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Original Article

Growth Rates and Variances of Unexploited Wolf Populations in Dynamic Equilibria

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ABSTRACT Several states have begun harvesting gray wolves (*Canis lupus*), and these states and various European countries are closely monitoring their wolf populations. To provide appropriate perspective for determining unusual or extreme fluctuations in their managed wolf populations, we analyzed natural, long-term, wolf-population-density trajectories totaling 130 years of data from 3 areas: Isle Royale National Park in Lake Superior, Michigan, USA; the east-central Superior National Forest in northeastern Minnesota, USA; and Denali National Park, Alaska, USA. Ratios between minimum and maximum annual sizes for 2 mainland populations ($n = 28$ and 46 yr) varied from 2.5–2.8, whereas for Isle Royale ($n = 56$ yr), the ratio was 6.3. The interquartile range (25th percentile, 75th percentile) for annual growth rates, N_{t+1}/N_t, was (0.88, 1.14), (0.92, 1.11), and (0.86, 1.12) for Denali, Superior National Forest, and Isle Royale respectively. We fit a density-independent model and a Ricker model to each time series, and in both cases we considered the potential for observation error. Mean growth rates from the density-independent model were close to 0 for all 3 populations, with 95% credible intervals including 0. We view the estimated model parameters, including those describing annual variability or process variance, as providing useful summaries of the trajectories of these populations. The estimates of these natural wolf population parameters can serve as benchmarks for comparison with those of recovering wolf populations. Because our study populations were all from circumscribed areas, fluctuations in them represent fluctuations in densities (i.e., changes in numbers are not confounded by changes in occupied area as would be the case with populations expanding their range, as are wolf populations in many states). © 2015 The Wildlife Society.

Gray wolf (*Canis lupus*) populations have recovered in the Upper Midwest and the northern Rockies and have been removed from the Federal Endangered Species List in several states. Thus, wolf management has been returned to individual states, and 6 states have been managing wolves via public harvesting with varying degrees of regulation (Mech 2013). Public harvesting of wolves has been met with considerable dismay by a large segment of the public, and lawsuits challenging the delisting have been filed in attempts to restore federal protection to these populations (Mech 2013). This sensitivity to public wolf hunting has brought scrutiny to harvest regulations, quotas, seasons, and population estimates (Creel and Rotella 2010 but see Gude et al. 2012).

Most state wolf-population estimates are necessarily minimum estimates, but the media and the public have interpreted and disseminated them as actual numbers. Furthermore, the media and the public then erroneously interpret decreases in consecutive, annual, minimum estimates as actual population decreases and attribute the apparent decreases to public harvesting. However, wolf populations fluctuate considerably under natural conditions (Fuller et al. 2003), and such natural fluctuations can be mistakenly attributed to public harvesting.

Because of all these issues, it is useful to characterize long-term trajectories of protected wolf populations to elucidate the fluctuations that occur naturally. One way to characterize population trajectories is to fit simple population-dynamic models to observed counts (Dennis et al. 1991, Morris and Doak 2002). For example, density-independent models are frequently used for performing population-viability assessments, and although forecasts of future dynamics are often imprecise (e.g., Fieberg and Ellner 2000), these models have been shown to provide useful approximations to complex population models, including those with age-structure and density dependence (e.g., Holmes 2004, Sabo et al. 2004, Holmes et al. 2007). New statistical methods also have been recently developed that allow one to account for observation errors when fitting population models, which should result in more accurate estimates of natural (or process) variability when population size is estimated with error (e.g., de Valpine 2002, 2003; Staples et al. 2004; Nadeem and Lele 2012). We fit 2 simple population-dynamic models—a density-independent model and a Ricker model (Ricker 1954)—to 3 long-term data sets available from national

parks and protected populations, while allowing for various forms of observation error. These population trajectories, and the summaries provided by the fitted parameters, can provide an appropriate context for interpreting fluctuations in harvested populations, thus helping inform managers, the media, and the public.

STUDY AREAS

The 3 areas where long-term data on wolf-population trajectories have been collected are Isle Royale National Park in Lake Superior, Michigan, USA, the east-central Superior National Forest in northeastern Minnesota, USA, and Denali National Park, Alaska, USA. We chose data from these 3 areas rather than from the recently recovered populations of various states and Yellowstone National Park because the latter populations were still establishing. In addition, the populations other than that in Yellowstone National Park were expanding in range, so population changes there do not necessarily reflect density fluctuations.

Isle Royale was a 544 km^2 island in northern Lake Superior that had supported moose (*Alces alces*) since the early 1900s and wolves since 1949. No other ungulate or large carnivore existed there. Beavers (*Castor canadensis*) formed the only other significant prey and were only available part of the year. Isle Royale was 24 km from the nearest mainland, with little documented wolf immigration or emigration (Vucetich et al. 2012). The wolf population had been highly inbred since its founding in late 1949 (Wayne et al. 1991, Adams et al. 2011). The Isle Royale wolves were legally protected throughout the study, and population data had been recorded since 1959. Additional background information is available from Mech (1966), Allen (1979), Peterson (1977), and Vucetich and Peterson (2009).

The east-central Superior National Forest wolf-study area in northeastern Minnesota comprised 2,060 km2 of the Minnesota wolf range, which is contiguous with the Ontario, Canada, wolf range. Wolves were legally protected there since 1971, and most of the area was relatively inaccessible during autumn hunting seasons, although some poaching did occur around the edges of the study area. The area supported white-tailed deer (*Odocoileus virginianus*), moose, and beavers as the main wolf prey; black bears (*Ursus americanus*) also inhabited the area as a competitor. Further information about the study area is available from Mech (2009).

Denali National Park and Preserve lay in south-central Alaska, and its 17,270 km^2 wolf-count area was part of the entire Alaska wolf population range and harbors wolves as well as moose, caribou (*Rangifer tarandus*), Dall's sheep (*Ovis dalli*), and beavers as prey. The park also supported both black bears and grizzly bears (*Urcus arctos*). Wolves were protected in the park but could be hunted and trapped in the preserve, and some park wolves ventured out of the park and were subjected to human harvesting. From 1986 to 2002 an estimated 4–7% of Denali wolves were killed by humans each year (Mech et al. 1998, Adams et al. 2008). Additional background information about the area is available from Murie (1944) and Mech et al. (1998).

METHODS

Wolf counts in all 3 areas were conducted in late winter, when wolf populations were close to their annual minimum. On Isle Royale, wolves were counted each winter from 1959 through 2014 by tracking them in snow via light, fixed-wing aircraft until the wolves were seen (Mech 1966, Jordan et al. 1967, Wolfe and Allen 1973, Peterson 1977, Vucetich and Peterson 2014). Aerial radio tracking supplemented the snow-tracking in various years since 1989. The relatively small study area allows a complete count of the wolves to be made each winter.

In the Superior National Forest study area, wolves were counted each winter from 1967 through 2012 in a circumscribed area primarily by radiotracking and observation from light, fixed-wing aircraft (Mech 1973, 1986, 2009). When not all packs in the study area were radio tagged, aerial snow-tracking was used, similar to Isle Royale, to locate and count pack members via direct observation, but sometimes by counting tracks in snow. The wolves were legally protected from 1971 through early 2012; from 1967 through 1970, few wolves were killed by hunters and/or trappers because most of the area was inaccessible except on foot.

Similar techniques were used to count the wolves in Denali National Park using aerial telemetry (Mech et al. 1998) from 1986 through 2013. However, because of the park's much larger size, the approach was modified by applying the density of counted wolves (no. of wolves per total area of their aggregate home ranges based on minimum-convex polygons) to the entire wolf habitat in the park. The aggregate area of wolf packs radiotracked each year averaged 14,208 km^2 $\pm$ 490 (SE) or 82% of the study area (U.S. National Park Service 2013).

Because all 3 of our study populations were from circumscribed areas, we emphasize that changes in their numbers reflect changes in wolf densities, assuming no change in detection probabilities or counting efficiency. By contrast, populations having no boundaries, such as those in most states and countries, can increase or decrease in number by expansion of their total distribution, aside from changes in density.

STATISTICAL METHODS

To compare the characteristics of the wolf-population trajectories from the 3 studies (Table 1), we fit 2 different stochastic population models—a density-independent model and a Ricker model (Ricker 1954)—to each time series of wolf population counts. Let N_t represent the true population size at time t and $X_t = \log(N_t)$. The Ricker model is given by the following:

$$N_{t+1} = N_t \exp(a + b N_t + \varepsilon_t); \varepsilon_t \sim N(0, \sigma_p^2); \text{ or equivalently}$$

$$(1)$$

$$X_{t+1} = X_t + a + b N_t + \varepsilon_t; \varepsilon_t \sim N(0, \sigma_p^2),$$

A value of $b < 0$ is suggestive of density dependence, in which case the parameter a describes the growth rate at low population densities. The density-independent model is formed by setting $b = 0$ in Equation 1. In both models, the ε_t's represent normally distributed deviations of the true log-population size from

Table 1. General characteristics of 3 population trajectories of wolves from protected areas in Isle Royale National Park in Lake Superior, Michigan, USA (1959–2014); the east-central Superior National Forest in northeastern Minnesota, USA (1967–2012); and Denali National Park, Alaska, USA (1986–2013).

Characteristic	Denali National Park	Isle Royale	Superior National Forest
Area (km^2)	2,060	544	17,270
No. of yr	28	56	46
Mean size (SE)	91 (4.4)	23 (1.2)	63 (2.3)
Annual range	53–134	8–50	35–97
Percent yr above mean	54	43	39
Percent yr below mean	46	57	61
Max.:min. population	2.5	6.3	2.8
Max. annual growth rate, $\lambda_t = (N_{t+1}/N_t)$	1.49	1.79	1.54
Min. annual growth rate	0.71	0.47	0.65
No/1,000 km^2	3.1–7.8	14.7–91.9	17.0–47.1

model-based expected values. The process variance, σ_p^2, quantifies the magnitude of these deviations.

As with most population surveys, the true population size may differ from the reported count (i.e., observation errors are likely present in the data). Yet these errors are expected to be small because wolf packs in each of the populations were intensely monitored with the aid of radio collared animals and snow-track surveys. Although sampling error is relevant to the Denali counts, errors associated with the Isle Royale and Superior National Forest counts most likely result from lone wolves that do not commonly associate with a single pack; these errors are not likely to follow a common statistical distribution. Thus, to assess robustness of the estimators of population dynamic parameters to the assumed form of the observation error model, we considered 2 alternatives (along with a model that assumed no observation error). Let O_t represent the observed count and $Y_t = \log(O_t)$. We considered the following models:

1. No observation error: $O_t = N_t$ or equivalently, $Y_t = X_t$.

2. Poisson observation errors: $O_t \sim \text{Poisson}(N_t)$.

3. Log-normal observation errors: $Y_t \sim N(X_t, \sigma_{obs}^2)$.

Models that allow for observation errors are most easily fit using Markov chain Monte Carlo techniques frequently used in Bayesian applications, although data cloning, which uses multiple copies of the data to swamp out any influence of prior distributional assumptions, also allows for a frequentist interpretation (Lele et al. 2007). The latter approach can be implemented using the 'pva' function in the PVAClone package of Program R (Nadeem and Lele 2012, Nadeem and Solymos 2012, R Core Team 2013). We find the Bayesian approach to inference appealing in this case because it allows one to visualize uncertainty in the estimated parameters using the full posterior distribution, but we also considered data cloning as part of a sensitivity analysis to evaluate the influence of our assumed priors. Although we report only the results from the Bayesian implementation, we compare these results to frequentist estimates in a supplementary appendix (Supplementary Tables S1 and S2; available on-line).

Bayesian methods require specification of a prior distribution for all model parameters (a, b, σ_p, and σ_{obs} [log-normal observation error model only]). We used the default prior distributions specified in the PVAClone package when fitting models: $a \sim N(1, 100$; no observation error and Poisson observation error models), $a \sim N(0, 100$; log-normal observation error), $b \sim N(0, 0.1)$, $\log(\sigma_p) \sim N(0,1)$, and $\log(\sigma_{obs}) \sim N(0,1$; log-normal observation error model only). For the Bayesian implementation, we fit the models using open-source software, Program R (R Core Team 2013) and JAGS (Plummer 2003), with the R package R2jags used to communicate between the 2 software platforms (Su and Yajima 2012). We assessed convergence by running 3 independent chains and then inspecting the Gelman–Rubin statistic (Brooks and Gelman 1998). This statistic compares between- and within-chain variation, with values close to 1 suggesting convergence. We ran the models for 20,000 iterations after an initial burn-in of 5,000 iterations. In all cases, the Gelman–Rubin statistics were ≤1.010, suggesting convergence. We evaluated sensitivity of the estimates to the assumed priors by also implementing the approach using data cloning with 20 data clones, via the 'pva' function in the PVAClone package (Nadeem and Lele 2012, Nadeem and Solymos 2012; Supplementary Tables S1 and S2). Data and R code to fit each of the models have been archived with the University of Minnesota's Digital Conservancy and are accessible through a permanent Universal Resource Locater (Fieberg and Mech 2014).

RESULTS

The 3 wolf-population trajectories we studied included 130 total years of data (Fig. 1). Minimum and maximum annual growth rates, given by N_{t+1}/N_t, among the 3 populations
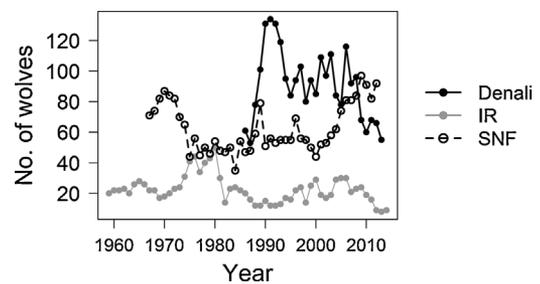

Figure 1. Wolf population trajectories totaling 130 years for Denali National Park, Alaska, USA; Isle Royale (IR) National Park, Michigan, USA; and the east central Superior National Forest (SNF), Minnesota, USA.

were 0.47 and 1.79, respectively (Table 1). Annual densities varied from 3.1/1,000 km² in Denali to 91.9/1,000 km² on Isle Royale and cover almost the full range of known wolf densities (Fuller et al. 2003). Ratios between highest and lowest annual densities within a population varied from 2.5–6.3. Of these measures, the Isle Royale population included the most years of data and had the most extreme ratio as well as the most extreme maximum annual increase and density.

Estimates of a from the fit of the density-independent model were similar and close to 0 for all 3 populations, with 95% credible intervals containing 0 regardless of the assumed observation error model (Fig. 2; Table 2). When plotted against the previous year's population size, annual log-growth rates, $\log(\lambda_t) = \log(N_{t+1}/N_t)$, exhibited a slight negative trend (Supplementary Fig. S1), and estimates of b in the Ricker model were negative for all 3 populations with 95% credible intervals that abutted 0 regardless of the assumed observation error model (Fig. 3; Table 3). In general, however, the 2 models (density-independent, Ricker) provided similar fits to the data (Fig. 4).

Estimates of the process standard deviation, σ_p, should be smaller in models that account for observation error, and this was the case for the Superior National Forest population and to a lesser extent for Isle Royale (Figs. 2 and 3; Tables 2 and 3). By contrast, the estimate of σ_p for Denali was close to 0.2

for both stochastic population models and for all 3 models of the observation error process (Tables 2 and 3). As a result, the relative comparisons involving σ_p were somewhat dependent on the assumed observation error model (Figs. 2 and 3). Nonetheless, σ_p was always smaller for Superior National Forest than Isle Royale (Figs. 2 and 3; Tables 2 and 3). The estimate of σ_p for Denali was in-between (except in the Poisson observation error model, where it was on par with the Isle Royale estimate).

The observation error standard deviation, σ_{obs}, in the log-normal observation error model was close to 0.1 for all 3 populations and for both population models, but estimates were more uncertain for Denali and Superior National Forest populations (Tables 2 and 3). Lastly, Bayesian and frequentist implementations resulted in similar parameter estimates. The main exceptions were the a parameter in the Ricker model for Denali and the estimates of σ_{obs} for Denali and Isle Royale, all of which were slightly closer to 0 in the frequentist implementations (Supplementary Tables S1 and S2). Differences were small, however, relative to the range of uncertainty encompassed by the posterior distributions.

DISCUSSION

The 3 wolf populations we assessed represent the best approximation available of the performance of unharvested
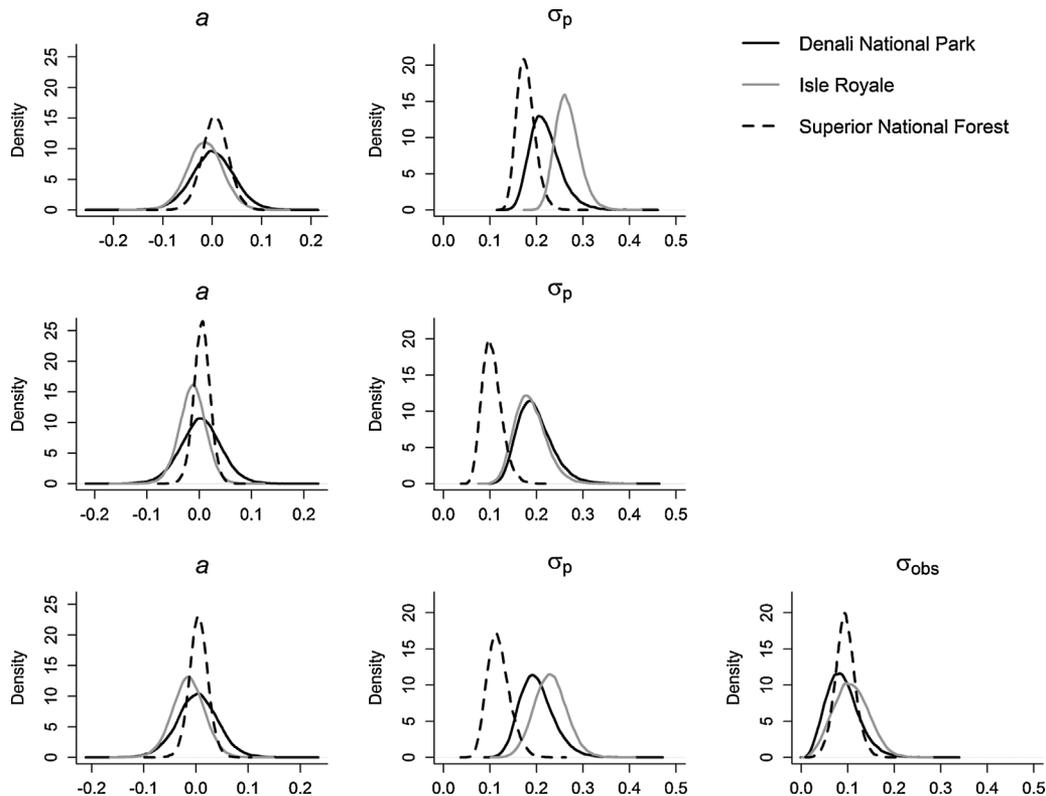

Figure 2. Posterior distributions from the fit of the density-independent model to the 3 time series of wolf population trajectories totaling 130 years in Denali National Park, Alaska, USA (1986–2013); Isle Royale National Park, Michigan, USA (1959–2014); and the east central Superior National Forest, Minnesota, USA (1967–2012). The top row corresponds to the model without observation error, the middle row corresponds to the model that assumes Poisson observation error, and the last row corresponds to the model that assumes log-normal observation error. The density-independent model is given by $N_{t+1} = N_t \exp(a + \varepsilon_t); \varepsilon_t \sim N(0, \sigma_p^2)$. The log-normal observation error model is given by $Y_t \sim N(X_t, \sigma_{obs}^2)$, where Y_t is the log-observed count and X_t is the log of the true population size.

Table 2. Estimated parameters and 95% credible intervals from the fit of the density-independent model[a] to each of the 3 time series of wolf counts conducted in Isle Royale National Park in Lake Superior, Michigan, USA (1959–2014); the east-central Superior National Forest in northeastern Minnesota, USA (1967–2012); and Denali National Park, Alaska, USA (1986–2013). Counts totaled 130 years.

Parameter	Observation model	Denali National Park		Isle Royale		Superior National Forest	
		Estimate	95% CI	Estimate	95% CI	Estimate	95% CI
a	No error	0.00	(−0.08, 0.09)	−0.01	(−0.09, 0.06)	0.01	(−0.05, 0.06)
	Poisson	0.00	(−0.08, 0.08)	−0.01	(−0.06, 0.04)	0.01	(−0.03, 0.04)
	Log-normal	0.00	(−0.08, 0.08)	−0.01	(−0.08, 0.05)	0.01	(−0.03, 0.04)
σ_p	No error	0.22	(0.17, 0.29)	0.27	(0.22, 0.32)	0.18	(0.14, 0.22)
	Poisson	0.20	(0.14, 0.28)	0.19	(0.13, 0.26)	0.11	(0.07, 0.15)
	Log-normal	0.20	(0.14, 0.29)	0.23	(0.16, 0.30)	0.12	(0.08, 0.17)
σ_{obs}[b]	Log-normal	0.09	(0.03, 0.17)	0.11	(0.04, 0.19)	0.09	(0.05, 0.14)

[a] The density-independent model is given by $N_{t+1} = N_t \exp(a + \varepsilon_t); \varepsilon_t \sim N(0, \sigma_p^2)$.
[b] The log-normal observation error model is given by $Y_t \sim N(X_t, \sigma_{obs}^2)$, where Y_t is the log-observed count and X_t is the log of the true population size.

wolf-population trajectories. Both the Superior National Forest and Denali populations have been extant for many decades and legally protected for most of their duration under study, but the Isle Royale population was founded in 1949 (Mech 1966). All 3 fluctuated greatly in relation to changes in the availability of their prey, which in turn were usually related to extremes in winter weather (Mech 1973, Peterson 1977, Mech et al. 1998). It is of interest that the Isle Royale population, although inbred, insular, and more variable, had a trajectory in many ways similar to that of the other populations. Founded by 1 female and 1 or 2 males and having incorporated genes from only 2 known immigrants (Wolfe and Allen 1979, Adams et al. 2011, but

see Hedrick et al. 2014), the population has persisted for 65 years.

Much progress has been made in recent years developing methods for fitting population dynamic models to count data while allowing for both observation and process errors (e.g., de Valpine 2002, 2003; Staples et al. 2004; Nadeem and Lele 2012); yet these methods have had mixed success when applied to real and simulated data. In particular, identifying the correct form of the model, both in terms of its deterministic and stochastic elements, can be challenging (Dennis et al. 2006, Polansky et al. 2009, Clark et al. 2010, Knape et al. 2011, Knape and de Valpine 2012). Further,
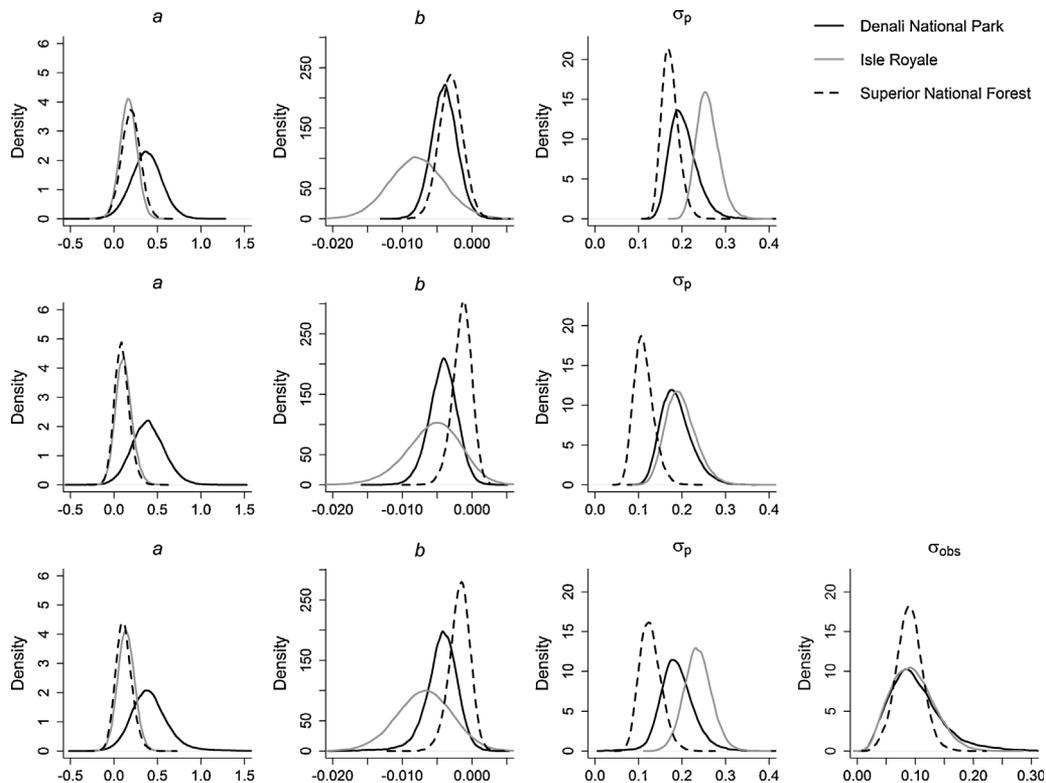

Figure 3. Posterior distributions from the fit of the Ricker model to the 3 time series of wolf population trajectories totaling 130 years in Denali National Park, Alaska, USA (1986–2013); Isle Royale National Park, Michigan, USA (1959–2014); and the east central Superior National Forest, Minnesota, USA (1967–2012). The top row corresponds to the model without observation error, the middle row corresponds to the model that assumes Poisson observation error, and the last row corresponds to the model that assumes log-normal observation error. The Ricker model is given by $N_{t+1} = N_t \exp(a + bN_t + \varepsilon_t); \varepsilon_t \sim N(0, \sigma_p^2)$. The log-normal observation error model is given by $Y_t \sim N(X_t, \sigma_{obs}^2)$, where Y_t is the log-observed count and X_t is the log of the true population size.

Table 3. Estimated parameters and 95% credible intervals from the fit of Ricker model[a] to each of the 3 time series of wolf counts conducted in Isle Royale National Park in Lake Superior, Michigan, USA (1959–2014); the east-central Superior National Forest in northeastern Minnesota, USA (1967–2012); and Denali National Park, Alaska, USA (1986–2013). Counts totaled 130 years.

Parameter	Observation model	Denali National Park Estimate	Denali National Park 95% CI	Isle Royale Estimate	Isle Royale 95% CI	Superior National Forest Estimate	Superior National Forest 95% CI
a	No error	0.370	(0.02, 0.73)	0.170	(−0.02, 0.36)	0.190	(−0.02, 0.41)
	Poisson	0.390	(0.03, 0.79)	0.110	(−0.06, 0.32)	0.090	(−0.07, 0.28)
	Log-normal	0.410	(0.03, 0.9)	0.140	(−0.05, 0.33)	0.110	(−0.06, 0.31)
b	No error	−0.004	(−0.008, 0)	−0.008	(−0.016, 0)	−0.003	(−0.006, 0)
	Poisson	−0.004	(−0.008, 0)	−0.006	(−0.014, 0)	−0.001	(−0.004, 0)
	Log-normal	−0.004	(−0.01, 0)	−0.007	(−0.015, 0)	−0.002	(−0.005, 0)
σ_p	No error	0.200	(0.15, 0.28)	0.260	(0.21, 0.32)	0.170	(0.14, 0.22)
	Poisson	0.190	(0.13, 0.27)	0.200	(0.14, 0.27)	0.110	(0.07, 0.16)
	Log-normal	0.190	(0.12, 0.27)	0.240	(0.18, 0.3)	0.130	(0.08, 0.18)
σ_{obs}[b]	Log-normal	0.100	(0.03, 0.22)	0.100	(0.03, 0.18)	0.090	(0.04, 0.14)

[a] The Ricker model is given by $N_{t+1}=N_t \exp(a + bN_t + \varepsilon_t); \varepsilon_t \sim N(0, \sigma_p^2)$.
[b] The log-normal observation error model is given by $Y_t \sim N(X_t, \sigma_{obs}^2)$, where Y_t is the log-observed count and X_t is the log of the true population size.

population projections can be highly sensitive to model assumptions (e.g., Nadeem and Lele 2012). Given the challenges of identifying the most appropriate model structure, and also the simplified dynamics implied by these models, we refrain from interpreting the parameters too literally. In particular, we caution against interpreting the large estimate of a in the Ricker model fit to the Denali population as reflecting the growth rate that would occur when population size is near 0 (a value well outside the range of the observed data). Instead, we view the simple stochastic population models as providing useful summaries of the population trajectories of these populations. For example, estimates of a from the density-independent model suggest that annual changes in the populations have been positive as often as negative over the length of the time series, and estimates of σ_p suggest that fluctuations in size have been greatest at Isle Royale, and lowest at Superior National Forest, with Denali most likely lying somewhere in-between. Possible reasons for the greater variability of the Isle Royale population include the larger sample size (10–28 more yr than the others, which may have captured more environmental variation), the smaller population abundance (thus less buffering and greater demographic stochasticity), the

relative lack of immigration and emigration, and the inbred nature of the population.

The above conclusions were robust to the form of observation error model. By contrast, estimates of σ_p, and a and b in the Ricker model for the Superior National Forest and Isle Royale populations were somewhat sensitive to the assumed observation error model and implementation approach. One could attempt to average posterior distributions across the different models, once provided with a set of model weights. Information theoretic methods (e.g., Deviance Information Criterion) are sometimes used for this purpose, but these methods are not straightforward to implement when models contain missing data—as in the case of the Poisson and log-normal observation error models (Celeux et al. 2006). More importantly, summaries of individual models, each with a different set of assumptions, can often be more informative than a single weighted summary (Ellner and Fieberg 2003).

MANAGEMENT IMPLICATIONS

We present estimates of population parameters that can serve as benchmarks for comparison with those calculated
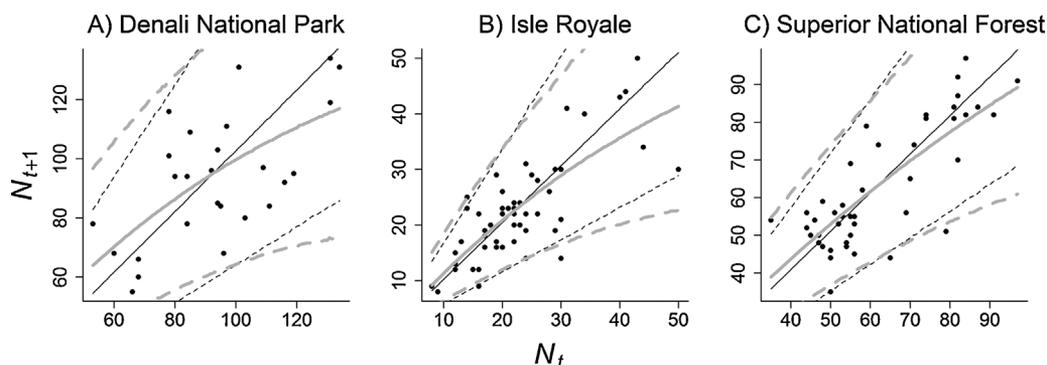

Figure 4. Fit of the density-independent (straight black lines) and Ricker model (curved gray lines) to each of the 3 time series of population counts, assuming no observation error, of wolf population trajectories totaling 130 years in Denali National Park, Alaska, USA (1986–2013); Isle Royale (IR) National Park, Michigan, USA (1959–2014); and the east central Superior National Forest (SNF), Minnesota, USA (1967–2013). Dotted lines give point-wise 95% prediction intervals, accounting for both uncertainty in the estimated parameters and year-to-year variability in annual growth rates (due to the ε_t terms).

from other wolf populations repopulating other areas. Wolf densities in national parks such as Yellowstone and in inaccessible wilderness can be expected to fluctuate similarly, and wolf densities in populations subject to harvesting can be compared with the 3 in this study so that regulations can be adjusted to minimize chances of driving wolf populations lower than managers might wish or to prevent wolf populations from increasing more than managers might want. Because our study populations were all from circumscribed areas, fluctuations in them represent fluctuations in densities (i.e., changes in numbers are not confounded by changes in occupied area as would be the case with populations expanding their range as are wolf populations in many states). Thus care must be taken to distinguish their behavior from those of uncircumscribed populations.

ACKNOWLEDGMENTS

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SUPPORTING INFORMATION

Additional supporting information may be found in the online version of this article at the publisher's web-site.

Supplementary Tables: Frequentist versus Bayesian comparisons.

Supplementary Figure S1. Log growth rates, $\log(N_{t+1}/N_t)$, plotted against Nt for each of the 3 wolf population time series, along with expected log-growth rates and 95% credible intervals from the fit of the density-independent model (top row) and the Ricker model (bottom row), assuming no observation error.

Supplementary Table S1. Comparison of frequentist and Bayesian parameter estimates for the density-independent model.

Supplementary Table S2. Comparison of frequentist and Bayesian parameter estimates for the Ricker model.

Growth Rates and Variances of Unexploited Wolf Populations in Dynamic Equilibria

Rrf: Mech et al. • Unexploited Wolf Populations

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## SUPPORTING INFORMATION

Supplementary Tables: frequentist versus Bayesian comparisons

Supplementary Table 1. Comparison of frequentist and Bayesian parameter estimates for the density-independent model.

Parameter	Observation model	Denali National park		Isle Royale		Superior National Forest	
		Bayessian	**Frequentist**	**Bayesian**	**Frequentist**	**Bayesian**	**Frequentist**
a	No error	0.00	0.00	–0.01	–0.01	0.01	0.01
	Poisson	0.00	0.00	–0.01	–0.01	0.01	0.01
	Log-normal	0.00	0.00	–0.01	–0.01	0.01	0.01
σ_p	No error	0.22	0.20	0.27	0.26	0.18	0.17
	Poisson	0.20	0.15	0.19	0.17	0.11	0.09
	Log-normal	0.20	0.18	0.23	0.24	0.12	0.10
σ_{obs}	Log-normal	0.09	0.07	0.11	0.06	0.09	0.09

Supplementary Table 2. Comparison of frequentist and Bayesian parameter estimates for the Ricker model.

Parameter	Observation model	Denali National park		Isle Royale		Superior National Forest	
		Bayessian	**Frequentist**	**Bayesian**	**Frequentist**	**Bayesian**	**Frequentist**
a	No error	0.38	0.30	0.17	0.17	0.19	0.19
	Poisson	0.39	0.26	0.11	0.09	0.09	0.07
	Log-normal	0.41	0.29	0.14	0.16	0.11	0.09
b	No error	−0.004	−0.003	−0.008	−0.008	−0.003	−0.003
	Poisson	−0.004	−0.003	−0.006	−0.005	−0.001	−0.001
	Log-normal	−0.004	−0.003	−0.007	−0.008	−0.002	−0.001
σ_p	No error	0.20	0.19	0.26	0.25	0.17	0.16
	Poisson	0.19	0.15	0.20	0.18	0.11	0.09
	Log-normal	0.19	0.18	0.24	0.24	0.13	0.11
σ_{obs}	Log-normal	0.10	0.05	0.10	0.04	0.09	0.09
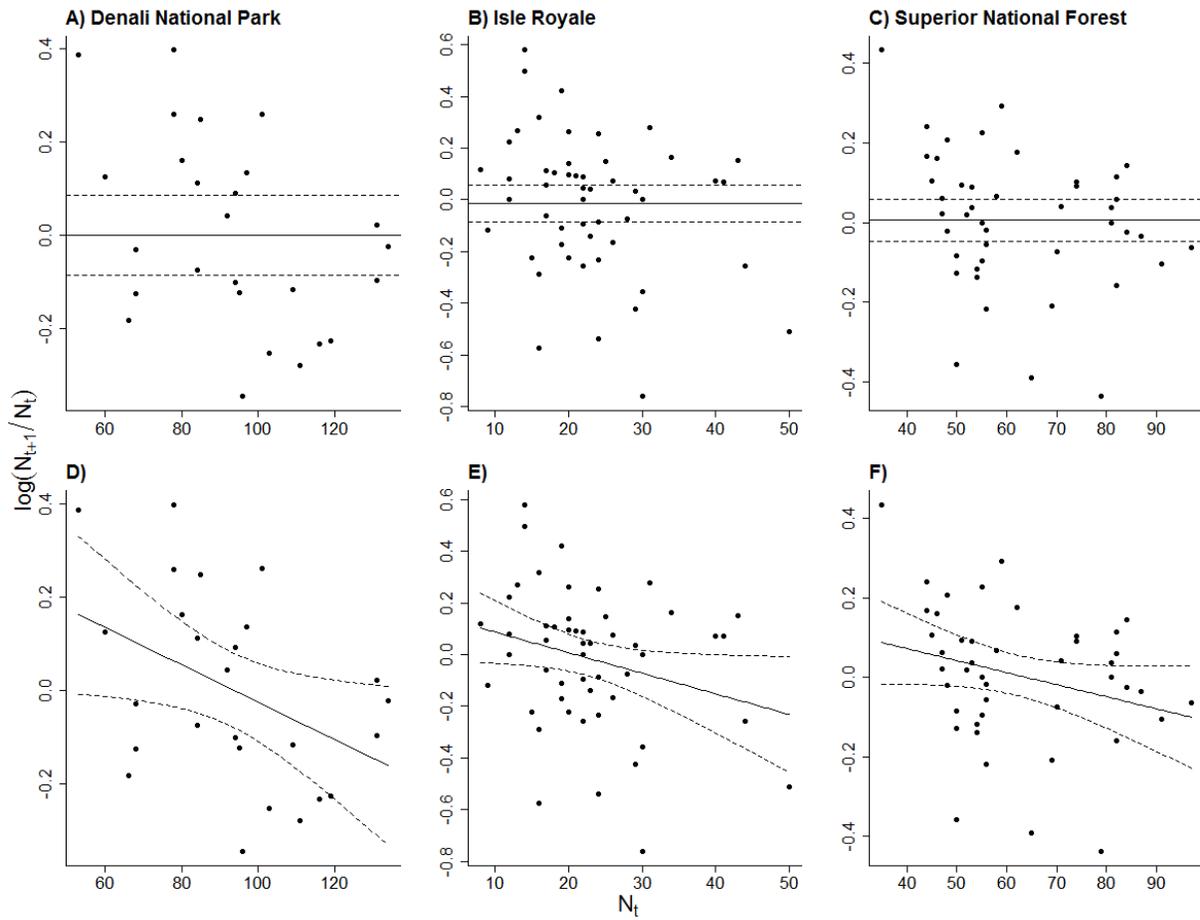
Supplementary Figure 1. Log growth rates, log(N_{t+1}/N_t), plotted against N_t for each of the 3 wolf population time series, along with expected log-growth rates and 95% credible intervals from the fit of the density-independent model (top row) and the Ricker model (bottom row), assuming no observation error.