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Effects of Social Structure and Prey Dynamics on Extinction Risk in Gray Wolves

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Abstract: *Extinction models based on diffusion theory generally fail to incorporate two important aspects of population biology—social structure and prey dynamics. We include these aspects in an individual-based extinction model for small, isolated populations of the gray wolf (Canis lupus). Our model predicts mean times to extinction significantly longer than those predicted by more general (diffusion) models. According to our model, an isolated population of 50 wolves has a 95% chance of surviving just 9 years and only a 30% chance of surviving beyond 100 years. Reflecting the influence of social structure, a wolf population initially comprising 50 individuals is expected to persist only a few years longer, on average (71 years), than is a population initially comprising just a single reproductive pair (62 years). In contrast, substantially greater average prey abundance leads to dramatically longer expected persistence times. Autocorrelated prey dynamics result in a more complex distribution of extinction times than predicted by many extinction models. We contend that demographic stochasticity may pose the greatest threat to small, isolated wolf populations, although environmental stochasticity and genetic effects may compound this threat. Our work highlights the importance of considering social structure and resource dynamics in the development of population viability analyses.*

Efectos de la Estructura Social y Dinámica de las Presas Sobre el Riesgo de Extinción de Lobos Grises

Resumen: *Los modelos de extinción basados en la teoría de difusión generalmente no incorporan dos aspectos importantes de la biología de poblaciones: la estructura social y la dinámica de las presas. Incluimos estos aspectos en un modelo de extinción basado en individuos para poblaciones pequeñas, aisladas de lobo gris (Canis lupus). Neustro modelo predice tiempos medios de extinción significativamente más largos que los que predicen modelos más generales (difusión). Según nuestro modelo, una población aislada de 50 lobos tiene un 95% de probabilidad de sobrevivir solo 9 años y solo un 30% de probabilidad de sobrevivir más de 100 años. Por influencia de la estructura social, se espera que una población de lobos compuesta inicialmente por 50 individuos persista solo unos cuantos años más en promedio (71 años), que una población inicialmente compuesta por solo una pareja reproductora (62 años). En contraste, la substancialmente mayor abundancia promedio de presas conduce a tiempos de persistencia dramáticamente mayores a los esperados. La dinámica autocorrelacionada de presas resulta en una distribución más compleja de tiempos de extinción que la predicha por muchos modelos de extinción. Sostenemos que la estocacidad demográfica puede ser la mayor amenaza para poblaciones pequeñas y aisladas de lobos, aunque la estocacidad ambiental y los efectos genéticos pueden complicar esta amenaza. Nuestro trabajo resalta la importancia de considerar la estructura social y la dinámica de los recursos en el desarrollo de análisis de viabilidad de poblaciones.*

Introduction

Extinction models based on diffusion theory have been used to gain seemingly robust insights about the relative

importance of demographic and environmental stochasticity (and random catastrophes) as determinants of extinction risk (e.g., Richter-Dyn & Goel 1972; Leigh 1981; Brockwell 1985; Goodman 1987; Lande & Orzack 1988; Lande 1993). Diffusion-based models have also been widely used for the purpose of assessing the extinction risk of specific populations. This application is straightforward

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because it requires nothing more than census data (Braumann 1983; Dennis 1989; Dennis et al. 1991; Foley 1994). The performance of such models applied to specific populations is suspect, however, because a simple form of environmental stochasticity is the only factor explicitly considered (Foley 1994); demographic stochasticity is ignored because its estimation is infeasible and because it is assumed to be important only for very small populations (Dennis et al. 1991; Caughley 1994; Foley 1994).

Models incorporating biologically realistic assumptions may generate predictions that differ, perhaps vastly, from those generated by diffusion models. For example, models that treat births and deaths as interdependent events predict shorter persistence times (Gilpin 1992; McCarthy et al. 1994), and those that include spatially explicit assumptions predict persistence times that are independent of initial population size (Liu 1993; but see Harrison 1991). We develop an individual-based model (DeAngelis & Gross 1992) in which we incorporate social structure and prey dynamics, factors typically ignored in species-specific extinction models (Boyce 1992; but see Hartt & Haefner 1995).

Social structure may inflate the importance of demographic stochasticity by restricting the number of breeding units to the number of social groups (Caro & Durant 1995). Many species exhibit this type of social organization (e.g., Brown 1987; Stacey & Koenig 1990; Moehlman 1979; Malcolm & Marten 1982; Creel & Creel 1990; Keane et al. 1994). Wolves, for example, live in social units (packs) that rarely produce more than one litter of pups annually (Wolfe & Allen 1973; Packard & Mech 1980; Van Ballenberghe 1983*a*). In such cases social organization may increase extinction risk by amplifying demographic stochasticity.

Prey dynamics are also likely to influence extinction risk (Hartt & Haefner 1995). A number of threatened and endangered predator populations depend on long-lived prey (e.g., Jhala 1993; Scheel & Packer 1995; Fuller & Kat 1990) that often exhibit autocorrelated annual fluctuations. Most models do not examine the effect of such fluctuations on extinction risk, and those that do so yield conflicting results (Foley 1994; Tuljapurkar & Orzack 1980). We explore the effect of prey dynamics, a potentially important component of environmental fluctuations.

The Model

Our model is based on empirical data collected between 1959 and 1995 from the gray wolf (*Canis lupus*) and moose (*Alces alces*) population in Isle Royale National Park, Michigan (ISRO), a 544-km^2 island in Lake Superior (Mech 1966; Peterson 1977; Peterson & Page 1988; Thurber & Peterson 1993). The population declined from 50 to 12 wolves in a 2-year period in the mid-1980s (Peterson & Page 1988) and since has failed to recover com-

pletely (Wayne et al. 1991; Thurber & Peterson 1993). Moose comprise nearly the entire diet of ISRO wolves. Beaver occur in the diet only seasonally, during open-water periods (Peterson & Page 1988). Human-caused mortality (hunting) has not confounded population dynamics. Therefore, ISRO wolves and moose can be realistically viewed as a single-predator single-prey system.

The ISRO wolf-moose system has been interpreted as both a top-down (McLaren & Peterson 1994) and a bottom-up trophic system (Peterson et al. 1984; Pastor & Naiman 1992). Both processes probably operate simultaneously in the ISRO predator-prey system; however, the relative contribution of each force remains to be elucidated.

The mechanisms and significance of top-down processes are matters of debate; the influence of wolves on the moose population may be additive, compensatory, or both (Peterson 1977; Peterson & Page 1988). Although wolf predation is known to have a major effect on calf survival (Gasaway et al. 1992), the complex effects of nutritional condition and weather on calf survival and moose dynamics are problematic (Mech et al. 1987). Thus, because our current knowledge of top-down effects is inadequate, we make no attempt to incorporate such effects.

In contrast, numerous studies have documented the bottom-up influence of ungulate abundance on wolf populations (Keith 1983; Peterson & Page 1988; Fuller 1989). The abundance of moose >9 years old (hereafter "old moose") may have an important influence on wolves in the ISRO system, reflecting the wolves' strong reliance on old (senescent) moose (Peterson 1977). Old moose are the primary component of the ISRO wolf diet, whereas calves are a much smaller component of the diet (Peterson 1977). We contend that the relationship between the number of wolf packs and the abundance of old moose is likely to be at least as important as the relationship between the number of wolves and the abundance of old moose (Fig. 1). Therefore, we model wolf population dynamics as influenced by moose population dynamics.

We constructed an individual-based, bottom-up model, where the dynamics of moose abundance influence the wolf population. Moose abundance is modeled as a statistical autoregressive process, with parameters estimated from empirical data. The wolf population consists of individual wolves belonging to individual packs. The number of packs are determined in part by the number of moose. Young are born within each pack and wolves experience an age-specific mortality risk.

Wolf Population

Initial conditions for the wolf population include the number of packs, the number of wolves belonging to each pack, and the age and sex of each wolf. A litter is added annually to each pack comprising at least one
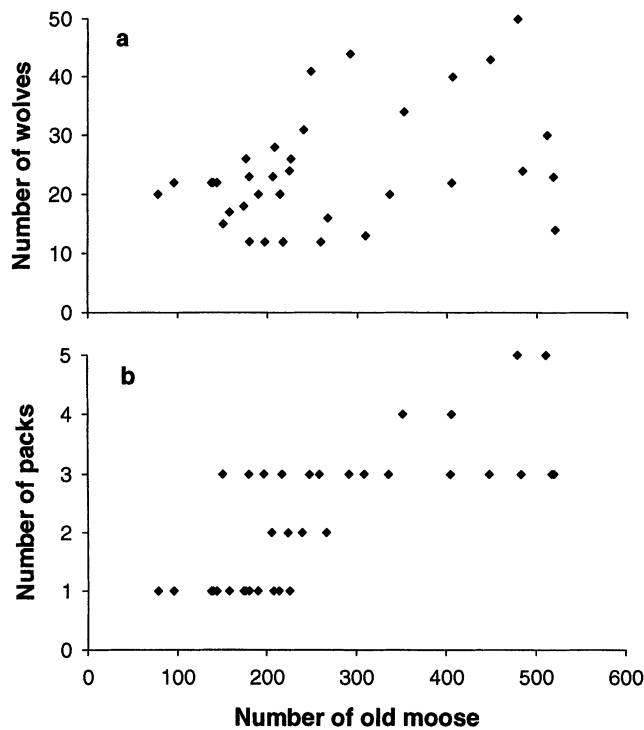
Figure 1. Relationships between the number of old moose (>9 years old) and the number of individual wolves (a) or the number of wolf packs (b) in Isle Royale National Park, 1959-1994.

Table 1. The observed and fitted age-specific mortality rates for Isle Royale wolves.

Age (years)	Age-specific mortality	
	Observed	Fitted
0	0.35	0.47
1	0.27	0.23
2	0.19	0.13
3	0.15	0.08
4	0.18	0.07
5	0.11	0.08
6	0.19	0.10
7	0.07	0.16
8	0.17	0.26
9	0.60	0.45
10	0.75	0.79
11	1.00	1.00

male and one female. Litter size is selected randomly from an empirical distribution. Each individual's sex is assigned randomly at birth. During each year of the simulation, each wolf has an age-dependent probability of survival until the next year (Appendix and Table 1).

Pack Structure

The dynamic nature of pack structure is not well understood, but the number of packs is positively correlated with the number of moose (Fig. 1a). Therefore, in each year of the simulation, the number of packs is selected randomly from a probability distribution that depends on the number of moose. A multinomial response model (Agresti 1990) was used to predict the probability distribution of the number of packs given the number of old moose (Appendix).

This model closely mimics empirical pack dynamics (Fig. 2), although it is statistical in nature and does not rely explicitly on knowledge of any biological process. The simulated number of packs changes slowly over time, resembling the empirical trajectory. This inertia arises from gradual changes in the old moose population that lead to gradual changes in the probability distribution of the number of wolf packs. The process is analogous to a slowly changing random walk model. Although the number of packs is randomly selected each

year, there is a high probability that the number of packs will remain unchanged from one year to the next.

Each time the simulation predicts the formation of a new pack, the youngest male (>1 year old) from the pack with the most males and the youngest female from the pack with the most females are combined to form the pack. A pack is reconstituted similarly if it has gone extinct due to demographic chance (rather than due to any change in moose abundance). This process is based
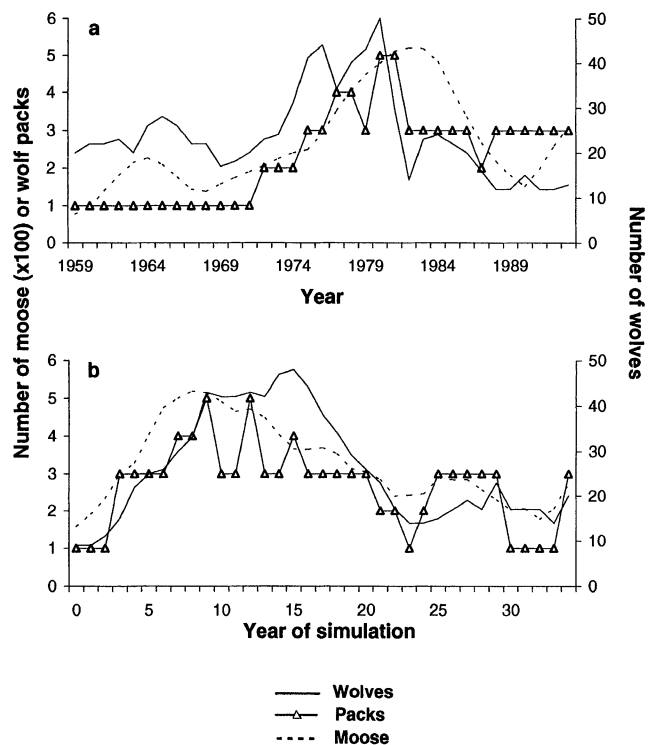

Figure 2. Trajectories for the number of wolves, packs, and old moose estimated empirically for Isle Royale National Park, 1959-1994 (a) and predicted by a typical run of the simulation model (b).

Table 2.   Effect of mortality rates (probability of death each year) of adult and juvenile wolves on mean time to extinction (MTE).

| | *Juveniles* | | | | *Adults* | | | | |
| | *Age (years)* | | | | *Age (years)* | | | | |
Mortality rate	*0*	*1*	*2*	*MTE (years)*	*3*	*4*	*5*	*6*	*MTE (years)*
Low	0.30	0.15	0.07	193	0.05	0.05	0.05	0.05	87
Predicted*	0.47	0.23	0.13	71	0.08	0.07	0.08	0.10	71
High	0.60	0.40	0.20	18	0.15	0.15	0.15	0.15	47

Predicted mortality rates (see Table 1 and Appendix) were used to evaluate sensitivity of MTE to other variables.

on the assumption that wolves will occupy the vacated territory. Coincidental with the prediction of the loss of a pack due to reduced moose abundance, the members of the smallest pack are assumed to disperse, as occurs in nature (Van Ballenberghe 1983*b*). Each wolf in the dispersing pack experiences an elevated mortality (60%) for the year of the dispersal event, and surviving wolves are recruited randomly into existing packs.

Old Moose (Prey) Population

For simplicity we also used a statistical model to simulate moose population dynamics. We chose an autoregressive-moving average (ARMA) model (Pankratz 1991) to describe the serial correlation in the moose trajectory (Fig. 2b). We adopted this statistical (rather than process-based) approach for the same reasons that we ignore potential top-down effects. The specific model used to describe the moose population was selected according to standard model-selection techniques (Appendix).

Simulations and Results

Simulated trajectories of the numbers of old moose, wolves, and packs were qualitatively similar to empirical trajectories from ISRO (Fig. 2). With all parameter values fixed, we calculated the mean time to extinction (MTE) based on the extinction times of 10,000 simulated populations. We evaluated the sensitivity of MTE by varying one parameter at a time.

Table 3.   Theoretical and observed distributions of wolf litter size.

| *Litter size* | *Theoretical distribution[a]* | *Observed distributions[b]* | |
		1980-1994	*1970-1979*
0	0.37	0.11	0.46
1	0.37	0.00	0.08
2	0.18	0.11	0.08
3	0.06	0.20	0.17
4	0.02	0.32	0.17
5	0.00	0.21	0.04
6	0.00	0.05	0.00

[a]*The theoretical distribution is Poisson with mean of one pup.*
[b]*The observed distributions have means of two (1980-1994; n = 24) and three pups (1970-1979; n = 19).*

Wolf Demographic Parameters

We obtained estimates of age-specific mortality (Table 1; Appendix) from a life table calculated according to Caughley (1966) and based on observations of the age at death of 35 ISRO wolves (R. O. Peterson, unpubl. data). The model's sensitivity to age-specific mortality was assessed by varying mortality rates for different age classes (Table 2). Briefly, increases in juvenile mortality lowered MTE more than did increases in adult mortality.

We assessed the model's sensitivity to average litter size by calculating MTE for simulations based on distributions of litter sizes with different mean values. These distributions were based on the observed litter size for every ISRO pack from 1970 until 1995. The average litter size was approximately three pups prior to the crash of the wolf population (1971-1979; Table 3). Since the crash (1980-1994), the average litter size has been approximately two pups. This reduced fecundity has put the ISRO wolf population at increased risk of extinction (Wayne et al. 1991). Hence, we compared MTE for simulations assuming distributions of litter size observed

Table 4.   Effect of parameters on mean time to extinction (MTE).[a]

Parameter/value	*MTE (years)*
Average litter size	
1	10.7
2 (observed 1980-1994)	25.4
3 (observed 1971-1979)[b]	71.3
Initial number of packs[c]	
1	62.3
2	66.0
3	70.7
4	77.6
5	87.8
Average size of old moose population	
200	50.3
250	77.8
300	148.0
305	155.4
350	207.9
400	229.0

[a]*Predicted adult and juvenile mortalities and observed distributions of litter sizes are given in the Appendix.*
[b]*Values used in sensitivity analysis.*
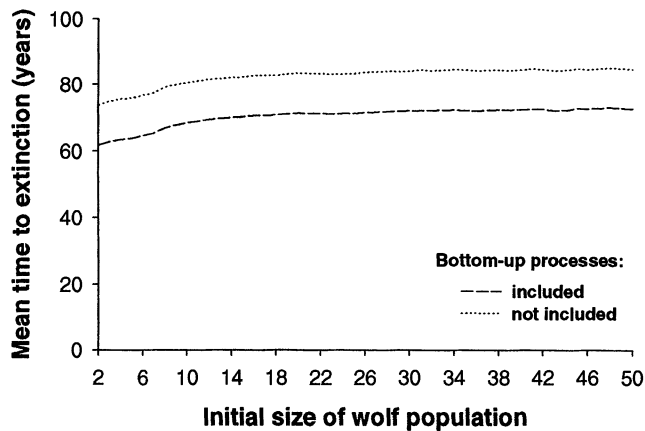[c]*Initial population size was 10 for all trials.*

Figure 3. The influence of initial size of the wolf population on the mean time to extinction (MTE) of simulated wolf populations assuming bottom-up processes and no bottom-up processes. When the initial number of wolves was 2-3, the initial number of packs was one; when the initial number of wolves was 4-30, the initial number of packs was two; and when the initial number of wolves was >30, the initial number of packs was three.

both prior to and since the population crash. To evaluate the effect of even lower fecundity, we also calculated MTE assuming an average litter size of one pup (based on Poisson expectation; Table 3). The model predicted relatively large increases in MTE as average litter size increased (Table 4).

Mean Time to Extinction and Initial Population Size

Increases in the initial size of the wolf population had little effect on MTE. An increase by one wolf raised MTE only 0.25 years on average (Fig. 3). In contrast, an increase in the initial number of packs by one (when initial population size is constant) raised MTE 5.7 years, on average (Table 4). This insensitivity of MTE to initial population size is attributable to the social structure of gray wolves. To evaluate this claim, we isolated the influence of social structure on demographic stochasticity by removing bottom-up assumptions. We used a random walk model to simulate the number of packs independent of the abundance of old moose. This model relies on empirically derived transition probabilities (i.e., the probability of observing some number of packs in year t, given the number of packs observed in year $t-1$). The MTE was insensitive to initial population size in this model as well (Fig. 3).

To compare our predictions with those based on diffusion theory, we also predicted MTE based on empirical estimates of average log growth rate ($\bar{r} = -0.08$), variation of that rate ($V_r = 0.31$), and carrying capacity ($K = 50$, the maximum number of wolves observed in ISRO).

We used Equations 6 and 8 in Foley (1994) to generate the relationship between MTE and initial population size (Fig. 4). Diffusion-based predictions differed from our predictions in two ways. First, the diffusion model predicted that the MTE will more than triple as initial population increases from two (MTE = 7 years) to approximately 25 wolves (MTE = 27 years). In contrast, our model predicts no significant increase in MTE as initial population size increases over the same range. Second, the diffusion model predicted overall MTEs less than half of what our model predicted.

Average Prey Abundance

Although constant prey abundance is an ecologically unrealistic assumption, simulations based on the assumption of constant old moose abundance are potentially useful because they reveal the effects of average prey abundance and, by comparison, fluctuations in prey abundance. Our simulations predicted that MTE would increase four fold if constant prey abundance were doubled (from 200 to 400 old moose; Table 4). This increase is plausible because greater abundance of old moose results in a higher average number of packs and, thereby, a greater MTE. We tentatively evaluated the contribution of environmental stochasticity to extinction risk by comparing MTE when prey abundance was held at 305 moose versus when prey abundance was modeled as a stochastic ARMA process (where average prey abundance was 305 moose). The MTEs were 155 and 70 years for the simulations with constant and stochastic prey abundance, respectively.

Cyclic Prey Dynamics

Several mammalian and avian species exhibit significant cyclic fluctuations (Moran 1953; Bulmer 1975; Finnerty
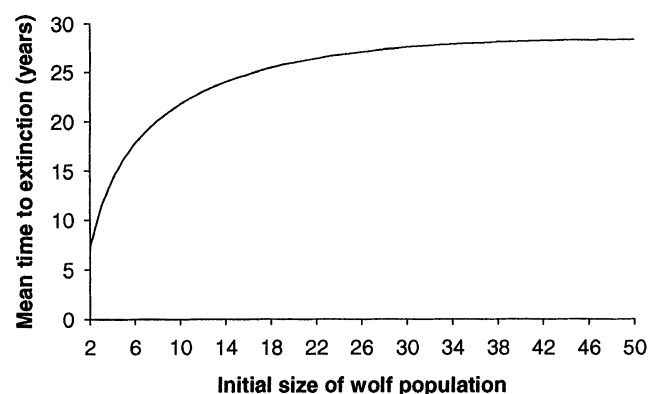

Figure 4. The influence of initial size of the wolf population on the mean time to extinction of simulated wolf populations as predicted by a diffusion model.
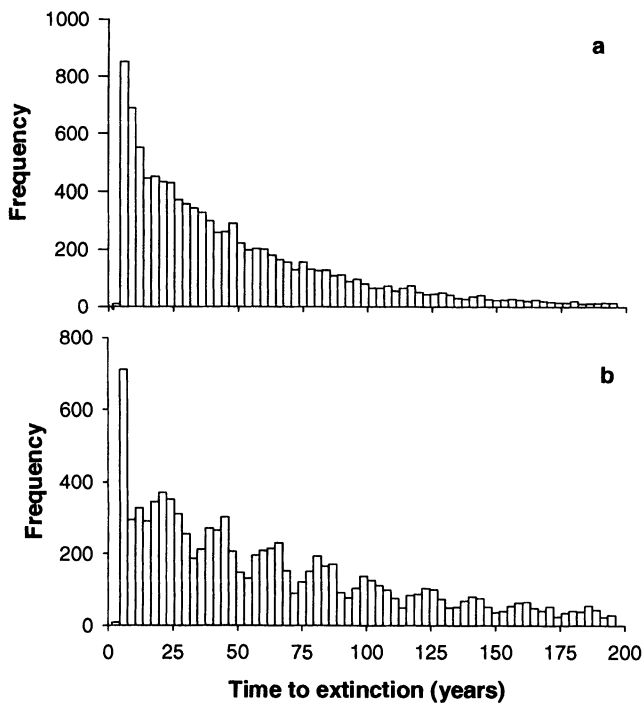
Figure 5. The distribution of extinction times of simulated wolf populations where the old moose population was constant (200 moose) (a) or cyclical (mean = 200 moose, period = 30 years, and amplitude = 150 moose) (b).

1980; Peterson et al. 1984; Boyce & Miller 1985). We assessed the effect of deterministic cyclicity by modeling moose abundance as a sine function. We ran simulations with various means, amplitudes, and periodicities approximating those observed in ISRO empirical data. Due to increased variance in prey abundance, cyclicity led to reduced MTE in all cases. For example, MTE was 155 years when prey abundance was a constant 305 old moose, but only 105 years when the abundance of old moose was modeled as a sine function with an average of 305 old moose (amplitude = 215, period = 20 years).

We evaluated another effect of deterministic cyclicity by examining the distribution of extinction times. This distribution was approximately exponential when moose abundance was constant (Fig. 5a). A more complex distribution of extinction times resulted when moose cycled with the same average abundance (Fig. 5b).

Discussion

In the absence of any consideration of social structure, the contribution of demographic stochasticity to extinction risk diminishes quickly with increases in population size (Lande 1993; Caughley 1994). However, numerous species exhibit social behavior where the number of

breeding units is limited to the number of social groups (e.g., reproductive suppression [e.g., Creel & Creel 1990; but see Keane et al. 1994] and cooperative breeding [reviews by Brown 1987; Stacey & Koenig 1990]). In such populations demographic stochasticity (due to variance in fecundity) decreases with increases in the number of social groups, not with increases in the number of individuals per se (Figs. 3, 4, and Table 4). For example, a larger wolf population (e.g., 45 in 1976) divided into a few packs (three) has the same reproductive potential (one litter per pack per year) as a smaller wolf population (e.g., 14 in 1982) divided into the same number of packs (Fig. 2). Social structure constrains MTE and leads to insensitivity of MTE to initial population size. Furthermore, it has a major influence on extinction risks regardless of whether population dynamics are influenced by prey dynamics (Fig. 3). Therefore, although the incorporation of any influence of wolves on prey dynamics would likely lead to increased complexity, it seems unlikely that this influence would supersede that of social structure.

Although low genetic variability has raised doubts about the population viability of ISRO wolves (Wayne et al. 1991), our results suggest that demographic risk alone constitutes a substantial threat. For example, the model predicts that a population of 50 wolves has an MTE of 73 years, a 95% chance of surviving just 9 years, and only a 30% chance of surviving beyond 100 years. These findings support the view that wolf populations of fewer than 100 individuals in natural reserves smaller than 500 km^2 may be inadequate for long-term survival (Fritts & Carbyn 1995; albeit our approach differs from theirs). This result also has significant implications for the viability requirements of species such as the African wild dog (*Lycaon pictus*), which exhibits a similar social structure but requires a substantially larger home range (Burrows 1995). Populations that are characterized by reproductive suppression and comprise a moderate number of individuals, and thus a small number of social groups, will suffer significant extinction risk due to demographic stochasticity alone.

Prey dynamics, a component of environmental stochasticity, also contribute to extinction risk. The MTE was lower when prey abundance was modeled as an ARMA process (versus when it was constant or deterministically cyclical; Table 4). A striking consequence of cyclic prey dynamics is the complex distribution of times to extinction, which reflects annual changes in the probability of extinction (Fig. 5). Years of declining prey abundance are associated with increasing extinction risk, and years of increasing prey abundance are associated with decreasing extinction risk. By contrast, many models, including those based on diffusion theory, predict an approximately exponential or inverse Gaussian distribution of extinction times (Lande & Orzack 1988; Foley 1994; Mangel & Tier 1994; for rationale see Goodman 1987).

Despite purported advantages of using diffusion mod-

els to predict MTE for specific populations of conservation concern, this approach can lead to gross errors in estimating population viability. Errors may result for at least two reasons. First, diffusion models ignore demographic stochasticity (Dennis et al. 1991; Foley 1994). The rationale for ignoring demographic stochasticity arises from the impracticality of its estimation (Foley 1994) and the theoretical finding that environmental stochasticity and random catastrophes are often stronger determinants of extinction risk (Lande 1993). However, our findings suggest that the effect of demographic stochasticity is significant, due to social structure, and may prevent MTE from increasing significantly as population size increases (cf. Figs. 3 and 4).

Second, diffusion models ignore density dependence which may result in underestimation of the MTE. Density dependence tends to increase the MTE by stabilizing a population trajectory toward its equilibrium (carrying capacity; Ginzburg et al. 1990; Stacey & Taper 1992). Our model does not explicitly incorporate density dependence; however, the interaction between wolf and moose population dynamics may act as a stabilizing force for the wolf population. This may explain the longer persistence times that we predict relative to the predictions of diffusion models.

Our recognition of the significance of social structure and prey dynamics prompts several recommendations for the conservation and management of wolf populations. The addition or removal of *individual* wolves should have little impact on expected persistence as influenced by demography (Fig. 3). Management efforts aimed at increasing the average number of *packs* may have greater impact on persistence. However, upon artificially adding or removing packs, a population may reconfigure itself, dividing into the number of packs sustainable by the current abundance of prey (Fig. 1). Efforts leading to an increase in average prey abundance may thus be the most effective tactic (Table 1). These considerations may be unimportant, though, when human activity elevates wolf mortality or degrades wolf habitat (Mech 1995; Mladenoff et al. 1995).

Diffusion models are useful tools for gaining insights regarding factors contributing to extinction risk; however, they may provide poor estimates of viability for specific populations. The disparity between MTEs predicted by our model versus those predicted by a diffusion-based model highlights the importance of developing species-specific models and incorporating social structure (and prey dynamics) wherever appropriate. Our work indicates that wolf populations limited to a few packs will have low viability largely because their social organization tends to inflate the effect of demographic stochasticity. The demographic and genetic contributions to extinction risk for a variety of complex social systems (e.g., Packer 1977; Packer et al. 1990; Caro 1994) remain to be explored.

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Appendix.

Multinomial Response Model: The model is designed to predict the distribution of a discrete dependent variable based on the value of a continuous independent variable (Agresti 1990). The model is given by

$$P[Y \le i | X = x] = \frac{\exp(\alpha_i + \beta^* x)}{1 + [\exp(\alpha_i + \beta^* x)]}, \tag{1}$$

where Y is the number of packs, X is the number of old moose, and α_i and β are coefficients estimated from the data in Fig. 1a. The estimates ($\alpha_1 = 4.01$, $\alpha_2 = 4.89$, $\alpha_3 = 9.55$, $\alpha_4 = 10.55$, $\beta = -0.02$) were obtained using the GLM procedure (SAS Institute 1989). Equation 1 is interpreted as the probability that the observed number of packs, Y, will be less than or equal to i ($i = 1, 2, \ldots, 4$) given that there are x moose. The probability distribution of the number of packs, given the observed number of old moose, was generated using Equation 1.

Autoregressive-Moving Average (ARMA) Model of Moose Dynamics: In general, ARMA models consist of a structural component reflecting the serial correlation in the empirical trajectory and a random component whose magnitude is also estimated from the empirical trajectory. An ARMA model was constructed by (1) inducing stationarity (constant mean and variance) through data transformation; (2) determining an initial estimate for the number of autoregressive and moving-average terms; (3) estimating the parameters; and (4) comparing the model's fit to that of alternative models with fewer or more parameters (Pankratz 1991).

Differencing, a standard transformation in ARMA modeling, led to a stationary time series of moose abundance. The difference transformation is given by

$$Z_t = M_t - M_{t-1}, \tag{2}$$

where M_t is the number of old moose at time t. Stationarity was confirmed by examining the empirical autocorrelation function (ACF; i.e., the correlation between all pairs of data points, Z_t and Z_{t-k}, where $k = 0, 1, \ldots N/4$, and N is the length of the time series). Comparison of the empirical ACF with theoretical ACFs also indicate that one autoregressive term (and no moving-average terms) adequately modeled the moose time series (Vandaele 1983). Expressed in terms of Z_t, this model is written as

$$Z_t = \mu + \phi(Z_{t-1}) + \varepsilon_t,$$
$$\varepsilon_t \sim N(0, \sigma^2), \tag{3}$$

where μ is the average value of the process and ϕ is the autoregressive

coefficient. The stochastic component of the model, ε_t, is a normally distributed random variable with mean zero and variance σ^2. Substituting $M_t - M_{t-1}$ for Z_t and rearranging, the model may be expressed in terms of the number of moose at time t:

$$M_t = \mu + M_{t-1} + \phi(M_{t-1} - M_{t-2}) + \varepsilon_t. \tag{4}$$

The parameter estimates ($\mu = 14.2$, $\phi = 0.296$, $\sigma^2 = 1547.6$) were obtained using the ARMA procedure (SAS Institute 1989).

The appropriateness of Equation 4 was assessed by comparing its performance to that of alternative models with different numbers of ARMA terms. Performance was assessed using standard criteria model evaluation, including Akaike's information criterion, ACF of model residuals, and the P-value for the null hypothesis that the residuals are white noise (Vandaele 1983; Pankratz 1991). For all criteria Equation 4 outperformed all alternative models.

Simulated moose trajectories were generated using Equation 4 by selecting seed values for M_{t-1} and M_{t-2} and selecting a random error term, ε_t, for each year of the simulation. The seed value for all simulations was 305 old moose. (The use of other seed values did not change the interpretation). We bounded the simulated old moose trajectories between 90 and 520 old moose, the minimal and maximal numbers of old moose observed on ISRO.

Age-specific Wolf Mortality Table: Age at death was estimated for 35 wolves in the ISRO population using cementum increment analysis (Waite 1994) and regressing radiocarbon activities of amino acids isolated from tooth dentin on northern hemispheric radiocarbon activity of atmospheric CO_2 from 1948 to 1984 (Bada et al. 1990). From these data we constructed a life table following Caughley (1966) and thereby obtained age-specific mortality rates (Table 1). Observed age-specific mortalities were fit to a mortality curve (Siler 1979):

$$q_x = a_1 e^{-b_1 x} + a_2 + a_3 e^{b_3 x}, \tag{5}$$

where x is age and q_x is the age-specific mortality rate. Estimates of other parameters ($a_1 = 0.4302$, $a_2 = 0.0336$, $a_3 = 0.0020$, $b_1 = 0.8073$, and $b_2 = 0.5933$) were obtained using the Marquardt algorithm in the NLIN procedure (SAS Institute 1989). The age-specific mortality function represented by Equation 5 (and Table 1) was used to assess the effect of age-specific mortality on MTE (Table 2).