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Density dependent matrix model for gray wolf population projection

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Abstract

A Leslie matrix model was developed for a small gray wolf (*Canis lupus*) population recolonizing an area with abundant resources and uncontrolled by humans. The model was modified to describe population growth in a limited environment using a discrete form of the logistic equation. The density dependent Leslie matrix model was applied to investigate gray wolf population recovery in the Upper Peninsula of Michigan. Estimates from the density dependent matrix model were compared with published winter count estimates from the Michigan Department of Natural Resources. The gray wolf population in the Upper Peninsula of Michigan was projected to reach a total of 929 wolves by the year 2012 with a 95% confidence interval of 662 to 1153 wolves.

Keywords: Gray wolf; Leslie matrix model; Logistic equation; Winter count estimates; Abundance

1. Introduction

Before European settlement, the gray wolf (*Canis lupus*) occupied an extensive range throughout North America including the Great Lakes States of Michigan, Wisconsin, and Minnesota. Alteration and loss of habitat, as well as direct extermination, resulted in the gray wolf largely disappearing from the Great Lakes States except within northeastern Minnesota by the middle of the 20th century (Fuller et al., 1992). Within Michigan, the gray wolf vanished from the Lower Peninsula in ca. 1910 and from the Upper Peninsula in ca. 1960 (Anonymous, 2000). The gray wolf was listed as federally endangered in 1974 (excluding Alaska) and is currently pending a delisting in status from endangered to threatened in both Michigan and Wisconsin. With legal protection, the gray wolf population in Minnesota has recolonized northern Wisconsin and the Upper Peninsula of Michigan. Successful recolonization of the gray wolf brings with it a corresponding increase in conflict between wolves and humans and between wolf abundance and other biodiversity (Anonymous, 1997).

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To plan for the management of recolonizing wolf populations in a given area, the extent of recovery needs to be understood. In this study, a matrix model was developed to describe the growth of an uncontrolled (a population that is not being hunted or trapped) gray wolf population introduced either naturally or via human intervention into a given landscape. The matrix model was applied to estimate the annual increase of abundance of the recolonizing gray wolf population in the Upper Peninsula of Michigan. The number of gray wolves determined annually from the Michigan Department of Natural Resources winter count was compared with the annual number of wolves projected with the matrix model for the years 1991 through 2000. In addition, the matrix model was used to project the Michigan gray wolf population for the years 1991 through 2018 with a 95% confidence interval for annual abundance to estimate how long it will take the Upper Peninsula population to reach carrying capacity.

2. Methods

2.1. Model development

A Leslie matrix model was developed using birth pulse fertilities and a prebreeding census (Caswell, 1989; Gotelli, 1998) whereby:

$$N_{t+1} = MN_t \quad (1)$$

where N_t is the vector of age structure at time t, N_{t+1} is the vector of age structure at time $t+1$, and M is the Leslie projection matrix. A prebreeding census is appropriate because application of the model will likely be used with data taken from winter track counts which occur just prior to the wolf breeding season. The wolf breeding season occurs in late January through April (Mech, 1970). The parameters of the Leslie matrix were determined from estimates of the survival rates and fertility values for a population growing at the maximum intrinsic rate of increase.

The Leslie matrix model describes exponential growth in an environment without limitation on resources. To describe population growth in a limited environment, the Leslie matrix model was modified. A simple density dependent matrix model based upon the discrete time scalar logistic equation:

$$P_{t+1} = P_t + \left[\frac{K - P_t}{K}\right] rP_t \quad (2)$$

was applied, where P_{t+1} is the population size at time $t+1$, P_t is the population size at time t, K is the carrying capacity and r is the intrinsic rate of increase. A matrix model analogous to (Eq. (2)) is (Jensen, 1995):

$$N_{t+1} = N_t + D_{(N)t}(M - I)N_t \quad (3)$$

where N_{t+1} is a vector of age classes at time $t+1$, N_t is a vector of age classes at time t, I is the identity matrix, $(M - I)$ is analogous to the intrinsic rate of increase of (Eq. (2)), and $D_{(N)t}$ is a density dependent function at time t:

$$D_{(N)t} = \frac{(K - T_{(N)t})}{K} \quad (4)$$

where $T_{(N)t}$ is the total number of wolves summed over all age classes at time t. The function $D_{(N)t}$ accounts for a carrying capacity in a resource limited environment. In the equations above, the number of individuals of age x at time t (for ages greater than zero) equals the number of age x at time $t-1$ plus a transition. The transition is equivalent to the quantity $D_{(N)t}$ multiplied by the difference between the number of individuals of age x at time $t-1$ and the projected number of individuals of age x at time t.

This modified matrix model was further altered by including a random variable that accounts for annual environmental variation that affects gray wolf population size annually as it affects each age class within the vector N_t. This results in the following equation:

$$N_{t+1} = N_t + D_{(N)t}(M - I)N_t + \xi N_t \quad (5)$$

where ξ is a normally distributed random variable with a mean of 0 and a standard deviation (S.D.) of 0.1; (Eq. (5)) was applied to generate a 95% confidence interval for the annual abundance of the wolf population.

The density dependent matrix model developed here is simple to apply to field populations. The model requires only survival and fecundity estimates, and an estimate for the carrying capacity of an area. The model can be easily integrated with habitat suitability analysis that provides an estimate of carrying capacity for an area.

2.2. Model parameter estimation

Estimates for the Leslie population projection matrix were taken from field studies of real populations. Pimlott et al. (1969) found the age distribution for a stationary wolf population under natural conditions was 31% pups, 18% yearlings, and 51% adults in 1964 and 31% pups, 15% yearlings, and 54% adults in 1965. Averaging the percentages for the 2 years yields ca. 31% pups, 17% yearlings, and 52% adults. These percentages were determined from animals trapped in August, September, October and November of 1964 and 1965 (Pimlott et al., 1969). Thus, pups would be ca. 0–10 months of age, yearlings 10–22 months of age, and adults would be greater than 22 months of age. Intensive study in Algonquin National Park by Pimlott et al. (1969) discovered no detectable change in wolf numbers from 1959 to 1964 (Mech, 1970). The annual survival rates for a stationary wolf population were estimated by Mech (1970) using data from the Pimlott et al. (1969) study and were determined to be ca. 43% for pups, 55% for yearlings, and 78% for adults. The ages used in Mech (1970) estimations allowed for a maximum age of 10 years. The study by Pimlott et al. (1969) found that within a stationary population ca. 59% of the adult females had borne young and that the average litter size was 4.9. In Mech (1970) estimation of survival rates for a stationary wolf population, an average litter size of five was used and an even sex ratio was assumed. Several field studies of gray wolves have documented an equal sex ratio (Mech, 1970).

Values for survival rates and percentage of females breeding taken from analysis of the stationary population were then compared with a population under natural control growing at the maximum intrinsic rate of increase in an environment where resources were abundant (a population that would characterize exponential growth) to determine parameters for use in the Leslie population projection matrix. The maximum intrinsic rate of increase for wolves was estimated to be between 0.28 and 0.33/year (Keith, 1983). The latter rate was the rate determined for wolves on Isle Royale during 1952–1959; a population initiated by a few individuals with abundant food (Keith, 1983). For the uncontrolled wolf population on Isle Royale, annual mortality of adult wolves was 13–16% when the population was increasing (Peterson and Page, 1988). Thus, annual adult survival was found to be as high as 87% on Isle Royale for an increasing, uncontrolled wolf population and this is an 11.54% increase over the stable population adult survival rate of 78% as determined by Mech (1970) from the Pimlott et al. (1969) study. The corresponding values for an 11.54% increase in pup survival and yearling survival from a stable population to a population growing at maximum intrinsic rate of increase would be ca. 47.96 and 61.34%, respectively. In support of these calculations, Fuller (1989) documented a pup survival of 0.48 from birth through mid- November for a growing, protected wolf population in Minnesota.

Wolves are capable of breeding at the age of 22 months (Rausch, 1967; Mech, 1970). The litter size per reproducing female was determined to be five (Mech, 1970) for the stationary population and this value was also used for a population growing at maximum intrinsic rate of increase. For the stationary population of Pimlott et al. (1969), 59% of females were determined to breed, but Rausch (1967) found that 89% of sexually mature females breed and this is considered to be the maximum percentage of females that would breed annually for the species (Mech, 1970). In constructing the Leslie matrix, we assumed that in an environment with unlimited resources (space and food) pack sizes will be smaller and thus a maximum percentage of females will breed.

The Leslie matrix, M, constructed for gray wolves using birth pulse fertilities, a pre-breeding census, and a maximum assumed age of 10 years was determined to be:

$$M = \begin{pmatrix} 0 & F & F & F & F & F & F & F & F & F \\ S_y & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & S_a & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & S_a & 0 & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & S_a & 0 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & S_a & 0 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & S_a & 0 & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & S_a & 0 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_a & 0 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & S_a & 0 \end{pmatrix} \quad (6)$$

where S_y was yearling survival and was equal to 0.61, and S_a was adult survival and was equal to 0.87. Fecundity, F, was equal to 1.07, and was calculated as the product of sex ratio, pup survival, the number of pups produced per female and the percentage of females bearing young (Caswell, 2001). The Leslie population projection matrix of (Eq. (6)) had an intrinsic rate of increase of ca. 0.30/year. This value was within the limits of the maximum intrinsic rate of increase for a gray wolf population as between 0.28 and 0.33/year as estimated by Keith (1983).

In generating a 95% confidence interval for annual gray wolf abundance, a normally distributed random variable with a mean of 0 and a standard deviation of 0.1. was used to compute annual environmental variation that affects all of the age classes in the vector N_t. The S.D. of 0.1 was used because it is consistent with estimates of variation in real populations (Fuller, 1989; Haight et al., 1998). An estimate for S.D. of pup mortality was calculated to be 0.12, and an estimate of the standard deviation of the annual reduction in the number of wolves due to dispersal and mortality between fall and spring was determined to be 0.07 by Haight et al. (1998) using published observations from a wolf population in northern Minnesota (Fuller, 1989).

As the density dependent matrix model was applied to investigate population recovery of gray wolves in the Upper Peninsula of Michigan, an estimate for the carrying capacity parameter within the model, K, was taken from a habitat suitability analysis for the gray wolf in the Upper Peninsula constructed using geographic information systems. A carrying capacity of 969 wolves was determined for the Upper Peninsula of Michigan based upon white-tailed deer abundance and road densities as an indicator of human interaction with wolves (Mladenoff et al., 1995, 1997).

Table 1
Michigan Department of Natural Resources winter estimates of population size for wolves in the Upper Peninsula of Michigan

Year	Estimated population
1991	17
1992	21
1993	30
1994	57
1995	80
1996	116
1997	112
1998	140
1999	174
2000	216

2.2.1. Study area/subject of application

The modified matrix model of Eqs. (3) and (4) was used to estimate the abundance of the recolonizing gray wolf population in the Upper Peninsula of Michigan. Michigan, with a total area of 58 527 square miles, is the largest of five states that make up the Midwest Region of the United States (Theisen, 2001). The Upper Peninsula of Michigan accounts for about 30% of the total land mass of the state, and has a maximum extent of 315 miles from west to east (Theisen, 2001). The Upper Peninsula of Michigan is bounded on the west by the state of Wisconsin, on the north by Lake Superior, on the south by Lake Michigan and Lake Huron, and on the east by the St. Marys River, which marks a border with the Canadian province of Ontario. Within the last ten years, there has been a resurgence of wolves into the Upper Peninsula of Michigan largely by dispersal from Minnesota (Mech et al., 1995; Mladenoff et al., 1995). The confirmed late winter wolf numbers for the Upper Peninsula of Michigan are listed in Table 1, and a mean rate of increase of 0.29/year was calculated from the annual population estimates in Table 1 by regressing $\ln N_t$ against time in years. This value

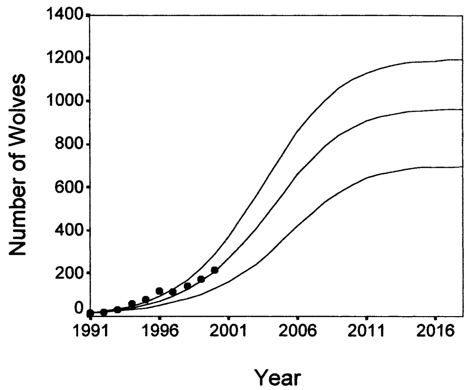

Fig. 1. The number of Upper Peninsula Michigan gray wolves estimated from the Michigan Department of Natural Resources winter wolf count (●) and as projected from the modified Leslie matrix model with a 95% confidence interval for the years 1991 through 2018.

was within the limits of 0.28 and 0.33/year as determined by Keith (1983) for the maximum rate of increase for a wolf population growing with abundant resources.

Estimates of the average annual abundance projected using the density dependent Leslie matrix model for the years 1991 through 2000 were compared with Michigan Department of Natural Resources winter wolf counts, and the projected counts for average annual abundance were used to investigate the number of years it will take the Upper Peninsula wolf population to reach 95% of its estimated carrying capacity of 969 wolves (ca. 920 wolves). In 1991, there were 17 wolves counted in the Upper Peninsula winter count (Anonymous, 1997), and an estimated initial population of eight pups, five yearlings, and four Age four adults (approximately two small packs) was used as an initial population vector in the matrix model. The model was executed 3000 times to generate a 95% confidence interval for gray wolf abundance at each year.

3. Results

Estimates of the average annual abundance of gray wolves in the Upper Peninsula of Michigan were generated using the modified matrix model of Eqs. (3) and (4) for the years 1991 through 2000. The Michigan Department of Natural Resources winter track count estimates of the recolonizing gray wolf population in the Upper Peninsula of Michigan can be compared directly with estimates of the average annual abundance generated using the modified matrix model of equations Eqs. (3) and (4) (Fig. 1). The density dependent Leslie matrix model predicted that, on average, the gray wolf population will reach 95% of carrying capacity which is equivalent to 920 wolves in ca. 21 years which corresponds to the year 2012 (the model actually predicts an average of 929 wolves for the year 2012). The estimated number of gray wolves that will be counted in the Michigan Department of Natural Resources winter count of 2001 is 269 wolves.

To investigate the effects of environmental variation on future gray wolf population size, the density dependent matrix model based upon Eqs. (4) and (5) was used to build a 95% confidence interval for abundance. The results indicated that the Upper Peninsula gray wolf population could reach 95% of its carrying capacity (ca. 920 wolves) as early as the year 2007.

4. Discussion

The estimated Michigan Department of Natural Resources winter wolf count for the year 1994 was 57 wolves, for 1995 it was 80 wolves and for the year 1996 it was 116 wolves. These values do not fall within the 95% confidence interval for annual abundance as predicted using the models presented above. However, this discrepancy between estimates could be explained by considering the impact that immigration could have on a small wolf population, the fact that the Michigan Department of Natural Resources estimates do not have any measure of variance associated with them, and also by considering the construction of the modified Leslie matrix model used in the analysis. The modified Leslie matrix model does not account for immigration, and when the wolf population size for the Upper Peninsula was small an unusual increase of 90% in one year (30 wolves were estimated in the Michigan Department of Natural Resources winter track count of 1993, and 57 were estimated in 1994) could be the result of a substantial amount of immigration from neighboring wolves in Wisconsin and Minnesota. Observations for wolves ear-tagged in Minnesota in 1991 and 1993 that dispersed into the Upper Peninsula of Michigan in 1994 (as well as Wisconsin in 1994) have been documented (Mech et al., 1995). A recent gray wolf population estimate for Minnesota was 2500 wolves (Mech, 1998), and dispersing wolves likely account for 5–20% of an established population (Fuller, 1989).

For each annual winter track count estimate of abundance by the Michigan Department of Natural Resources, there is no corresponding measure of variance. The 90% annual increase resulting from winter track count estimates between 1993 and 1994 is an unusually large increase compared with the range for maximum intrinsic rate of increase for a gray wolf population calculated by Keith (1983) of 0.28–0.33/year, upon which the models presented in this study were constructed. An estimate of variability associated with the Michigan Department of Natural Resources winter track counts may help to explain the large annual increase estimated from the winter track counts between 1993 and 1994.

The parameters used in the density dependent Leslie matrix model used in the present study were taken from observational studies which were

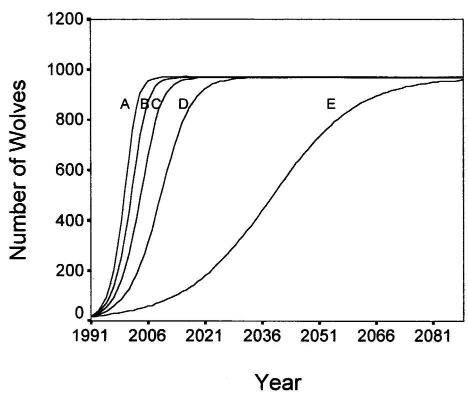

Fig. 2. The effect of pup survival rate on the projection of gray wolf population size using the density dependent matrix model. As shown, (A) pup survival = 0.75; (B) pup survival = 0.6; (C) pup survival = 0.48; (D) pup survival = 0.35; (E) pup survival = 0.2.

subject to variability. Variability in the estimation of survival rate for pups and the estimate of gray wolf carrying capacity for the Upper Peninsula influenced the dynamics of the model. A sensitivity analysis of the model was conducted by examining how years to 95% of carrying capacity was affected by change in pup survival and change in carrying capacity. The annual survival rate of pups has a broad range of reported values from 0.06 to 0.88 (Mech, 1970). Holding the carrying capacity constant at 969, a pup survival rate of 0.2 resulted in an average time period of 80 years to reach 95% of carrying capacity, and a maximum intrinsic rate of increase as determined from the Leslie matrix of only 0.08/year, which is small compared with the observed mean rate of increase of 0.29/year calculated above for the Upper Peninsula Michigan wolf population. In comparison, a pup survival rate of 0.75 resulted in an average of 14 years to carrying capacity, and a maximum intrinsic rate of increase as determined from the Leslie matrix of 0.43/year, which is larger than the range of values of between 0.28 and 0.33/year as estimated by Keith (1983) for intrinsic rate of increase for gray wolf populations (Fig. 2). Within the Great Lakes Region, from field studies it was estimated that survival of pups through the summer was between 0.48 and 0.89 (Fuller, 1989; Fuller, 1995) and during the winter pup survival was estimated to be slightly lower than survival rates of yearlings and adults which were reported as varying from 0.61 to 0.82 (Fuller, 1989). As illustrated in Fig. 2, the projection of average population size over time was less sensitive to changes in pup survival when using a value for pup survival greater than or equal to 0.48. In examining the model sensitivity to carrying capacity, values for carrying capacity were varied from 600 to 1400 (Fig. 3). This is consistent with the estimated 90% confidence interval for carrying capacity for the gray wolf in the Upper Peninsula of Michigan as reported by Mladenoff et al. (1997) of 581 to 1357 wolves. A sensitivity analysis indicated that carrying capacity did not affect the change in average population size over time predicted by the density dependent matrix model when the population size was small, but differences in projected population size increased

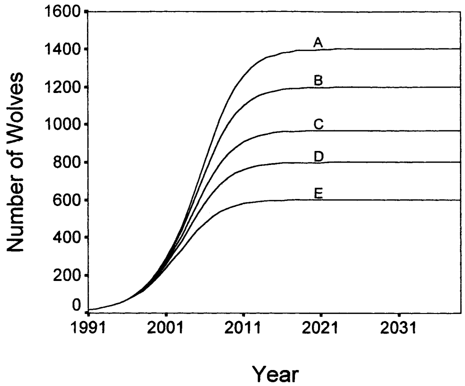

Fig. 3. The effect of carrying capacity on the projection of gray wolf population size using the density dependent matrix model. As shown, (A) carrying capacity = 1400; (B) carrying capacity = 1200; (C) carrying capacity = 969; (D) carrying capacity = 800; (E) carrying capacity = 600.

as population size increased due to the effect of the density dependent function of (Eq. (4)).

5. Management implications

The model applied here can be used to predict future population size for a wolf population where estimates of the vital rates, carrying capacity, and an initial population vector are available. Estimates of abundance will prove useful to wildlife managers in considering a time scale in which to deal with the economic and social consequences of gray wolf recolonization. The model could also be used to examine growth of wolf populations in areas currently being considered for gray wolf population reintroduction such as the northeast states of New York, New Hampshire, Vermont and Maine which were previously identified as a potential location for restoration of the gray wolf (Anonymous, 1992). This model also could be used to address considerations resulting from reclassification of the gray wolf from endangered to threatened when options available to wildlife managers for control of the wolf population will change. The future gray wolf population size in the Upper Peninsula may require direct methods to control the wolf population through legalized government hunting or sterilization. The Michigan Department of Agriculture and the Michigan Department of Natural Resources have recently established a wolf compensation fund targeted to reimburse verified loss of livestock due to wolf predation.

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