (Koehler and Hornocker 1977, Soutiere 1979, Steventon and Major 1982), little in-depth research has been done in the Pacific states. Also, the influences of specific forest attributes on marten selection of resting and foraging sites have been insufficiently quantified. This study details marten selection of resting and foraging habitats in the northern Sierra Nevada.

STUDY AREA

Marten were studied in the 40-km² Sagehen Creek Basin in Tahoe National Forest, Nevada County, California. Elevations range from 1,880 to 2,620 m. Summers are short and dry with great diurnal temperature variations; winters are long and nocturnally cold, but with mid-day temperatures often above 0 C. Most of the 91 cm of annual precipitation falls as snow. Average winter snow pack is 112

cm at 1,950 m elevation and may be substantially deeper at higher elevations.

Xeric areas are dominated by Jeffrey pine (*Pinus jeffreyi*) and mixed Jeffrey pine-white fir (*Abies concolor*) (Jeffrey pine associations). Mixtures of lodgepole pine (*P. contorta*) and white fir (mixed conifer associations) dominate below 2,050 m elevation (lower basin). Above 2,050 m elevation (upper basin), red fir (*A. magnifica*) dominates, with admixtures of mountain hemlock (*Tsuga mertensiana*) and western white pine (*P. monticola*) (red fir associations). Moist areas, comprising about 5% of the drainage, are dominated by lodgepole pine and a dense cover of sedges, forbs, and willow shrubs (*Salix* spp.) (riparian lodgepole associations). Large brushfields resulting from wildfire cover one-third of the study area.

METHODS

We captured 14 marten (7M:7F) in Tomahawk livetraps (National Live Trap Co., Tomahawk, Wis.) and radio-collared 6 (2M:4F). Four of these (1M:3F) were located several times each week using hand-held, 2-element Yagi antennas (Telonics Inc., Mesa, Ariz.), yielding 213 observations from July 1979 through August 1980. Observations were classified as "active" or "resting" using signal variability prior to and during the location attempt (Spencer 1981). Pre-observational monitoring of activity ensured that observations in which a marten was inadvertently chased into or out of a refuge by the observer were not misclassified. The obser-

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