ADAPTIVE HARVEST MANAGEMENT OF WOLVES: THE ROLE OF RECRUITMENT AND HIERARCHICAL DEMOGRAPHY IN POPULATION DYNAMICS OF A SOCIAL CARNIVORE

By

ALLISON CHRISTINE KEEVER

B.S., University of Illinois, Champaign-Urbana, Illinois, 2011
M.S., Auburn University, Auburn, Alabama, 2014

Dissertation

presented in partial fulfillment of the requirements
for the degree of

Doctor of Philosophy
in Wildlife Biology

The University of Montana
Missoula, MT

May 2020

Approved by:

Scott Whittenburg,
Graduate School Dean

Dr. Michael S. Mitchell, Chair
U.S. Geological Survey, Montana Cooperative Wildlife Research Unit

Dr. David E. Ausband,
U.S. Geological Survey, Idaho Cooperative Fish and Wildlife Research

Dr. Mark Hebblewhite,
Wildlife Biology Program

Dr. Angela D. Luis,
Wildlife Biology Program

Dr. Paul M. Lukacs,
Wildlife Biology Program

Dr. James T. Peterson,
U.S. Geological Survey, Oregon Cooperative Fish and Wildlife Research Unit

Kevin M. Podruzny,
Montana Fish, Wildlife and Parks

Keever, Allison C., Ph.D., December 2019 Wildlife Biology

Adaptive Harvest Management of Wolves: the Role of Recruitment and Hierarchical Demography in Population Dynamics of a Social Carnivore

Chairperson: Dr. Michael S. Mitchell

Regulated public harvest became an important management tool following recovery of gray wolves (*Canis lupus*) in the U.S. Northern Rocky Mountains. Decisions on harvest regulations, however, can be contentious due to conflicting stakeholder values, uncertainties in the effects of harvest on wolves, and difficulty in monitoring wolves. We addressed challenges associated with wolf management by 1) developing methods to estimate recruitment, 2) evaluating the role of hierarchical demography in wolf population dynamics, 3) developing competing population models to address uncertainty, and 4) developing an adaptive management framework to identify harvest regulations that best meet objectives for wolf management. We developed integrated population models (IPM) with and without social structure to evaluate the role of hierarchical demography in population dynamics of wolves. We tested and compared the IPMs on simulated populations with known demographic rates. We then used the IPM with hierarchical demography to estimate recruitment and population dynamics in wolves when productivity data were lacking. In addition, we developed a model to predict recruitment based on empirical data from Idaho and then tested the model in Montana. To better understand wolf population dynamics, we tested competing hypotheses of additive or compensatory harvest mortality and density dependent or density independent recruitment using population models and Bayesian model weight updating. Finally, we used stochastic dynamic programming and passive adaptive learning to find optimal season lengths and bag limits for wolf management in Montana. This framework accounted for uncertainty and included biological and societal objectives. We found that accounting for hierarchical demography improved estimation of demographic rates and population dynamics of wolves. Although regulated public harvest has appeared to decrease recruitment of pups and survival of adults, the population remained relatively stationary or only slightly declined. Using passive adaptive management, we found support for the hypothesis that net immigration into Montana was zero. Additionally, we found the optimal harvest strategy became more liberal as the wolf population grew. Following the optimal harvest strategy, we found that the wolf population was maintained around 650 wolves, which suggests that maintaining the population at this size best meets objectives.

ACKNOWLEDGMENTS

I am very grateful to the numerous people that have helped and supported me throughout this process. First and foremost, however, I would like to thank Montana Fish, Wildlife and Parks (MFWP) for funding and supporting this research. This project truly would not have been possible without the generous contributions of wolf specialists, biologists, and managers at MFWP.

Completing this PhD was more challenging than I thought and more rewarding than I could have ever imagined. None of this would have been possible without my advisor, Dr. Mike Mitchell. I am eternally grateful for his encouragement and mentorship. Mike, with your guidance I have grown as a scientist, a writer, and a person. You helped me find clarity when my writing or thoughts were muddled, you believed in me when I had trouble believing in myself, and you taught so much about how to conduct good science. Thank you for being a wonderful advisor.

My committee members have also been invaluable during this endeavor. Thank you to Kevin Podruzny for the support and constructive feedback. I greatly appreciate your contributions. To Dr. Dave Ausband, thank you for your profound insights into wolf ecology and, more importantly, for your good humor during this stressful experience. I am also very appreciative of Dr. Paul Lukacs for helping me wade through the world of Bayesian hierarchical modeling and emerge on the other side a much better coder and population ecologist. Dr. Mark Hebblewhite, thank you for your endless enthusiasm and encouragement. Your passion for research and learning helped me craft well thought out questions and hypotheses, and it is truly inspiring. To Dr. Angie Luis, I am grateful for your insightful questions and guidance throughout

this process. I also want to thank Dr. Jim Peterson. I appreciate you sharing your knowledge and expertise in quantitative decision analysis. You helped me develop the skills needed to complete this research.

Finding balance in grad school can be difficult. I am therefore very grateful to my fellow grad students for making life in and outside of the office enjoyable. I am indebted to past and present Mitchell lab members: Sarah Sells, Sarah Bassing, Teagan Hayes, Shannon Forshee, Kenneth Loonam, Kristin Barker, James Goerz, Collin Peterson, Kari Eneas, Jesse DeVoe, Alex Welander, and Brandon Kittson. The white boarding sessions, jokes, and shenanigans made this experience so much more enjoyable. Misery loves company, and so does jubilation. Thank you for sharing in my ups and downs. I also want to extend my thanks to Dr. Will Janousek, Dr. Colter Chitwood, Dr. Josh Nowak, and Dr. Charlie Henderson for their helpful advice and assistance at various stages of this project. I am very appreciative of Tina Anderson, Debora Simmons, and Jeanne Franz for keeping the well-oiled machine of grad student life running smoothly. I would not have been able to handle the paper work and logistics without your help.

Last, and most importantly, I want to thank my family and friends, near and far. Without your love and support I would not have been able to make it through the lows of grad school, and you made the highs much more rewarding. Whether it was listening to me vent about grad school, offering comforting or supporting words when I needed them, or celebrating my accomplishments with me, I thank you. My parents have always been supportive, and I cannot begin to thank them enough.

A note on authorship

Throughout this document, I use the pronoun “we” in recognition and appreciation of the contributions of my collaborators and coauthors.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

CHAPTER 1:

ACCOUNTING FOR HIERARCHICAL DEMOGRAPHY IMPROVES ESTIMATION OF RECRUITMENT IN GROUP-LIVING SPECIES

ABSTRACT

Populations that are structured into social groups have complex population dynamics that occur in a hierarchy. Hierarchical demography, which links processes within groups to processes among groups and overall population growth rate, is often not accounted for when modeling dynamics of social species. Many large carnivores, which are challenging to monitor, are also social, and estimating demographic rates and population dynamics can be difficult. We evaluated how accounting for hierarchical demography affects understanding and estimation of demographic processes in simulated populations of gray wolves (*Canis lupus*) using integrated population models. Further, because demographic data can be costly to collect, we evaluated the accuracy of estimates of demographic rates without explicit data to inform them. We simulated populations of wolves structured into packs to generate data, and compared estimates from the models to truth from the simulations to assess model performance. We found that accounting for hierarchical demography greatly improved accuracy of estimates of recruitment, however accuracy of other demographic rates were similar with and without accounting for social structure. We also found that we could produce accurate estimates of recruitment in absence of productivity data. Our results suggest this could be a viable method to estimate population dynamics in social species. More importantly, accounting for structure in population models can affect the resulting patterns and processes of population change.

INTRODUCTION

Dynamics of populations structured into social groups often depend on hierarchical demography (Al-Khafaji et al. 2009; Clutton-Brock 2016). Hierarchical demography links processes within groups and group growth rate to processes among groups and overall population growth rate. In non-social species, a population is a collection of individuals that survive, disperse, and reproduce. These processes yield the observed patterns of population growth rate over time. For a social species, however, a population is a hierarchy: a collection of groups, and a collection of individuals within groups. Within groups, individuals can survive, disperse, and reproduce (Packer et al. 2005; Bateman et al. 2018). These processes yield observed patterns in growth rates within groups; however population growth rate in social species also depends on survival or persistence of existing groups and formation of new groups (Brainerd et al. 2008; Bateman et al. 2018). To understand drivers of growth rate in socially-structured populations, it is therefore necessary to determine how processes within and among groups influence observed population dynamics.

Traditional models that fail to account for hierarchical demography may fail to detect or underestimate the importance of some demographic processes that occur within groups in socially-structured populations (Bateman et al. 2011, 2018). Demographic rates of individuals in social groups may be influenced by component Allee effects, in which components of growth rate increase with group size (Stephens et al. 1999; Lerch et al. 2018). For example, larger packs of gray wolves (*Canis lupus*) recruit more pups than do smaller packs (Ausband et al. 2017*a*; Ausband 2018), and meerkats (*Suricata suricatta*) in larger groups experience greater survival than those in smaller groups (Bateman et al. 2012). Group characteristics can also lead to greater variation in demographic rates among groups and years in socially-structured populations. In African lions (*Panthera leo*), turnover of males in the pride can lead to infanticide, causing highly variable recruitment (Elliot et al. 2014). Similarly, disease in social species can cause extreme variation in recruitment and survival among groups or years (Almberg et al. 2010).

Processes within social groups, such as survival of individuals and recruitment of offspring, are interrelated with group formation and group persistence (Brainerd et al. 2008; Bateman et al. 2018). In particular, dispersal of individuals from social groups provides an important link of dynamics within and among groups. Dispersal directly affects group size creating smaller groups and decreasing group growth rate, however it can increase group formation rates and indirectly increase population growth rates (Bateman et al. 2018; Woodroffe et al. 2019). Group and population characteristics (e.g., group size and number of groups) can influence dispersal rates, creating density-dependent dispersal (Bateman et al. 2012). In both African wild dogs (*Lycaon pictus*) and meerkats, dispersal increases with group size, creating density-dependent growth in group size (Bateman et al. 2018; Woodroffe et al. 2019). The slow growth of larger groups, however, did not translate to the population growth rate because larger groups produced more daughter groups through successful dispersal (Bateman et al. 2018; Woodroffe et al. 2019). Models that do not consider hierarchical demography may fail to adequately account for these demographic processes, which could bias results when estimating dynamics in social species.

Integrated population models (IPM) could offer greater insights into how accounting for hierarchical demography in social species influences understanding of dynamics because they simultaneously evaluate both patterns and processes of population change (Besbeas et al. 2002; Schaub and Abadi 2011). IPMs simultaneously analyze data on abundance and demographic parameters to estimate population growth and vital rates (Newman et al. 2014). A state-space model for the population count data, which separately models the true population state and observation process, combined with additional models that directly estimate demographic parameters forms the IPM (Schaub and Abadi 2011; Newman et al. 2014). There are many benefits of an integrated modelling approach, including more precise estimates of abundance and demographic rates, explicit consideration of covariation of demographic rates, and parameters without explicit data can often be estimated (Besbeas et al. 2002; Abadi et al. 2010, 2017; Schaub and Abadi 2011; Newman et al. 2014). Because changes in abundance over time are a function of survival and recruitment (assuming a closed population), if data were available for abundance and survival over time then recruitment could be estimated by essentially solving for it (Abadi et al. 2010). For example, Abadi et al. (2010) estimated immigration and recruitment for a population of little owls (*Athene noctura*) in southern Germany using an IPM without data for the rates because they had data for survival and abundance. This can be particularly important for species that are difficult or costly to monitor.

Large carnivores exhibit many of the characteristics that make monitoring populations and estimating demographic rates challenging. Large carnivores are generally rare, elusive, and occur at low densities, and even with intensive effort, data are often insufficient to understand population dynamics (Wilson and Delahay 2001; Karanth and Chellam 2009). Data collection involving repeated capture of individuals is labor-intensive and prohibitively expensive for many large carnivore populations (Wilson and Delahay 2001). Although camera-trap studies may provide a cost-effective means of monitoring abundance or occupancy of large carnivores (Kane et al. 2015; Steenweg et al. 2016; Rich et al. 2017; Loonam 2019), these data often provide inadequate information to estimate demographic parameters. Despite these challenges, demographic data are needed to better understand implications of conservation and management actions as many carnivore populations are threatened or endangered (Karanth and Chellam 2009;

Di Marco et al. 2014). Further, some large carnivores that are difficult to monitor are also social, such as wolves, African wild dogs, killer whales (*Orcinus orca*), and African lions. Therefore, new methods are needed to estimate demographic rates with limited data that also accounts for social structure.

We developed an IPM that explicitly accounts for hierarchical demography (hereafter hierarchical demography IPM) to estimate dynamics in a social species with limited data, and used simulations to assess the utility of the model. Our objective was to evaluate how accounting for hierarchical demography affects understanding and estimation of demographic processes in a social species. To do this, we simulated hypothetical populations of a social species based on the life-history of gray wolves. Wolves form family units called packs, which are traditionally comprised of a breeding pair and offspring from current and past litters (Mech and Boitani 2003). Pup survival and recruitment is positively correlated with pack size, suggesting a component Allee effect on recruitment within packs (Ausband et al. 2015, 2017*a*). Dispersal may also be density dependent, with evidence suggesting positive density dependence of dispersal within packs (i.e., increase in dispersal with pack size) and negative density dependence of dispersal among packs (i.e., decrease in dispersal with population size; (Fuller et al. 2003; Jimenez et al. 2017). We then simulated datasets by surveying the virtual populations of wolves and fit IPMs to the simulated datasets. Finally, we compared estimates of abundance, survival, recruitment, and dispersal from different IPM model structures. The first model structure explicitly accounted for sociality (hierarchical demography IPM), and the second did not include social structure (per capita IPM). Within those two IPM model structures, we then evaluated four scenarios of model misspecification to test the robustness of the model: 1) unmodeled temporal variability in recruitment and dispersal, and unmodeled density dependence in recruitment and dispersal (Constant Scenario), 2) unmodeled density dependence in dispersal with a modeled component Allee effect on recruitment within groups (Allee Scenario), 3) unmodeled density dependence in recruitment with modeled density dependence in dispersal (Dispersal Scenario), and 4) modeled density dependence in dispersal and a component Allee effect on recruitment (Full Scenario). These scenarios were selected because there is evidence of density dependence in both recruitment and dispersal in social species (Courchamp and Macdonald 2001; Ausband et al. 2017*a*; Bateman et al. 2018; Woodroffe et al. 2019), and not accounting for it may bias results. Furthermore, because detailed demographic data may be sparse for social carnivores, we assumed we did not have data for recruitment to evaluate the effects of missing data and incorrect model structure on estimates of demographic rates.

METHODS

We conducted a simulation study to evaluate how accounting for hierarchical demography in social species affects estimation and understanding for demographic processes using IPMs. We used a four step process to test the robustness of the overall modeling approach: 1) we initiated a virtual population and simulated dynamics for 15 years, 2) we sampled time series of abundance and group counts, and simulated fates of individuals based on demographic rates to generate datasets, 3) we fit eight IPMs with different model structure (two social structure models times four misspecification scenarios) to estimate demographic rates and abundance, and 4) we calculated performance metrics of the estimates from the eight IPM models.

Simulating Virtual Populations

We initiated and simulated 1000 virtual populations based on the life-history characteristics of wolves. We limited our analysis to 1000 simulations due to computational time of fitting the IPMs. We initiated each virtual population with 70 packs. We included variation in pack size using a Poisson distribution (Morris and Doak 2002; Kéry and Schaub 2011; McGowan et al. 2011) with the mean of 5.5 wolves per pack. The initial population size was the sum of the individuals in the 70 packs, and varied for each of the 1000 virtual populations. We recorded pack sizes for the initial 70 groups and initial abundance for each of the virtual populations. We then projected each virtual population for 15 years based on survival and dispersal of individuals, recruitment of offspring, new pack formation, and pack persistence (Morris and Doak 2002).

We included demographic and temporal variability in each of the demographic rates used to project the population (Morris and Doak 2002; McGowan et al. 2011). We simulated a population similarly to steps outlined by (Kéry and Schaub 2011). For survival and group persistence, we drew random rates for each year from uniform distributions to account for temporal variation (Morris and Doak 2002; Kéry and Schaub 2011). We incorporated demographic variability using a binomial distribution for either the number of individuals in each pack that survive to next year, or the number of packs that persist to next year, based on the random annual rates (Kéry and Schaub 2011; McGowan et al. 2011). The number of pups recruited in each pack was a function of pack size and temporal variation, and we included demographic variability using a Poisson distribution:

$$\mu_{gt} = \exp\left(\beta_0 + \beta_1 \, log\left(G_{gt-1}\right) + \varepsilon_{t-1}\right) \quad \varepsilon_t \sim Normal(0, \sigma^2)$$

$$r_{gt} \sim Poisson(\mu_{gt})$$

where μ_{gt} is the expected number of pups recruited for pack g in year t, β_0 and β_1 are the intercept and coefficient for the effect of pack size (G_{gt}) on recruitment, ε_t is the year random effect, and r_{gt} is the number of pups recruited for pack g in year t. To determine the per capita recruitment rate for each year, we added up the total number of offspring recruited, and divided by total population size. Dispersal rate for each pack and year (d_{gt}) was modeled similarly to recruitment (i.e., dispersal was a function of pack size), however we used a logit-transformation of the linear model. The equation for the projection of group size (G_{gt}) was then

$$\eta.G_{gt} \sim Binomial\left(s_{t-1} * \left(1 - d_{gt-1}\right), G_{gt-1}\right),$$

$$G_{gt} = \eta.G_{gt} + r_{gt},$$

where s_t was survival rate and $\eta.G_{gt}$ was the number of individuals that survived and remained in group g in year t. We assumed the number of packs formed (F_t) was a function of dispersal rate, and modeled F_t as

$$F_t = 0.30 * 0.50 * D_t$$

where 0.30 was the proportion of wolves that survived dispersal and successfully formed packs (Marescot et al. 2012; Jimenez et al. 2017), 0.50 was to account for a pair needed to form a pack, and D_t was the number of wolves that dispersed. We initialized each new pack with two wolves (Mech and Boitani 2003). The equation to project the number of groups (Z_t) was

$$\eta.Z_t \sim Binomial(\psi_{t-1}, Z_{t-1})$$

$$Z_t = \eta.Z_t + F_t$$

where ψ_t was pack persistence rate and $\eta.Z_t$ was the number of packs that persisted to year t. Population size for any given year was the sum of the individuals within the extant groups. We recorded demographic rates, group sizes, the number of groups, and population size each year for each of the 1000 virtual populations.

In simulating these virtual populations, we assumed the population consisted of juveniles (< 1 year) and adults (> 1 year). Further, we assumed the group was the breeding unit with a single breeding pair and non-breeding helpers (i.e., cooperative breeding; Solomon and French 1997). We did not include immigration into groups or the population when projecting the virtual populations. Although immigration of individuals into social groups occurs (Kokko et al. 2001;

Clutton-Brock 2016; Ausband et al. 2017*b*), immigration of non-related individuals into wolf packs may occur infrequently (Bassing 2017). We focused estimation on other demographic processes in a social species, and therefore did not include immigration. We included dispersal of individuals from packs, and if the individual did not form a new pack, we assumed it emigrated from the population.

Generating Datasets

We simulated seven datasets for each of the 1000 virtual populations. We assumed we had estimates of total abundance and the number of groups. Therefore, we simulated data for abundance and the number of groups by drawing values from a normal distribution with a mean of the true abundance or number of groups from the simulated population, and a standard deviation of 75 or 20, respectively. We assumed we had imperfect observations of new groups that formed, and generated data by drawing the observed number of groups that formed from a binomial distribution with a detection probability of 0.60 and the true number of groups that formed. For group persistence, we assumed we monitored the fate of 50 groups, and generated data (the number of groups that did not persist) using a binomial distribution with one minus the annual probability of pack persistence and 50 for the number of trials. We assumed we had observed counts of group size for 50 groups, and generated data by drawing group counts from a binomial distribution with a detection probability of 0.85 and the true group size for the number of trials. Survival and dispersal data were similarly generated. We assumed we monitored 40 individuals each for survival and dispersal, and generated data by drawing the fate of each individual (i.e, died/survived or stayed/dispersed) from a binomial distribution with a probability of the demographic rate and one trial. Dispersal rate was group specific, therefore we randomly selected 40 groups each year, with replacement, and used the group specific dispersal rate to generate the data and recorded the group size associated with the individual fate.

Integrated Population Model Structures

IPMs are formed by state-space models that include 1) a state process that describes how population size changes over time (i.e., population projection model) and 2) an observation process that describes how the observed data relate to the state process (Besbeas et al. 2002; Newman et al. 2014). We expanded this basic framework to account for hierarchical demography by modeling the processes among groups and within groups using state-space models with time-series count data for abundance and group size, respectively (hierarchical demography IPM; Figure 1.1). In addition to the hierarchical demography IPM, we also developed a per capita IPM based on Stenglein et al. (2015) to evaluate performance of models with and without accounting for social structure under four scenarios of model misspecification.

Per capita IPM – The per capita IPM was based on Stenglein et al. (2015), however we included dispersal and did not include a correction factor for survival. We assumed that the population count data ($y.N_t$) in year t was normally distributed with a population size of N_t, and sampling variance of σ_N^2. The population size (N_t) in year t was a function of population size (N_{t-1}), recruitment rate (ρ_{t-1}), survival rate (ϕ_{t-1}), and dispersal rate (δ_{t-1}) in the previous year, $t-1$:

$$y.N_t \sim Normal(N_t, \sigma_N^2),$$

$$N.adult_t \sim Binomial(\phi_{t-1}(1-\delta_{t-1}), N_{t-1}),$$

$$N.pup_t \sim Poisson(N_{t-1}\rho_{t-1})$$

$$N_t = N.adult_t + N.pup_t.$$

The annual, per capita recruitment rate (ρ_t) was the number of offspring per individual that survived one year. We assumed we did not have available data, and therefore did not have an observation process for recruitment. We compared two different generalized linear models with a logit-link function for ρ_t to use in the scenarios of model misspecification. The first model was a constant ρ_t, and the second model included density dependence with a simple linear relationship between ρ_t and N_t (Stenglein et al. 2015) and a random year effect ($\varepsilon_{R,t}$):

$$logit(\rho_t) = \beta_0,$$

$$logit(\rho_t) = \beta_0 + \beta_1 \log(N_t) + \varepsilon_{R,t}, \quad \varepsilon_{R,t} \sim Normal(0, \sigma_R^2).$$

The constant ρ_t was used in the Constant Scenario, which did not account for density dependence or temporal variation, and the Dispersal Scenario, which included density dependence and temporal variability in dispersal but not recruitment. The density dependent ρ_t was used in the Allee Scenario, which included density dependence and temporal variability in recruitment but not dispersal, and the Full Scenario, which included density dependence and temporal variability in both recruitment and dispersal.

We estimated survival (ϕ_t) using a discrete-time proportional hazards model with a complimentary log-log (cloglog) link function (Prentice and Gloeckler 1978, Kalbfleisch and Prentice 2011). We used the year as a discrete period, and included a year random effect ($\varepsilon_{S,t}$) to account for annual variation. We modeled the individual contribution to the survival likelihood as independent Bernoulli random variables for the observation of individual i as either alive (0) or dead (1). The probability of the individual dying, $\mu.surv_{i,t}$, was modeled as a generalized linear mixed-effects model:

$$cloglog(\mu.surv_{i,t}) = \beta_0 + \varepsilon_{S,t}, \qquad \varepsilon_{S,t} \sim Normal(0, \sigma_S^2),$$

$$y.surv_i \sim Bernoulli(\mu.surv_i),$$

$$y.surv_i = \{0,1\}.$$

The cumulative hazard for each year was $H_t = -\log(1 - \mu.surv_t)$, and survival was calculated as $\phi_t = \exp(-H_t)$ (Prentice and Gloeckler 1978, Hosmer and Lemeshow 2000, Heisey et al. 2007).

We modeled the dispersal data (i.e., whether or not a monitored individual dispersed) using a Bernoulli distribution with the probability of dispersal (δ_t) and population size of the previous year (N_{t-1}). We compared two different generalized linear models with a logit-link function for δ_t to use in the scenarios of model misspecification. The first model was a constant δ_t, and the second model included density dependence with a simple linear relationship between δ_t and N_t and a random year effect ($\varepsilon_{D,t}$):

$$y.disp_{it} \sim Bernoulli(\delta_t)$$

$$logit(\delta_t) = \beta_0,$$

$$logit(\delta_t) = \beta_0 + \beta_1 \log(N_t) + \varepsilon_{D,t}, \quad \varepsilon_{D,t} \sim Normal(0, \sigma_D^2).$$

The constant δ_t was used in the Constant Scenario, which did not account for density dependence or temporal variation, and the Allee Scenario, which included density dependence and temporal variability in recruitment but not dispersal. The density dependent δ_t was used in the Dispersal Scenario, which included density dependence and temporal variability in dispersal but not recruitment, and the Full Scenario, which included density dependence and temporal variability in both recruitment and dispersal.

Hierarchical demography IPM – For the hierarchical demography IPM, we used state-space models for both the population count data ($y.N_t$) and the group count data ($y.G_{gt}$). Changes in group size (G_{gt}) for group g in year t was a function of survival rate (ϕ_t), the number of pups recruited per pack (γ_{gt}), and dispersal rate (δ_{gt}). We used a binomial distribution to account for process error, and modeled the group count data ($y.G_{gt}$) using a binomial distribution with a detection probability (p_G) for individuals within the group, and the true, but unknown group size (G_{gt}):

$$y.G_{gt} \sim Binomial(p_G, G_{gt}),$$

$$\eta.G_{gt} \sim Binomial\big(\phi_{t-1}(1-\delta_{gt-1}), G_{gt-1}\big)$$

$$G_{gt} = \eta.G_{gt} + \gamma_{gt-1}.$$

Population size in a social species is a function of the number of groups, and the number of individuals within those groups. We assumed we only had group count data for a proportion (P_t) of the total number of groups (Z_t) in the population. Therefore, we modeled population size (N_t) and the population count data ($y.N_t$) in year t as

$$y.N_t \sim Normal(N_t, \sigma_N^2),$$

$$N_t = \sum_{g=1}^{P_t} G_{gt} + (Z_t - P_t)\bar{G}_t,$$

where $\bar{G}_t$ was the estimated mean group size for year t. Changes in the total number of groups (Z_t) was a function of the number of groups that formed (F) and group persistence rate (ψ):

$$y.Z_t \sim Normal(Z_t, \sigma_Z^2),$$

$$Z_t \sim Binomial(\psi_{t-1}, Z_{t-1}) + Poisson(F_{t-1}),$$

$$y.persist_t \sim Binomial(1-\psi_t, P_t),$$

$$logit(\psi_t) = \beta_0 + \varepsilon_{P,t}, \;\; \varepsilon_{P,t} \sim Normal(0, \sigma_P^2),$$

$$y.form_t \sim Binomial(p_F, F_t),$$

$$F_t = \exp\big(\beta_0 + \varepsilon_{F,t}\big), \;\; \varepsilon_{F,t} \sim Normal(0, \sigma_F^2)$$

where $y.Z_t$ was the estimate of the number of groups, σ_Z^2 was the estimated error term for the number of groups, $y.persist_t$ was the observed number of groups that did not persist, P_t was the number of groups that were monitored, $\varepsilon_{P,t}$ was a year random effect for group persistence rate, $y.form_t$ was the observed number of groups that formed, p_F was an estimated detection probability for group formation, F_t was the estimated number of groups that formed, and $\varepsilon_{F,t}$ was a year random effect for group formation.

Survival rate in the hierarchical demography IPM was modeled exactly as survival rate in the per capita IPM. Dispersal was modeled similarly to dispersal rate in the per capita IPM, however, density dependence in dispersal for the hierarchical demography IPM was a relationship between dispersal rate and group size. We used the constant and density dependent dispersal models in the hierarchical demography IPM in the same scenarios of model misspecification as the dispersal models for the per capita IPM.

The annual recruitment rate (γ_{gt}) was the number of offspring per group (g) in year t that survived one year. Again, we assumed we did not have available data, and compared two different generalized linear models to use in the scenarios of model misspecification. Instead of using the logit-link function, however, we used a log-link function:

$$\gamma_{gt} = \exp(\beta_0),$$

$$\gamma_{gt} = \exp(\beta_0 + \beta_1 \log(G_{gt}) + \varepsilon_{R,t}), \quad \varepsilon_{R,t} \sim Normal(0, \sigma_R^2),$$

where $\varepsilon_{R,t}$ was a year random effect and G_{gt-1} was group size for group g. We used the constant and density dependent γ_{gt} in the same scenarios as the recruitment models for the per capita IPM.

Model Implementation and Performance Metrics

We used the data generated from the 1000 simulated populations in the hierarchical demography and per capita IPMs to estimate demographic rates under all four scenarios of model misspecification. Therefore, for each IPM model type (hierarchical demography or per capita) and model misspecification scenario (Constant, Allee, Dispersal, or Full), we fit the model to 1000 datasets (for each virtual population). We used Markov chain Monte Carlo (MCMC; Brooks 2003) methods in a Bayesian framework to fit the IPMs using program R 3.4.1 (R Core Team 2017) and package R2Jags (Su and Yajima 2015) that calls on program JAGS 4.2.0 (Plummer 2003). We ran three chains for 60,000 iterations. We discarded the first 10,000 iterations as a burn-in period and used a thinning rate of three. We monitored convergence of models using the Gelman-Rubin diagnostic (Gelman and Rubin 1992) and randomly selected one of the 1000 virtual populations for each scenario and model type to visually inspect convergence of the MCMC chains. We provide the JAGS code to fit the hierarchical demography and per capita IPMs for the Constant scenario in Supplementary Materials 1.A.

We assessed whether the parameter for recruitment rate was identifiable for the base scenario by comparing the prior and posterior distributions. When the data supply little to no information about a parameter, the model is considered weakly identifiable (Gimenez et al. 2009). A parameter is considered identifiable if the posterior distribution differs from the prior and is unaffected by specification of the prior distribution (Gimenez et al. 2009; Abadi et al. 2010). We specified three prior distributions: $Uniform(-10{,}10)$, $Uniform(-2{,}2)$, and $Normal(0{,}0.5)$. For all other parameters, we used non-informative priors.

To evaluate model performance, we computed the bias, coefficient of variation (CV), root mean squared error (RMSE), and the 90% credible interval coverage (coverage) of the posterior estimates of abundance, survival, dispersal, and recruitment rate (Sokal and Rohlf 1995; Walther and Moore 2005). All performance metrics were averaged across years and simulated datasets for each model type and misspecification scenario, and calculated as

$$bias = \sum_{j=1}^{1000} \sum_{t=1}^{15} \frac{(\hat{x}_{tj} - x_{tj})}{x_{tj}} \Big/ (15 \times 1000)$$

$$CV = \sum_{j=1}^{1000} \sum_{t=1}^{15} \left(\frac{100SD_{tj}}{\hat{x}_{tj}} \right) \Big/ (15 \times 1000)$$

$$RMSE = \sqrt{\sum_{j=1}^{1000} \sum_{t=1}^{15} (\hat{x}_{tj} - x_{tj})^2 \Big/ (15 \times 1000)}$$

where $\hat{x}_{tj}$ is the parameter estimate, x_{tj} is the true parameter value from the virtual population, and SD_{tj} is the standard deviation of the estimate in year t for the dataset from the virtual population i. We calculated coverage as the proportion of simulated datasets for which the true value for the parameter was between the 5th and 95th posterior quantiles of the estimated parameter value.

RESULTS

Models for all simulations and scenarios converged and had Gelman-Rubin statistics of < 1.1 for all parameters. Additionally, the randomly selected model simulation runs for each scenario had good mixing of chains with visual inspection of diagnostic plots, indicating models converged. The prior distributions had little effect on the posterior distribution of recruitment rate. Prior-posterior overlap was ≤20% for all priors, which is below the maximum 35% guideline specified by Gimenez et. al. (2009) that indicates an identifiable parameter. Further, the posterior means for the different prior distributions were similar. Therefore, the parameter for recruitment rate was identifiable from the other data sources using the hierarchical demography IPM.

Estimates of recruitment rates were more accurate when we accounted for hierarchical demography (Figure 1.2). The per capita IPM model structure with constant recruitment (i.e., models with no component Allee effect) did not produce viable estimates of recruitment, as mean bias was > 0.10 (Figure 1.3). Mean CV for these models was ≤ 0.07, and due to the high precision and bias, coverage by the 90% credible interval was poor (Table 1.1). The per capita IPM models with a component Allee effect on recruitment, however, were unbiased (Figure 1.3). Coverage for estimates of recruitment by the 90% credible interval was greatest for the hierarchical demography IPM with a component Allee effect on recruitment and density dependent dispersal (i.e., the Full Scenario), and was closest to the expectation of 90% coverage (Table 1.1). CV for estimates of recruitment from the hierarchical demography IPMs were ~ 0.20 with constant recruitment and ~ 0.45 with a component Allee effect on recruitment.

In general, estimates of dispersal and survival from the hierarchical demography and per capita IPM model structures had comparable accuracy and bias within scenarios of model misspecification (Figure 1.2, Figure 1.3). Whereas bias of estimates of survival was similar across scenarios, estimates of dispersal were less biased when density dependence was included in dispersal (Figure 1.3). Coverage for estimates of dispersal was also greatest for scenarios that included density dependence in dispersal (Table 1.1). Similarly to recruitment, CV for estimates of dispersal was greater for scenarios with density dependence compared to scenarios with constant dispersal (> 0.45 and ~ 0.20, respectively). Notably, estimates of survival were more accurate in scenarios that included a component Allee effect on recruitment (Figure 1.2) and had greater coverage by the 90% credible intervals (Table 1.1). CV for estimates of survival under both IPM model structures and all scenarios was approximately 0.12.

Accuracy for estimates of abundance was greatest for models with hierarchical demography (Figure 1.2); however, both per capita and hierarchical demography IPM model structures produced estimates of abundance that were unbiased (Figure 1.3). CV for estimates of abundance under both model structures and all scenarios was ≤ 0.08. Additionally, coverage by the 90% credible interval was ≤ 0.78, which indicates that the estimated variance is likely too low (Table 1.1).

DISCUSSION

Population dynamics for group-living species depend on the processes within groups (survival, dispersal, and recruitment) and the processes that occur among groups (group formation and persistence). It is unclear how explicitly accounting for hierarchical demography (Al-Khafaji et al. 2009) of a socially-structured population affects estimation of population dynamics in group-living species. We tested IPMs with and without accounting for social structure under four scenarios of model misspecification to evaluate how accounting for hierarchical demography affects estimation and inference of population dynamics in a social species. Through simulations, we found that accounting for hierarchical demography greatly improves accuracy for estimates of recruitment. Further, with this framework we were able to accurately estimate recruitment when productivity data were lacking. Our results suggest this could be a viable method to estimate population dynamics in social species. More importantly, accounting for structure in population models can affect the resulting patterns and processes of population change.

Hierarchical demography affected accuracy for estimates of recruitment and abundance, however estimates of dispersal and survival were comparable. Estimates of recruitment rate and abundance were more accurately estimated with the IPM model structure that explicitly accounted for hierarchical demography under all four scenarios of model misspecification (Figure 1.2). Generally, all models provided viable estimates of demographic rates and abundance. This suggests that any of the models would be adequate for simply providing estimates. However, similarly to other studies (Stephens et al. 2002; Bateman et al. 2018; Woodroffe et al. 2019), our results suggest that models that account for social structure can offer advantages at detecting complex dynamics that arise in socially structured populations. Per capita models often fail to detect an Allee effect (Bateman et al. 2011), whereas those that explicitly account for social structure may perform better, as demonstrated here. Recruitment can be highly variable in social species due to factors like group characteristics or reproductive suppression (Solomon and French 1997; Elliot et al. 2014; Bateman et al. 2018). Per capita models would fail to account for this variation, as shown here by the poor coverage of the 90% credible interval (Table 1.1). Coverage of estimates by the 90% credible intervals was generally greater for the hierarchical demography IPM structure, indicating that the estimated variance was more similar to variance observed in the simulated populations.

In general, we found the IPMs provided accurate estimates of demographic rates even when explicit data were lacking. Accuracy of recruitment and dispersal estimates were similar despite the lack of data to inform recruitment. An advantage to using an integrated modeling framework is that demographic rates can be estimated without explicit data because the time-series count data contain information on the processes (Besbeas et al. 2002; Abadi et al. 2010). We found that the prior distribution had little influence on the posterior distribution of mean recruitment rate. Further, the posterior means and 95% credible intervals were similar under different priors. This suggests that the posteriors were dominated by the observed data (i.e., group count, abundance, survival, and dispersal data) and that recruitment rate is identifiable. An integrated modeling framework can be particularly useful for rare or elusive species that are difficult to sample because detailed demographic data can be more costly to collect than count or abundance data (Wilson and Delahay 2001; Thompson 2004). Dispersal data can also be difficult to collect, and this IPM framework may be useful to estimate not only recruitment but also dispersal without explicit data. Abadi et al. (2010) were able to estimate both immigration rate and recruitment without data for either demographic rate. Therefore, we could likely estimate both dispersal and recruitment of social species without explicit productivity or movement data.

There are several areas for further developing this framework for estimating demographic rates and evaluating the role of sociality. Although we developed the hierarchical demography IPM with species that form stable social groups in mind, the approach could readily be applied to other socially-structured populations. Sociality also includes more ephemeral group formations that exhibit fission-fusion dynamics (Aureli et al. 2008). This model could be adapted to determine effects of fission-fusion dynamics in population dynamics in species with flexible group membership such as bison (*Bison bison;* Merkle et al. 2015). Additionally, this approach could be applied to spatially-structured populations (i.e., metapopulations). For a metapopulation, naïve counts or estimates from sub-populations would replace the group counts. With the IPM, not only would we be able to provide estimates of population size and demographic rates, but also improve understanding of how processes within sub-populations and processes among sub-populations affect overall population growth rate. An application of this model to metapopulations might complement existing matrix models (Hunter and Caswell 2005) or occupancy models (Sjögren-Gulve and Hanski 2000) of metapopulations.

In the context of stable social groups, other nuances of group living could easily be incorporated into this modelling framework. First, sex and stage structure could be included to account for differences between males and females or, in the case of cooperative breeders, reproductive skew (Keller and Reeve 1994). In Serengeti lions (*Panthera leo*) males and females disperse at different rates (Packer and Pusey 1987) and in gray wolves typically only the breeding pair reproduces (Mech and Boitani 2003). Second, group formation and persistence rates could be a function of processes within and among groups. We assumed that group formation and extinction rates only varied over time to focus on estimating recruitment with limited data, however this is likely unrealistic. Environmental conditions might also interact with dispersal to affect group formation rates as is the case for meerkats (Bateman et al. 2012, 2018). Group extinction rates, which also includes groups dissolving when all members leave, could be a function of group density, environmental conditions, or fate of the dominate individuals in a group (Courchamp et al. 2002; Brainerd et al. 2008; Bateman et al. 2013). In wolves, for example, groups that lost the breeding male or female were more likely to dissolve (Brainerd et al. 2008; Borg et al. 2015). Last, immigration into the population or groups could be included to account for group augmentation (Kokko et al. 2001). We simulated the populations without immigration into groups or the population, however immigration rate could be modeled based on group or population characteristics. For social species, immigration into the population would likely increase group formation rates (Clutton-Brock 2016), therefore group formation can be viewed similarly to an apparent recruitment rate that accounts for groups formed by both immigrants and individuals in the population. Using this IPM for species that exhibit different within-group processes would improve our understanding of the importance of hierarchical demography in socially-structured populations.

This model provides a useful tool to estimate demographic rates and evaluate patterns and processes of population change in group-living species. In general, IPMs offer many advantages over the traditional approach of estimating demographic rates in separate analyses, such as improved precision of estimates or estimation or rates without data (Abadi et al. 2010; Schaub and Abadi 2011). When the species of interest is socially-structured, an IPM that explicitly accounts for hierarchical demography can improve estimates even more and lead to greater understanding of the influence of social structure on population dynamics. The use of an

IPM that accounts for hierarchical demography does require more data sources than an IPM without social structure, however socially structured populations are often observed in groups and group count data are often collected incidentally when abundance data are collected. Our results also indicate that hierarchical demography is important to consider when managing socially-structured populations. For a social species of conservation concern, if hierarchical demography is ignored, then important demographic processes that influence population growth rates (e.g., Allee effect) may not be detected which may affect results of population viability analyses or probabilities of persistence.

LITERATURE CITED

Abadi, F., C. Barbraud, and O. Gimenez. 2017. Integrated population modeling reveals the impact of climate on the survival of juvenile emperor penguins. Global Change Biology 23:1353–1359.

Abadi, F., O. Gimenez, B. Ullrich, R. Arlettaz, and M. Schaub. 2010. Estimation of immigration rate using integrated population models. Journal of Applied Ecology 47:393–400.

Al-Khafaji, K., S. Tuljapurkar, J. R. Carey, and R. E. Page. 2009. Hierarchical demography: a general approach with an application to honey bees. Ecology 90:556–566.

Almberg, E. S., P. C. Cross, and D. W. Smith. 2010. Persistence of canine distemper virus in the Greater Yellowstone Ecosystem’s carnivore community. Ecological Applications 20:2058–2074.

Aureli, F., C. M. Schaffner, C. Boesch, S. K. Bearder, J. Call, C. A. Chapman, R. Connor, A. D. Fiore, R. I. M. Dunbar, S. P. Henzi, K. Holekamp, A. H. Korstjens, R. Layton, P. Lee, J. Lehmann, J. H. Manson, G. Ramos-Fernandez, K. B. Strier, and C. P. van Schaik. 2008. Fission-fusion dynamics. Current Anthropology 49:627–654.

Ausband, D. E. 2018. Multiple breeding individuals within groups in a social carnivore. Journal of Mammalogy 99:836–844.

Ausband, D. E., M. S. Mitchell, C. R. Stansbury, J. L. Stenglein, and L. P. Waits. 2017a. Harvest and group effects on pup survival in a cooperative breeder. Proceedings of the Royal Society of London B: Biological Sciences 284:20170580.

Ausband, D. E., M. S. Mitchell, and L. P. Waits. 2017b. Effects of breeder turnover and harvest on group composition and recruitment in a social carnivore. L. Prugh, editor. Journal of Animal Ecology 86:1094–1101.

Ausband, D. E., C. R. Stansbury, J. L. Stenglein, J. L. Struthers, and L. P. Waits. 2015. Recruitment in a social carnivore before and after harvest. Animal Conservation 18:415–423.

Bassing, S. 2017. Harvest and persistence of wolf populations: variable effects of harvest on wolf packs in the Rocky Mountains. University of Montana.

Bateman, A. W., T. Coulson, and T. H. Clutton-Brock. 2011. What do simple models reveal about the population dynamics of a cooperatively breeding species? Oikos 120:787–794.

Bateman, A. W., A. Ozgul, T. Coulson, and T. H. Clutton-Brock. 2012. Density dependence in group dynamics of a highly social mongoose, Suricata suricatta. Journal of Animal Ecology 81:628–639.

Bateman, A. W., A. Ozgul, M. Krkošek, and T. H. Clutton-Brock. 2018. Matrix models of hierarchical demography: linking group- and population-level dynamics in cooperative breeders. The American Naturalist 192:188–203.

Bateman, A. W., A. Ozgul, J. F. Nielsen, T. Coulson, and T. H. Clutton-Brock. 2013. Social structure mediates environmental effects on group size in an obligate cooperative breeder, Suricata suricatta. Ecology 94:587–597.

Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. Biometrics 58:540–547.

Borg, B. L., S. M. Brainerd, T. J. Meier, and L. R. Prugh. 2015. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. The Journal of Animal Ecology 84:177–187.

Brainerd, S. M., H. Andrén, E. E. Bangs, E. H. Bradley, J. A. Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. A. Jozwiak, O. Liberg, C. M. Mack, T. J. Meier, C. C. Niemeyer, H. C. Pedersen, H. Sand, R. N. Schultz, D. W. Smith, P. Wabakken, and A. P. Wydeven. 2008. The effects of breeder loss on wolves. Journal of Wildlife Management 72:89–98..

Brooks, S. P. 2003. Bayesian computation: a statistical revolution. Philosophical Transactions of the Royal Society A 361:2681–2697.

Clutton-Brock, T. 2016. Mammal societies. John Wiley & Sons, New York.

Courchamp, F., and D. W. Macdonald. 2001. Crucial importance of pack size in the African wild dog Lycaon pictus. Animal Conservation 4:169–174.

Courchamp, F., G. S. A. Rasmussen, and D. W. Macdonald. 2002. Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog Lycaon pictus. Behavioral Ecology 13:20–27.

Elliot, N. B., M. Valeix, D. W. Macdonald, and A. J. Loveridge. 2014. Social relationships affect dispersal timing revealing a delayed infanticide in African lions. Oikos 123:1049–1056.

Fuller, T. K., L. D. Mech, and J. Fitts-Cochran. 2003. Wolf population dynamics. Pages 161–191 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation.

University of Chicago Press, Chicago, Illinois.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–472.

Gimenez, O., B. J. T. Morgan, and S. P. Brooks. 2009. Weak identifiability in models for mark-recapture-recovery data. Pages 1055–1067 in D. L. Thomson, E. G. Cooch, and M. J. Conroy, editors. Modeling demographic processes in marked populations. Springer, New York.

Heisey, D. M., T. L. Shaffer, and G. C. White. 2007. The ABCs of nest survival: theory and application from a biostatistical perspective. Studies in Avian Biology 34:13–33.

Hosmer, D. W. J., and S. Lemeshow. 2000. Applied logistic regression. 2nd edition. Wiley, New York, New York.

Hunter, C. M., and H. Caswell. 2005. The use of the vec-permutation matrix in spatial matrix population models. Ecological Modelling 188:15–21.

Jimenez, M. D., E. E. Bangs, D. K. Boyd, D. W. Smith, S. A. Becker, D. E. Ausband, S. P. Woodruff, E. H. Bradley, J. Holyan, and K. Laudon. 2017. Wolf dispersal in the Rocky Mountains, Western United States: 1993-2008. The Journal of Wildlife Management 81:581–592.

Kalbfleisch, J. D., and R. L. Prentice. 2011. The statistical analysis of failure time data. Volume 360. John Wiley & Sons.

Kane, M. D., D. J. Morin, and M. J. Kelly. 2015. Potential for camera-traps and spatial mark-resight models to improve monitoring of the critically endangered West African lion (Panthera leo). Biodiversity and Conservation 24:3527–3541.

Karanth, K. U., and R. Chellam. 2009. Carnivore conservation at the crossroads. ORYX 43:1–2.

Keller, L., and H. K. Reeve. 1994. Partitioning of reproduction in animal societies. Trends in Ecology & Evolution 9:98–102.

Kéry, M., and M. Schaub. 2011. Bayesian population analysis using WinBUGS: a hierarchical perspective. Academic Press.

Kokko, H., R. A. Johnstone, and C.-B. T. H. 2001. The evolution of cooperative breeding through group augmentation. Proceedings of the Royal Society of London. Series B: Biological Sciences 268:187–196.

Lerch, B. A., B. C. Nolting, and K. C. Abbott. 2018. Why are demographic Allee effects so rarely seen in social animals? Journal of Animal Ecology 87:1547–1559.

Loonam, K. 2019. Assessing the robustness of time-to-event abundance estimation. Graduate Student Theses, Dissertations, & Professional Papers. University of Montana , Missoula.

Di Marco, M., L. Boitani, D. Mallon, M. Hoffmann, A. Iacucci, E. Meijaard, P. Visconti, J. Schipper, and C. Rondinini. 2014. A retrospective evaluation of the global decline of carnivores and ungulates. Conservation Biology 28:1109–1118.

Marescot, L., O. Gimenez, C. Duchamp, E. Marboutin, and G. Chapron. 2012. Reducing matrix population models with application to social animal species. Ecological Modelling 232:91–96.

McGowan, C. P., M. C. Runge, and M. A. Larson. 2011. Incorporating parametric uncertainty into population viability analysis models. Biological Conservation 144:1400–1408.

Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1–34 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, Illinois.

Merkle, J. A., M. Sigaud, and D. Fortin. 2015. To follow or not? How animals in fusion-fission societies handle conflicting information during group decision-making. Ecology Letters 18:799–806.

Morris, W. F., and D. F. Doak. 2002. Quantitative conservation biology. Sinauer, Sunderland, Massachusetts, USA.

Newman, K. B., S. T. Buckland, B. J. T. Morgan, R. King, D. L. Borchers, D. J. Cole, P. Besbeas, O. Gimenez, and L. Thomas. 2014. Modelling population dynamics. Springer, New York, NY.

Packer, C., R. Hilborn, A. Mosser, B. Kissui, M. Borner, G. Hopcraft, J. Wilmshurst, S. Mduma, and A. R. E. Sinclair. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. Science 307:390–393.

Packer, C., and A. E. Pusey. 1987. Intrasexual cooperation and the sex ratio in African lions. The American Naturalist 130:636–642. University of Chicago Press.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling. <http://citeseer.ist.psu.edu/plummer03jags.html>.

Prentice, R. L., and L. A. Gloeckler. 1978. Regression analysis of grouped survival data with application to breast cancer. Biometrics 34:57–67.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. <http://www.r-project.org/>.

Rich, L. N., D. A. W. Miller, H. S. Robinson, J. W. McNutt, and M. J. Kelly. 2017. Carnivore distributions in Botswana are shaped by resource availability and intraguild species. Journal of Zoology 303:90–98.

Schaub, M., and F. Abadi. 2011. Integrated population models: a novel analysis framework for deeper insights into population dynamics. Journal of Ornithology 152:227–237.

Sjögren-Gulve, P., and I. Hanski. 2000. Metapopulation viability analysis using occupancy models. Ecological Bulletins 48:53–71.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. Freeman.

Solomon, N. G., and J. A. French, editors. 1997. Cooperative breeding in mammals. Cambridge University Press, Cambridge.

Steenweg, R., J. Whittington, M. Hebblewhite, A. Forshner, B. Johnston, D. Petersen, B. Shepherd, and P. M. Lukacs. 2016. Camera-based occupancy monitoring at large scales: Power to detect trends in grizzly bears across the Canadian Rockies. Biological Conservation 201:192–200. Elsevier.

Stenglein, J. L., J. Zhu, M. K. Clayton, and T. R. Van Deelen. 2015. Are the numbers adding up? Exploiting discrepancies among complementary population models. Ecology and Evolution 5:368–376.

Stephens, P. A., F. Frey-roos, W. Arnold, and W. J. Sutherland. 2002. Model complexity and population predictions. The alpine marmot as a case study. Journal of Animal Ecology 71:343–361. John Wiley & Sons, Ltd.

Stephens, P. A., W. J. Sutherland, and R. P. Freckleton. 1999. What is the Allee effect? Oikos 87:185–190.

Su, Y.-S., and M. Yajima. 2015. R2jags: using R to run “JAGS.” <http://cran.r-project.org/package=R2jags>.

Thompson, W. L., editor. 2004. Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters. Island Press, London.

Walther, B. A., and J. L. Moore. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. Ecography 28:815–829.

Wilson, G. J., and R. J. Delahay. 2001. A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. Wildlife Research 28:151–164.

Woodroffe, R., H. M. K. O'Neill, and D. Rabaiotti. 2019. Within- and between-group dynamics in an obligate cooperative breeder. Journal of Animal Ecology 89:530–540.

TABLES

Table 1.1: 90% credible interval coverage (coverage) for estimates of survival, dispersal, recruitment, and abundance from integrated population models (IPM) based on 1000 simulated populations of gray wolves (*Canis lupus*) for 15 years. Each value represents the proportion of simulations for which the true value of the parameter was between the 5th and 95th quantiles of the posterior distribution. We simulated the populations with social structure, positive density dependence in recruitment (i.e., a component Allee effect), and conventional density dependence in dispersal. We estimated parameters using two types of IPM model structure: 1) a model that explicitly accounted for hierarchical demography (HD), and 2) a per capita (PC) model. Additionally, under each IPM model structure we estimated parameters using four scenarios: 1) constant model with no density dependence or temporal variability, 2) a component Allee effect on recruitment, 3) density dependent dispersal, and 4) the full model with a component Allee effect on recruitment and density dependent dispersal.

	Hierarchical demography				Per capita			
Parameter	Constant	Allee	Dispersal	Full	Constant	Allee	Dispersal	Full
Survival	0.67	0.91	0.75	0.89	0.58	0.89	0.68	0.89
Dispersal	0.65	0.73	0.78	0.91	0.66	0.51	0.78	0.93
Recruitment	0.32	0.75	0.32	0.88	0.10	0.66	0.10	0.77
Abundance	0.78	0.71	0.71	0.71	0.52	0.78	0.57	0.77

FIGURES

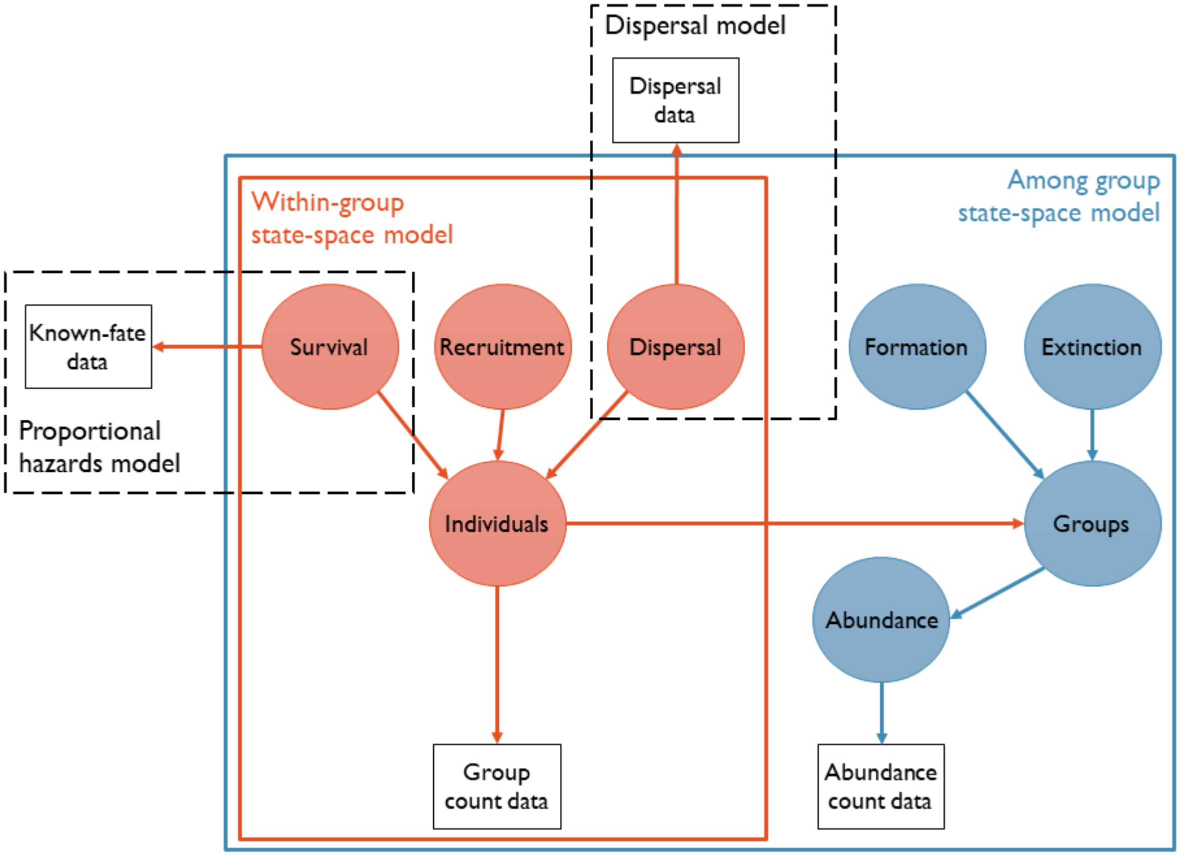

Figure 1.1: Directed acyclic graph of an integrated population model that accounts for social structure modeled after gray wolves (*Canis lupus*) in Montana, USA. The model includes state-space models for processes that occur within in groups (red) and for processes that occur among groups (blue). Estimated or fixed parameters are represented by circles and the data are represented by rectangles. Arrows represent dependencies, e.g., the observed known-fate data depends on survival of individuals within a group or the number of groups depends on group formation and extinction.

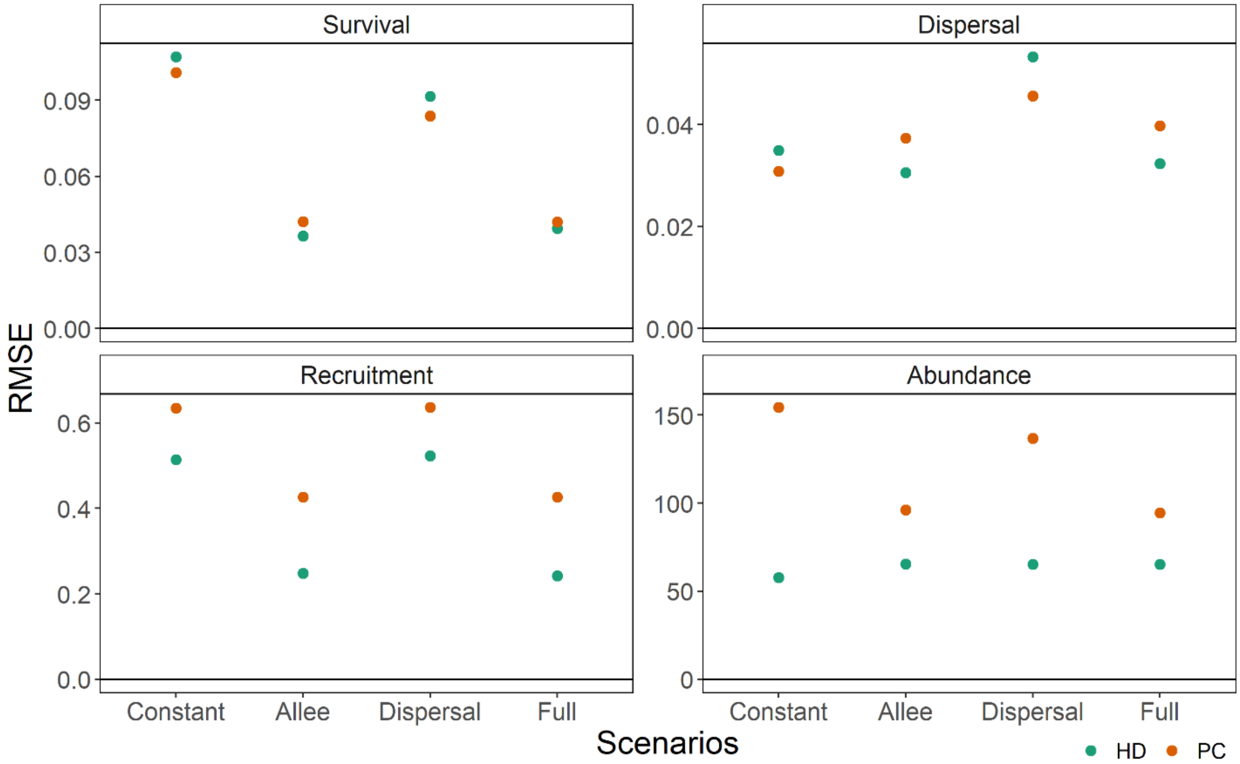

Figure 1.2: Root mean squared error (RMSE) of mean posterior estimates of survival, dispersal, recruitment, and abundance from integrated population models (IPM) based on 1000 simulated populations of gray wolves (*Canis lupus*) for 15 years. RMSE was averaged across simulations and years, and we scaled RMSE for recruitment by dividing by mean recruitment from the simulations. We simulated the populations with social structure, positive density dependence in recruitment (i.e., a component Allee effect), and conventional density dependence in dispersal. We estimated parameters using two types of IPM model structure: 1) a model that explicitly accounted for hierarchical demography (HD), and 2) a per capita (PC) model. Additionally, under each IPM model structure we estimated parameters using four scenarios: 1) constant model with no density dependence or temporal variability, 2) a component Allee effect on recruitment, 3) density dependent dispersal, and 4) the full model with a component Allee effect on recruitment and density dependent dispersal.

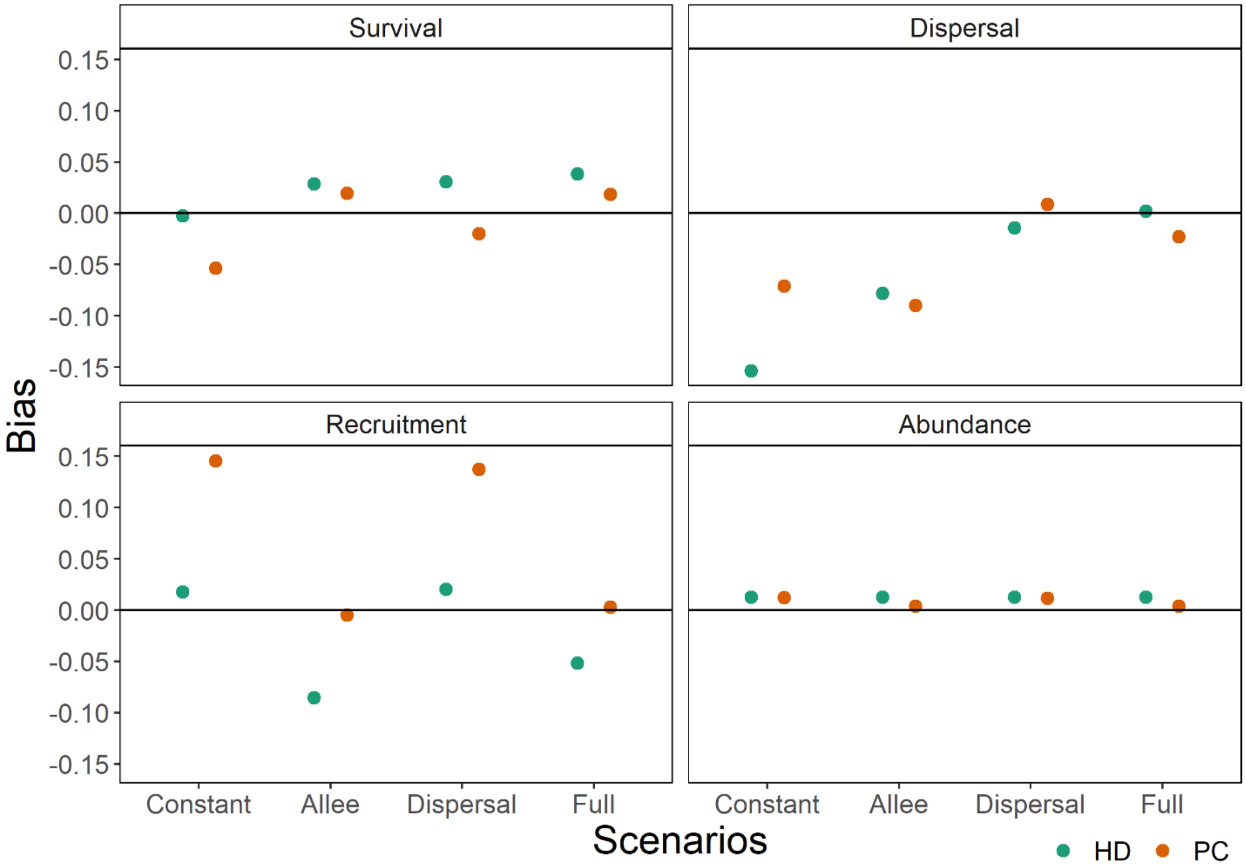

Figure 1.3: Bias (averaged across simulations and years) for estimates of survival, dispersal, recruitment, and abundance from integrated population models (IPM) based on 1000 simulated populations of gray wolves (*Canis lupus*) for 15 years. We simulated the populations with social structure, positive density dependence in recruitment (i.e., a component Allee effect), and conventional density dependence in dispersal. We estimated parameters using two types of IPM model structure: 1) a model that explicitly accounted for hierarchical demography (HD), and 2) a per capita (PC) model. Additionally, under each IPM model structure we estimated parameters using four scenarios: 1) constant model with no density dependence or temporal variability, 2) a component Allee effect on recruitment, 3) density dependent dispersal, and 4) the full model with a component Allee effect on recruitment and density dependent dispersal.

CHAPTER 2:

DRIVERS OF VARIATION IN RECRUITMENT AND EFFECTS ON POPULATION DYNAMICS IN GRAY WOLVES

ABSTRACT

Recruitment is an important vital rate affecting population growth of large mammals, and understanding patterns in this rate is crucial to effective management of wildlife populations. However, obtaining reliable estimates of recruitment remains challenging, particularly for social carnivores as they are often difficult to monitor. We developed an integrated population model to estimate recruitment in gray wolves (*Canis lupus*) and to evaluate factors influencing spatio-temporal variation in that vital rate. We used annual estimates of abundance and the number of packs, annual group count data, and known-fate data from global positioning system (GPS) and very-high-frequency (VHF) radiocollared adult wolves collected in Montana from 2007-2018 to estimate recruitment and evaluate the relative importance of intrinsic and extrinsic factors influencing variation in recruitment. Many factors may lead to spatio-temporal variation in recruitment of wolves, and these may either be extrinsic factors (e.g., mortality risk, food availability) or intrinsic factors (e.g., population or pack size). Studies have highlighted the importance of food availability or anthropogenic mortality in wolf population dynamics, and these factors may drive variation in recruitment. Due to the social structure of wolves, however, population density or pack size may be an important source of variation in recruitment. Therefore, we hypothesized that variation in recruitment was driven primarily by intrinsic factors such as pack size or population size. Alternatively, we hypothesized that extrinsic factors primarily influence variation in recruitment and predicted that indices of prey availability or

harvest would explain the most variation in recruitment. We found that the main factors explaining variation in recruitment of wolves was population size, pack size, and harvest. Mean number of pups recruited per pack varied slightly over time with changes in management practices and decreased survival of adults following harvest implementation. Recruitment does not appear to compensate for changes in survival, however the population has remained relatively stationary with mean annual harvest rates of 0.23 during our study.

INTRODUCTION

Understanding spatio-temporal variation in demographic parameters is a focus of population ecology (Hanski 1999; Williams et al. 2002; Tilman and Kareiva 2018). Recruitment and survival vary over both space and time, and information of that variation is needed to understand species distributions, dynamics of metapopulations, and the role of density dependence in population regulation (Bjørnstad et al. 1999; Sjögren-Gulve and Hanski 2000). Patterns of spatio-temporal variation in demographic rates can be used to identify source-sink habitat, predict the response of a population to environmental stressors such as climate change, and assess management actions (Horne 1983; Chandler et al. 2018). Understanding variation in recruitment may be particularly important for harvested populations because it influences the level of harvest a population could sustain (Mills 2013). Further, for long-lived species, recruitment of juveniles typically varies more than adult survival and can thus more strongly influence population growth rates (Gaillard et al. 1998, 2000).

Although understanding variation in recruitment is important for management, this information can be challenging to obtain, especially for social carnivores. Evaluating spatio-temporal variation in recruitment requires long-term demographic studies over broad spatial scales. Many large carnivores, however, occur at low densities and are wide-ranging which makes them difficult to monitor (Thompson 2004). Traditional methods to estimate recruitment include visual observation of offspring (e.g. Bateman et al. 2013) or mark-recapture data (Williams et al. 2002). These methods, however, can be expensive and labor intensive at broad spatial scales (Wilson and Delahay 2001). Although camera trap data are used to estimate abundance of unmarked populations (Royle 2004; Keever et al. 2017; Moeller et al. 2018), there have not been similar advances to estimate demographic parameters for unmarked populations from camera trap data (but see Dail and Madsen 2011; Zhao et al. 2017). Sociality also presents unique challenges when evaluating spatio-temporal variation in recruitment. In some social species, the group is the reproductive unit, and often only a few individuals are responsible for a majority of reproduction (Koenig et al. 2009). In those cases, treating recruitment as a per-capita rate is inappropriate. Further, sociality creates complex population dynamics that occur in a hierarchy, with variation in recruitment being influenced by individual, group, and population characteristics (Al-Khafaji et al. 2009; Clutton-Brock 2016). Hierarchical demography refers to the link between demographic processes at different levels of hierarchical social structure within a population (Al-Khafaji et al. 2009). Within social groups, individuals survive, reproduce, disperse, and immigrate. These rates depend on individual characteristics (e.g., age, sex, body size) similar to non-social species (Lindberg et al. 2013; Gimenez et al. 2018), but also depend on group characteristics (e.g., group size, group composition) and population size (Courchamp and Macdonald 2001; Packer et al. 2005; Bateman et al. 2018). For example, in common marmosets (*Callithrix jacchus*) breeding females had greater reproductive success with more adult males present (Koenig 1995). Therefore, accounting for hierarchical demography may be key to understanding variation in recruitment of social species.

Gray wolves (*Canis lupus*) are managed with harvest in parts of their range, and a better understanding of factors influencing spatio-temporal variation in recruitment are needed. Wolves are a social species that form stable groups (i.e., packs) and occur at low densities. Generally, the pack consists of a breeding pair and non-breeding adults from past litters that help guard and provision pups (Mech and Boitani 2003). Within a pack, dynamics are a function of recruitment of pups, adoption of unrelated adults (i.e., immigration), mortality, and dispersal (Fuller et al. 2003; Mech and Boitani 2003). Among packs, new packs can form and existing packs can disband (i.e., go locally extinct). Dynamics within and among packs determine growth rate of the population (Fuller et al. 2003; Packard 2003; Brainerd et al. 2008). Management of wolves with harvest is a contentious issue, and debate over the level of harvest a wolf population can sustain stems from the role of variable recruitment in population dynamics (Creel and Rotella 2010; Gude et al. 2012).

Many factors may lead to spatio-temporal variation in recruitment of wolves, and these may either be extrinsic factors (e.g., mortality risk, food availability) or intrinsic factors (e.g., population or pack size). Food availability and human-caused mortality are extrinsic factors that are strongly correlated with wolf density and population growth rate (Fuller et al. 2003; Creel and Rotella 2010), and may be most important for variation in recruitment. First, recruitment may vary both spatially and temporally with prey availability (Boertje and Stephenson 1992; Fuller et al. 2003). Annual fluctuations in prey populations were positively correlated with variations in wolf density (Mech and Fieberg 2015), and may be related to increased litter size and pup survival with prey availability (Boertje and Stephenson 1992). Spatio-temporal variation in harvest may also lead to variable recruitment in wolves. Harvest both directly and indirectly reduces recruitment (Ausband et al. 2015, 2017), and could cause significant spatial and temporal variation in recruitment. Spatial variation in harvest may be difficult to quantify, however Person and Russell (2008) used road density as a proxy for spatial risk of harvest because roads increase access for hunters and trappers. Forest cover has also been used as a proxy for escape cover from humans (Llaneza et al. 2012) and is positively associated with occupancy of wolves (Rich et al. 2013; Bassing et al. 2019). Conversely, recruitment could be primarily affected by intrinsic factors such as pack size and composition (Ausband et al. 2017; Ausband 2018) or population size. The number of non-breeding helpers in a group influences recruitment in many species that cooperatively breed, including wolves (Solomon and French 1997; Courchamp et al. 2002; Stahler et al. 2013; Ausband et al. 2017). Gude et al. (2012) and Stenglein et al. (2015*b*) found evidence of density-dependence in recruitment, and population size may be an important intrinsic factor driving variation in recruitment.

Our objective was to evaluate the relative importance of intrinsic and extrinsic factors influencing variation in recruitment in a large, social carnivore. We tested the hypothesis that variation in recruitment of wolves is influenced by intrinsic factors (pack size and population size). Alternatively, we hypothesized that extrinsic factors (prey availability and human-caused mortality) drive variation in recruitment. We tested our hypotheses using an integrated population model (IPM) we developed to estimate recruitment of wolves in Montana from 2007 to 2018. IPMs are an integrated modeling framework that typically combines time-series of count data and capture-mark-recapture data to estimate abundance and demographic rates (Besbeas et al. 2002; Newman et al. 2014). Time-series count data contain information on the demographic rates (i.e., abundance next year equals the number that survived and the number that were recruited in a closed population), therefore demographic rates without explicit data can be estimated with an IPM (e.g., Abadi et al. 2010). For example, if we had time-series of count data and data to inform survival we could essentially solve for recruitment in a closed population because we knew how the population changed and the number that survived. Thus, using an IPM was appropriate for our purpose because it allowed us to use existing data for abundance, pack size, and survival to estimate recruitment, for which we had no data.

STUDY AREA

Our study took place in the Montana portion of the U.S. Northern Rocky Mountains and primarily encompassed western Montana, where a majority of wolves were located within the state (Rich et al. 2013; Montana Fish Wildlife and Parks 2018). Western Montana was characterized by forested mountain ranges and rich river valleys. The area was dominated by pine (*Pinus spp.*) and spruce (*Picea spp.*) forest intermixed with grassland, agriculture, and rangeland. The main prey resources available for wolves were elk (*Cervus elaphus*), white-tailed deer (*Odocoileus virginianus*), mule deer (*O. hemionus*), and moose (*Alces alces*; USFWS 1994). Cattle and domestic sheep occurred throughout the region, and land ownership was a mixture of private and public lands (USFWS 1994).

Management of wolves in Montana changed over the course of this study. The wolf population in Montana was delisted in 2011 (U.S. Fish and Wildlife Service 2011) following successful natural recolonization of northern Montana and reintroductions into central Idaho and the Greater Yellowstone Area (Ream et al. 1989; Bangs and Fritts 1996; Bangs et al. 1998). Prior to 2011, excluding 2009 when wolves were temporarily delisted, wolves were protected. However, classification as experiment non-essential under the ESA in parts of their range allowed managing agencies and landowners to lethally remove wolves depredating or threatening livestock (USFWS 1994*b*). From 1996 to 2010, control actions removed 6% - 34% of wolves annually (mean = 14%, SD = 7.7%). Since delisting, responsibility for management and monitoring of wolves in Montana was performed by Montana Fish, Wildlife and Parks (MFWP), and regulated public harvest was used to manage the wolf population. From 2011 to 2018, control actions removed 5% - 12% (mean = 7%, SD = 1.8%) and harvest removed 12% - 32% annually (i.e., by calendar year; mean = 23%, SD = 6.0%) of wolves in Montana.

METHODS

We adjusted a traditional IPM framework to account for hierarchical demography by adding a state-space model for within-pack processes in addition to the state-space model for population size (Figure 2.1). We used estimates of abundance for changes in population size over time, estimates of the number of packs over time, group counts for changes in pack size over time (i.e., within-pack state-space model), and global positioning system (GPS) and very-high-frequency (VHF) radiocollar data to estimate adult survival (Glen et al. 2011; Rich et al. 2013; Inman et al. 2019) from 2007-2018. Because we did not have raw data to estimate dispersal within the IPM, we used published dispersal rates as an informative prior in our model (e.g., Besbeas et al. 2002; McCaffery and Lukacs 2016).

Population and Demographic Data

We used three types of data produced by ongoing monitoring in Montana: estimates of abundance and the number of packs, GPS and VHF radiocollars, and group counts (Rich et al. 2013; Inman et al. 2019). MFWP estimated the number of packs and abundance of wolves annually from 2007-2018 using patch occupancy models, mean territory size, and mean pack size (Miller et al. 2013; Rich et al. 2013; Inman et al. 2019). Dynamic occupancy models that account for false-positive detections provided an estimate of the area occupied by wolves (Miller et al. 2013; Rich et al. 2013; Inman et al. 2019). Mean territory size was assumed to be 600 km^2 (Rich et al. 2012), and was used to calculate the number of territories (i.e., packs) within the occupied area (Rich et al. 2013; Inman et al. 2019). Abundance was then calculated as the estimated number of packs multiplied by mean pack size (Rich et al. 2013; Inman et al. 2019). Reported estimates of abundance were assumed to represent the population size in December because mean pack size was determined using group counts at the end of the calendar year (Rich et al. 2013; Inman et al. 2019).

MFWP, United States Fish and Wildlife Service (USFWS), and University biologists began deploying VHF radiocollars on wolves consistently in 1995 (USFWS 2010). GPS radiocollars were deployed in 2008-2009 as part of another research initiative (Rich et al. 2012) and during 2014-2018. Wolves were captured using foothold traps or aerial darting, and all handling followed MFWP's biomedical protocol (Montana Fish Wildlife and Parks 2005) and guidelines from the American Society of Mammalogists (Sikes and Bryan 2016) and the Institutional Animal Care and Use Committee for the University of Montana (AUP # 070-17). We used data from 2007-2018 that included both VHF and GPS radiocollars that were deployed on adult wolves through ground trapping in spring, summer, and fall and aerial darting in winter. We censored wolves that were removed for livestock depredation in the time period preceding their last transmission because they represented a non-random sample (i.e., wolves were radiocollared because of livestock depredation; Murray et al. 2010).

Group counts were collected by USFWS, Tribal, and MFWP biologists annually. Field methods and effort varied over the course of wolf recovery. Biologists monitored radiocollared wolves to determine pack size via aerial and ground observations from late summer through winter (Mech 1973; Gude et al. 2012). Camera-trapping was also used to obtain group counts for packs that were not radiocollared (USFWS 2009; Bradley et al. 2015). MFWP biologists increased monitoring efforts each December to provide end-of-year counts. They classified counts as good, moderate or poor quality. We used group counts for wolves in Montana from 2007-2018 that the biologists classified as good or moderate quality (i.e., pack size was documented multiple times each year). Because counts were collected from late summer through December, we used the reported end-of-year counts plus the number of wolves harvested from the pack and assumed that counts were representative of immediately prior to the harvest season (i.e., September; see Supplementary Materials 2.A for a biological and monitoring timeline). Additionally, we added the number of wolves removed for livestock depredation for each pack to the group counts. Because we censored wolves that were removed for livestock depredation from the radiocollar data, this allowed us to account for livestock removals by subtracting known removals of wolves from packs.

Model Structure

We developed an IPM that accounted for hierarchical demography to estimate recruitment of wolves in Montana based on available data. Changes in population size each year was a function of the number of packs, and the number of individuals within those packs. We only had group count data for a portion of the total packs in the population. Therefore, we modeled changes in population size (N_t) and the total number of packs (Z_t) over time as

$$N_t = \sum_{g=1}^{P_t} G_{gt} \phi_t^H + (Z_t - P_t)\bar{G}_t,$$

$$Z_t \sim Normal(Z_{t-1}\rho_{t-1}, \tau_Z^2),$$

where P_t was the number of packs that were monitored in year t, G_{gt} was the number of individuals in pack g in September, ϕ_t^H was survival rate during the hunting only period from September through November, $\bar{G}_t$ was the estimated mean pack size from monitored packs after accounting for survival during the hunting period, ρ was the growth rate of packs (i.e., pack formation and persistence rates), and τ_Z^2 was process variance for the number of packs. We did not include additional process error in population size because we included it in group size (G_{gt}) and the total number of packs (Z_t). We related the observed estimates of abundance ($y.N_t$) and the number of packs ($y.Z_t$) to the actual population size (N_t) and number of packs (Z_t) with normal distributions and sampling variance (σ^2):

$$y.N_t \sim Normal(N_t, \sigma_N^2),$$

$$y.Z_t \sim Normal(Z_t, \sigma_Z^2).$$

Changes in group size (G_{gt}) over time were a function of survival probability (ϕ_t), dispersal from the pack (δ_t), and recruitment of pups within the pack (γ_{gt}) for year t in pack g. Because we censored wolves that were removed for livestock depredation from the radiocollar data, we accounted for livestock removals by subtracting known removals of wolves from packs (C_{gt}). We assumed observed group count data ($y.G_{gt}$) were collected 5 months after birth in September, therefore we modeled changes in group size in two ways. In the first year, we modeled changes in group size based on recruitment rate to 5 months of age (γ_{gt}^5). In subsequent years we modeled changes in group size based on recruitment rate to 5 (γ_{gt}^5) and 17 months of age (γ_{gt}^{17}):

$$muG_{gt} = G_{gt-1}\phi_{t-1}(1-\delta_{t-1}) + \gamma_{gt-1}^5 - C_{gt-1},$$

$$muG_{gt} = G_{gt-2}\phi_{t-1}\phi_{t-2}(1-\delta_{t-1})(1-\delta_{t-2}) + \gamma_{gt-1}^5 + \gamma_{gt-1}^{17} - C_{gt-1} - C_{gt-2}.$$

This allowed us to estimate recruitment rate of pups to 5 and 17 months of age. The group count data did not appear to be overdispersed, therefore we used a Poisson distribution to account for process error and modeled the observation process as

$$G_{gt} \sim Poisson(mu_{gt})$$

$$y.G_{gt} \sim Binomial(p, G_{gt}),$$

where $y.G_{gt}$ was the group count data and p was the estimated detection rate for group counts, which we assumed was constant. We did not have adequate raw data available to estimate dispersal, therefore we used the mean and variance of dispersal of wolves in the U.S. Northern Rocky Mountains from 2007-2008 (Jimenez et al. 2017) and estimated dispersal rates from Idaho, 2005 – 2016 (Horne et al. 2019) as an informative prior to estimate annual dispersal rates.

We estimated survival of adults using a discrete-time proportional hazards model with a complimentary log-log (cloglog) link function (Prentice and Gloeckler 1978). Kalbfleisch and Prentice (2011) recommended using cloglog transformation for continuous data that were grouped into discrete periods. We chose four discrete periods for analysis: the denning period (April-May), rendezvous period (June-August), hunting-only period (September-November), and the hunting and trapping period (December-March). We modeled the relocations of radiocollared wolves ($y.surv_i$) as independent Bernoulli random variables (Heisey et al. 2007) for the observation (i) of the individual wolf as either alive (0) or dead (1). The probability for an event occurring ($\mu.surv_{pt}$) was modeled using the cloglog link as

$$cloglog(\mu.surv_{pt}) = \beta_{Period} + \varepsilon_{S,t}, \qquad \varepsilon_{S,t} \sim Normal(0, \sigma_S^2),$$

$$y.surv_i \sim Bernoulli(\mu.surv_{pt}),$$

$$y.surv_i = \{0,1\},$$

where β_{Period} was the intercept for each time period and ε was a year random effect for observation i, year t, and period p. To estimate annual survival of adults (ϕ_t) from the probability of an event (i.e., death) occurring, we calculated the hazard for each period and year (h_{pt}) and the cumulative hazard (H_t) for each year (Prentice and Gloeckler 1978; Hosmer and Lemeshow 2000; Heisey et al. 2007):

$$h_{pt} = -\log(1 - \mu.surv_{pt}),$$

$$H_t = \sum_{p=1}^{4} h_{pt} w_p,$$

$$\phi_t = \exp(-H_t),$$

where w_p was the number of months in each period p. The cumulative hazard was therefore the cumulative sum of the hazard multiplied by the number of months in each period (Hosmer and Lemeshow 2000; Kalbfleisch and Prentice 2011). We had a random year effect on survival to account for yearly variation in this vital rate. We did not include other covariates on survival because we were primarily interested in estimating recruitment.

We estimated recruitment as the number of pups per pack that survived to 5 (γ_{gt}^{5}) and 17 (γ_{gt}^{17}) months of age using a Poisson distribution for process error and generalized linear models with a log link function. The linear predictor could then be described using covariates to test hypotheses about factors influencing recruitment as

$$\mu.gam_{gt}^{a} = \exp\left(\beta_0 + \beta_1 X_1 + \varepsilon_{R,t}\right), \qquad \varepsilon_{R,t} \sim Normal(0, \sigma_R^2),$$

$$\gamma_{gt}^{a} \sim Poisson\left(\mu.gam_{gt}^{a}\right),$$

where β_0 was the intercept and β_1 was the slope coefficient for covariate X_1 for recruitment to age a (i.e., either 5 or 17 months of age) and $\varepsilon_{R,t}$ was a year random effect. We accounted for potential overdispersion in recruitment by including extra variation in the year random effect. We estimated the total number of pups recruited to 5 and 17 months of age by multiplying the estimated number of packs and the appropriate recruitment rate. Additionally, we estimated annual population growth rate as N_t/N_{t-1}.

Assessing Role of Intrinsic and Extrinsic Factors on Recruitment

We ran six competing models of recruitment that represented intrinsic factors (population density or pack size) or extrinsic factors (human-caused mortality measured by low-use road density, harvest, or forest cover and prey availability measured by winter severity and catch-per-unit-effort) to assess the relative importance of each (Table 2.1). We ran the same models for both recruitment rates. We classified low-use road density as either 4-wheel-drive or 2-wheel-drive roads (U.S. Census Bureau Geography Division 2003, U.S. Department of Agriculture Forest Service 2007) and calculated road density within a 600 km^2 buffer around the pack centroid, which represented average territory size of wolves (Rich et al. 2012, 2013). We removed roads in areas with human population densities > 25 people/km^2 because we assumed these represented high-use roads. We also calculated the proportion of the buffer covered by forest using ArcGIS (ESRI 2011). Forest cover was assessed by reclassifying 90 m^2 land cover pixels into forest and non-forest (Redmond et al. 1998). Data for forest cover and road density were from 2013, and we assumed this varied little over time. Harvest was a binary variable that was 1 in years with harvest and 0 in years without harvest. Prey biomass is difficult to quantify, however some studies have used winter severity as a proxy measure for prey vulnerability (Mech and Peterson 2003; Mech and Fieberg 2015). Therefore, we used winter severity and catch-per-unit-effort (CPUE) of antlered elk as an index of prey abundance (Lancia et al. 1996). For winter severity we used the average daily snow depth for the water year (October 1 – September 30) from SNOTEL (https://www.wcc.nrcs.usda.gov/snow/). We estimated CPUE for elk in each administrative region as the number of harvested antlered elk divided by the number of hunter days using harvest statistics from MFWP (fwp.mt.gov). We used the estimated population size for density dependence and pack size for density dependence within a pack. We centered and scaled the covariate data for road density, forest cover, snow depth, and elk CPUE. We had two candidate models that represented the intrinsic hypothesis and four candidate models that represented the extrinsic hypothesis (Table 2.1), and selection was based on posterior deviance.

We only considered univariate models because we were interested in the relative influence of covariates on recruitment, and to avoid over-parameterizing the model for recruitment.

We used Markov chain Monte Carlo (MCMC; Brooks 2003) methods in a Bayesian framework to fit the IPM using program R 3.4.1 (R Core Team, 2017) and package R2Jags (Su and Yajima 2015) that calls on program JAGS 4.2.0 (Plummer 2003). Vague prior distributions were used for all parameters except for dispersal (see provided JAGS code in Supplementary Materials 2.B). We ran three chains for 300,000 iterations with the first 50,000 discarded as a burn-in period and a thinning rate of three. We ran an additional 100,000 iterations until convergence was reached or a maximum of an additional 500,000 iterations. We monitored convergence using visual inspection of the MCMC chains and the Gelman-Rubin diagnostic, and retained only models that successfully converged (Gelman and Rubin 1992). All results are presented with mean and 95% credible intervals unless otherwise specified. We calculated the probability a coefficient was greater than or less than zero using the MCMC samples from the posterior distribution.

RESULTS

We had a total of 163 radiocollared adult wolves (95 females and 68 males) from 2007 to 2018. The wolves were captured in 99 unique packs with an average of 1.65 (SD=0.993) radiocollared wolves captured per pack. The number of radiocollared wolves per year ranged from 19 in 2007 to 47 in 2016. Of the 163 radiocollared wolves, 81 had an unknown fate and were censored the time period of their last known location. Mortality sources for the 82 wolves with documented mortality included legal harvest (n=31), control removals (n=21), poaching (n=9), other human-caused mortality (e.g., vehicle collision or removed in defense of livestock; n=3), non-human mortality (e.g., natural mortality or conspecific aggression; n=6), and unknown cause of mortality (n=7).

We excluded 358 group count observations (24.8%) of the original group count dataset because they were not classified as “good” or “moderate” quality. The final dataset included 816 observations from 181 packs, 2007-2018. The mean observations per year was 68 (SD=21.8) with a range of 27 observations in 2007 to 102 observations in 2017. On average, each pack had 4.5 observations (SD=2.48), with one pack contributing 12 observations (i.e. 12 years of good or moderate quality counts).

All models except the model with snow depth and elk CPUE converged with Gelman-Rubin statistics of <1.1 for all parameters, which indicates model convergence. Additionally, parameters with Gelman-Rubin statistics close to 1.1 had good mixing of chains with visual inspection of diagnostic plots for models that converged. The model with the lowest mean deviance included a density-dependent effect on recruitment (Table 2.1). There was a 0.97 probability of a negative correlation between population size and recruitment rate to 17 months (Table 2.2), and we found a 2.5% (0 – 5.92%) decline in recruitment with a 10% increase in population size. The effect of population size on recruitment rate to 5 months was positive, however this relationship was uncertain (Table 2.2). There were two competing models within the standard deviation of the top model that included 1) harvest and 2) pack size (Table 2.1). We found a 0.91 probability that harvest was correlated with decreased recruitment to 17 months, and found recruitment decreased by 49% (149% decrease – 9.8% increase) in years with harvest (Table 2.2). The correlation between harvest and recruitment to 5 months of age was positive, however the relationship was uncertain (Table 2.2). Pack size had a positive effect on recruitment rate to 5 months of age (Table 2.2). We found for each additional wolf added to the pack, recruitment rate to 5 months of age increased by 6% (4.4 – 7.5%). The relationship between recruitment rate to 17 months and pack size was uncertain (Table 2.2).

Although not supported through model selection, we found correlations between recruitment rate and 4-wheel-drive road density and forest cover whereas the relationship between 2-wheel-drive road density and recruitment was uncertain (Table 2.2). We found a 0.95 probability that 4-wheel-drive road density was negatively correlated with recruitment to 17 months (Table 2.2). We also found a negative correlation between forest cover and recruitment to 17 months, and for each standard deviation increase in forest cover recruitment to 17 months decreased by 50% (103 – 5.7%; Table 2.2). The relationship between forest cover and recruitment to 5 months was the opposite, and for each standard deviation increase in forest cover recruitment to 5 months increased by 10% (7.9% decrease – 25.5% increase; Table 2.2).

Recruitment rate of pups to 5 months of age and to 17 months of age varied little across years. Mean recruitment rate to 5 months of age ranged from 3.25 (2.32 – 4.13) to 4.21 (3.28 – 5.26) whereas mean recruitment rate to 17 months of age ranged from 1.40 (0.57 – 2.15) to 3.06 (1.70 – 4.63; Figure 2.2). During years without harvest, the mean recruitment rate to 5 and 17 months of age was 3.86 (2.92 – 4.82) and 2.57 (2.14 – 3.48), respectively. During years with harvest, however, the mean recruitment rate to 5 and 17 months of age was 3.80 (3.14 – 4.55) and 1.51 (0.76 – 2.13), respectively. Mean annual number of pups recruited to 5 and 17 months was 516 (389 – 653) and 229 (103 – 347), respectively (Figure 2.2). We found that adult survival rates also varied annually, and was greatest during years without harvest (0.70, 0.585 – 0.814) than years with harvest (0.50, 0.434 – 0.555; Figure 2.3). The biological period with the greatest survival rate, based on non-overlapping CRIs, was the denning period (April-May; 0.99, 0.972 – 0.998) and rendezvous period (June-August; 0.91, 0.868 – 0.947), whereas survival for the the hunting-only period (September-November; 0.78, 0.745 – 0.807) and the hunting and trapping period (December-March; 0.77, 0.701 – 0.833) were similar. The greatest difference in survival by period during years with and without harvest, based on non-overlapping CRIs, was during the hunting and trapping period. Survival during the hunting and trapping period for years with harvest was 0.74 (0.660 – 0.814) compared to 0.86 (0.786 – 0.919) during years without harvest. Mean population growth rate for our study period was 1.02 (1.01 – 1.04; Figure 2.4). We found that the correlation between population growth rate and survival ($r = 0.21$; $Pr(r>0) = 0.78$) and recruitment to 17 months of age ($r = 0.55$; $Pr(r>0) = 0.98$) was positive, whereas there was no correlation between population growth rate and recruitment to 5 months of age ($r = 0.02$; $Pr(r>0) = 0.50$) or dispersal ($r = -0.16$; $Pr(r<0) = 0.61$).

DISCUSSION

Understanding the effects of intrinsic and extrinsic factors on recruitment can provide insight into drivers of population dynamics and aid in identifying management actions. Estimating recruitment for populations of species that cooperatively breed, however, can be challenging due to hierarchical demography (Al-Khafaji et al. 2009; Clutton-Brock 2016). Efforts to estimate recruitment are further hindered by cost and difficulty in collecting data. We used an IPM to evaluate how intrinsic and extrinsic factors affect variation in recruitment in a social, cooperatively breeding species when productivity data were lacking. Using available data from monitoring of wolves in Montana from 2007-2018, we found that recruitment was primarily affected by intrinsic factors such as population size and pack size. Both abundance and pack size appeared to affect recruitment of pups suggesting density dependence of population size and pack size, however these processes had opposite effects. Abundance had a negative correlation with recruitment to 17 months of age, suggesting a negative density dependent effect. Pack size had a positive correlation with recruitment of pups to 5 months of age and indicates positive density dependence within a pack. We also found support that harvest negatively affects recruitment of wolves. Although the credible interval contained zero for the coefficient of harvest, there was still a probability of 0.91 that harvest reduced recruitment to 17 months of age.

We found support for our hypothesis that recruitment to 17 months in wolves is density dependent. This suggests that wolves may have saturated the available habitat in the NRM (Oakleaf et al. 2006) and reached some carrying capacity, whether biological or social (i.e., human tolerance; Murray et al. 2010). Density dependence in recruitment could be due to decreasing per capita food availability affecting either pup survival, litter size, or both (Boertje and Stephenson 1992; Sidorovich et al. 2007). We found no support for a negative effect of abundance on recruitment to 5 months of age (Table 2.2), however, suggesting that density dependence may not influence litter size or neonatal pup survival in our study. Further, if recruitment to 5 months is not density dependent, it suggests that food availability, at least through September, may not be limiting. Instead, as the population grew and prime habitat became saturated, wolves likely expanded into marginal habitat with more human activity potentially resulting in density dependence in survival (Murray et al. 2010; Stenglein et al. 2018) and recruitment to 17 months (Figure 2.2). The asymptotic growth of wolves over time (Figure 2.1 and 2.4 in MFWP 2018) and the mean population growth rate of 1.02 we found also support this conclusion. Prior to reintroductions into central Idaho and Yellowstone National Park, the Montana wolf population was approximately 50 individuals, increased exponentially until 2007, and then grew more slowly until the population became relatively stationary after delisting began in 2011 (U.S. Fish and Wildlife Service et al. 2010; Montana Fish Wildlife and Parks 2018). Gude et al (2012) and Stenglein et al. (2015) also found negative density dependence in recruitment of wolves in the NRM and Wisconsin, respectively. Our findings of density dependent recruitment to 17 months may be confounded with dispersal. Although wolves generally remain in their natal pack until two years of age, yearling wolves may also disperse (Fuller et al. 2003; Jimenez et al. 2017). This may bias our estimates of recruitment low if wolves survived until 17 months but dispersed.

Our results support the hypothesis that the presence of non-breeding helpers increases recruitment to 5 months (i.e., positive density dependence with pack size). Positive density dependence in recruitment within a pack indicates that survival of pups increases with increasing pack size. This corroborates findings of increased survival and recruitment of pups with increasing pack size in wolves (Ausband et al. 2017) and other species that cooperatively breed (Koenig 1995; Solomon and French 1997; Courchamp and Macdonald 2001; Courchamp et al. 2002). For example, African wild dogs require a minimum number of helpers for hunting, pup defense, and feeding (Courchamp and Macdonald 2001). Similarly, meerkats recruit more offspring in larger groups because the burden of babysitting and predator surveillance is shared (Russell et al. 2003). Although the breeding female provides most care, non-breeders in the pack help guard and provision pups (Ausband et al. 2016) that could increase pup survival and recruitment. Alternatively, the increase in recruitment with group size could be due to increases in production of pups instead of survival. Typically only the breeding pair reproduces, however increases in both pack size and abundance are positively correlated with multiple breeding females in a pack (Ausband 2018). Therefore, increased recruitment in larger packs could be a result of multiple breeding females and larger litter sizes per pack. We did not find a component Allee effect in recruitment to 17 months with pack size, suggesting that the benefit of larger packs for recruitment to 5 months did not translate to recruitment to 17 months. After 5 months of age, pups begin moving with the pack and are less dependent on care from adults (Fuller et al. 2003; Mech and Boitani 2003). Additionally, harvest mortality occurs after pups are 5 months old, and any increase in recruitment to 5 months old in larger packs may be negated by harvest mortality. We did not find negative density dependence within a group; however, we only tested a monotonic relationship with pack size and both positive and negative density dependence may occur within a pack (Creel and Creel 1995; Bateman et al. 2012; Stenglein et al. 2015*b*). There could be a threshold beyond which increasing pack size results in decreased recruitment as demonstrated in meerkats (Bateman et al. 2012). In African wild dogs (*Lycaon pictus*), the per capita food intake adjusted for costs was greatest at intermediate pack sizes (Creel and Creel 1995), and less food available per individual could negatively affect recruitment of offspring. Stenglein et al. (2015*b*) found both positive and negative density dependence in recruitment of wolves in Wisconsin, however this relationship was with population size. Future work could evaluate non-linear relationships to determine if there is both positive and negative density dependence (i.e., parabolic shape where an intermediate pack size results in maximum recruitment) within a pack.

We also found support for our hypothesis that harvest negatively affected recruitment. We found evidence that harvest decreased recruitment to 17 months of age, but this relationship was uncertain (95% credible intervals contained zero). However, there was a probability of 0.91 that harvest reduced 17-month recruitment suggesting that harvest influenced recruitment of wolves. Studies from the Northern Rocky Mountain wolf population in Idaho found that harvest decreased pup survival and recruitment (Ausband et al. 2015, 2017). Our estimates of recruitment to 17 months were similar to those reported in Idaho for recruitment to 15 months before and after harvest (3.2 and 1.6 pups, respectively; Ausband et al. 2015) although our methods differed substantially. Because we found similar recruitment rates to Ausband et al. (2015) using different methods this lends more support to the negative effect of harvest on recruitment in wolves. Without explicit data for recruitment we were able to detect an effect of harvest, however the effect was less than that detected by Ausband et al. (2015) in Idaho. In general, harvest regulations were more liberal (i.e., longer season length and greater bag limit) in Idaho (Ausband 2016; www.idfg.idaho.gov) than in Montana (Montana Fish Wildlife and Parks 2018; fwp.mt.gov). This could explain the greater effect of harvest in Idaho than we detected. Uncertainty in the estimated coefficient for harvest is also likely an artifact of using a binary variable for harvest (i.e., years with and without harvest). Recruitment rate to 17 months included survival through the harvest season, therefore we could not account for variation in harvest rate. Harvest rates varied annually, and undoubtedly varied spatially. We attempted to account for spatial variation in risk of harvest using increased road density as an index to increased risk. Roads provide easy access for hunters, and have been correlated with increased risk of mortality (Person and Russell 2008; Stenglein et al. 2015*a*). Our results suggest that this increased risk of mortality also translated to reduced recruitment, however the negative correlation between 4-wheel-drive road density and recruitment to 17 months was uncertain (Table 2.2). Similar to Horne et al. (2019) that estimated recruitment to 6 months, we did not find an effect of harvest on recruitment to 5 months. This was unsurprising as recruitment to 5 months precedes the harvest season.

Our estimates of recruitment and survival were comparable to other studies for wolves. Recruitment rate to 5 and 17 months varied over time (Figure 2.2). Recruitment estimates for wolves in Idaho averaged 3.2 and 1.6 pups per pack to 15 months without harvest and with harvest, respectively (Ausband et al. 2015). Our estimates of recruitment to 17 months of age were similar to estimates in Idaho (2.57 and 1.51, without and with harvest). Recruitment of wolves in Idaho to 6 months was 4 (3.5 to 4.6) pups per pack, and similar to our estimates of recruitment to 5 months during years with (3.80 pups per pack) and without (3.86 pups per pack) harvest. Survival rate for wolves in the NRM prior to harvest implementation averaged 0.75 (Smith et al. 2010), which is slightly greater than we estimated for wolves in Montana during years without harvest (0.70, Figure 2.3). Similarly, survival rate for wolves in an unharvested population in Wisconsin was 0.76 (Stenglein et al. 2015*b*). Survival rates for wolves in harvested populations in Yukon and Alaska averaged 0.56 and 0.59, respectively (Ballard et al. 1987; Hayes and Harestad 2000), which is similar to our estimates for Montana during years with harvest (0.50, Figure 2.3). We found the greatest decline in survival during the hunting and trapping period in years with harvest. This suggests that harvest has decreased survival in adult wolves in Montana, however we did not explicitly test this.

Our results indicate that recruitment does little to compensate for changes in survival; however the population has remained relatively stationary (mean population growth rate of 1.02). We found the correlation with population growth rate was greatest for recruitment to 17 months of age followed by annual survival of adults. This suggests that these demographic rates have the strongest effect on population growth rate. Mean number of pups recruited to 17 months and survival of adults decreased over time with changes in management practices (Figures 2.2 and 2.3), which is concurrent with declines in annual population growth rate (Figure 2.4). Estimated mean total human-caused mortality, which includes harvest, control removals, and other (e.g., vehicle accident), in Montana was 0.28 (SD = 0.078) during our study, and is near the top of the range of human-offtake thought to result in stable or growing populations (Gude et al. 2012). We hypothesize that immigration into or local dispersal within Montana may partially compensate for decreased survival. Immigration of wolves is an important process in dynamics for many wolf populations (Hayes and Harestad 2000; Fuller et al. 2003). Packs may adopt unrelated individuals which can maintain pack stability in harvested populations (Rutledge et al. 2010; Bassing et al. 2019), and recolonization of unoccupied territories may occur quickly (Ballard et al. 1987; Hayes and Harestad 2000). Although we did not include immigration into packs (i.e., adoption), we accounted for immigration into the population through new pack formation. We estimated annual pack growth rate, and years with greater growth rate of packs may signify years with increased immigration or local dispersal within the population to form new packs. Dispersal rates are high for wolves in Yellowstone National Park (Jimenez et al. 2017), situated near the southwest border of Montana, and may supply immigrants for the Montana wolf population. Alternatively or in conjunction with immigration, reductions in dispersal may compensate for decreased survival and allow the Montana wolf population to remain stationary. Although we did not explicitly include density dependent dispersal, we allowed dispersal rates to vary annually which would allow dispersal rates to decrease as the population grew and available habitat became saturated (Jimenez et al. 2017). Adams et al. (2008) found that decreased dispersal rates compensated for harvest mortality and resulted in relatively stationary densities across years in Alaska. Conversely, despite reduction in the number of pups recruited to 17 months per pack post-harvest, wolves may still recruit enough pups to offset harvest mortality. Wolves have high capacity for reproduction and recruitment, and post-parturition pups comprise the largest age class of the population (Fuller et al. 2003). We found mean annual number of pups recruited in the population to 17 months was 229 (103 – 347), which is similar to the number of wolves harvested annually during our study (from 2011-2018, mean = 212, SD = 42.7; Inman et al. 2019).

We made several assumptions in our modeling that could have affected estimates of recruitment if violated. We assumed that lone wolves do not contribute to recruitment unless they establish a pack and did not include them in the population estimate. In order to breed successfully, individual wolves must find a potential mate and a territory with enough resources (Rothman and Mech 1979; Mech and Boitani 2003), therefore it is unlikely that lone wolves are contributing to recruitment of pups. We assumed that dispersal from a pack was constant across packs and consistent with past research. Wolves disperse in response to competition for food resources and mating opportunities (Mech and Boitani 2003), and likely varies across packs with pack size. Density dependence in dispersal with group size has been observed in other group living species (Bateman et al. 2018; Woodroffe et al. 2019). In wolves, however, there has been support (Hayes and Harestad 2000) and also lack of evidence (Jimenez et al. 2017) for density dependent dispersal. Density dependent dispersal likely becomes more important with decreasing prey availability (Fuller et al. 2003; Mech and Boitani 2003), and may have had minimal effects on our study if prey availability was not limiting. However, if mean dispersal was greater than we assumed, then our recruitment estimates are likely biased low, and if mean dispersal was less than we assumed then our estimates of recruitment are likely biased high. Future work could focus on estimating dispersal and incorporate dispersal rates that depend on pack characteristics in the IPM. Abadi et al. (2010) estimated both recruitment and immigration into a population without data for either rate; therefore, it may be possible to estimate both dispersal and recruitment in a pack without explicit data. We also assumed that adoption (i.e., immigration into a pack) of unrelated individuals into a pack was rare and would not affect pack dynamics. If adoption was frequent, our estimates of recruitment could be biased high. For harvested populations, adoption of non-breeding adults appears to be infrequent (Bassing 2017), however most male breeder vacancies in Idaho are filled by a non-related male and therefore may be more common than we suspected (Ausband et al. 2017). Horne et al. (2019) similarly estimated dispersal while assuming immigration was minimal. Therefore, we assume our estimates of recruitment are predominately pup production and survival, however immigration into the pack could also be included in those estimates. We also excluded radiocollared wolves that were removed for control actions from the survival analysis. Packs that depredated livestock were often radiocollared for close monitoring and future removal, therefore they represent a non-random sample. During this study, 10% (SD = 4.2%) of wolves were removed for control actions annually, and relatively more were removed during years without harvest (15%, SD = 2.1%) than during years with harvest (7%, SD = 1.8%). Therefore, our estimates of survival may be biased high, and, consequently, our estimates of recruitment may be biased low. However, this is likely a small effect because only 35% of packs had a control removal, and only 25% of packs had a control removal during years with harvest. Additionally, we accounted for control removals by subtracting wolves removed from group count data in our model. We also did not account for or evaluate the effects of disease (e.g., canine parvovirus, distemper; Mech and Goyal 1995, Mech et al. 2008) on recruitment or population growth. Disease outbreaks could cause declines in pup recruitment and contribute to spatial and temporal variation (Almberg et al. 2009). Lastly, as with all models, our results are contingent on the data used in analyses. We used estimates of abundance, the number of packs, and pack growth rate from monitoring of wolves in Montana from 2007-2016 (Inman et al. 2019). These estimates rely on assumptions of a constant average territory size and may be biased (Glen et al. 2011; Rich et al. 2013; Inman et al. 2019; Sells 2019). If this is a systematic bias and consistent through time (e.g., the population size is always 10% larger than the estimate), however, our estimates of the dynamics of the population may remain unbiased. Further, we accounted for uncertainty in the estimates in the observation process for abundance and the number of packs. Regardless, these results highlight the utility of an integrated modeling approach to estimate population dynamics and evaluate factors influencing recruitment even with limited data.

LITERATURE CITED

Abadi, F., O. Gimenez, B. Ullrich, R. Arlettaz, and M. Schaub. 2010. Estimation of immigration rate using integrated population models. Journal of Applied Ecology 47:393–400.

Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. Wildlife Monographs 170:1–25.

Al-Khafaji, K., S. Tuljapurkar, J. R. Carey, and R. E. Page. 2009. Hierarchical demography: a general approach with an application to honey bees. Ecology 90:556–566.

Almberg, E. S., L. D. Mech, D. W. Smith, J. W. Sheldon, and R. L. Crabtree. 2009. A serological survey of infectious disease in Yellowstone National Park’s canid community. PloS one 4:e7042.

Ausband, D. E. 2016. Gray wolf harvest in Idaho. Wildlife Society Bulletin 40:500–505.

Ausband, D. E. 2018. Multiple breeding individuals within groups in a social carnivore. Journal of Mammalogy 99:836–844.

Ausband, D. E., M. S. Mitchell, S. B. Bassing, A. Morehouse, D. W. Smith, D. Stahler, and J. Struthers. 2016. Individual, group, and environmental influences on helping behavior in a social carnivore. Ethology 122:963–972.

Ausband, D. E., M. S. Mitchell, C. R. Stansbury, J. L. Stenglein, and L. P. Waits. 2017. Harvest and group effects on pup survival in a cooperative breeder. Proceedings of the Royal

Society of London B: Biological Sciences 284:20170580.

Ausband, D. E., C. R. Stansbury, J. L. Stenglein, J. L. Struthers, and L. P. Waits. 2015. Recruitment in a social carnivore before and after harvest. Animal Conservation 18:415–423.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs 98:3–54.

Bangs, E. E., and S. H. Fritts. 1996. Reintroducing the gray wolf to central Idaho and Yellowstone National Park. Wildlife Society Bulletin 24:402–413.

Bangs, E. E., S. H. Fritts, J. A. Fontaine, D. W. Smith, K. M. Murphy, C. M. Mack, and C. C. Niemeyer. 1998. Status of gray wolf restoration in Montana, Idaho, and Wyoming. Wildlife Society Bulletin 26:785–798.

Bassing, S. 2017. Harvest and persistence of wolf populations: variable effects of harvest on wolf packs in the Rocky Mountains. University of Montana.

Bassing, S. B., D. E. Ausband, M. S. Mitchell, P. Lukacs, A. C. Keever, G. Hale, and L. Waits. 2019. Stable pack abundance and distribution in a harvested wolf population. The Journal of Wildlife Management 83:577–590.

Bateman, A. W., A. Ozgul, T. Coulson, and T. H. Clutton-Brock. 2012. Density dependence in group dynamics of a highly social mongoose, Suricata suricatta. Journal of Animal Ecology 81:628–639.

Bateman, A. W., A. Ozgul, M. Krkošek, and T. H. Clutton-Brock. 2018. Matrix models of hierarchical demography: linking group- and population-level dynamics in cooperative breeders. The American Naturalist 192:188–203.

Bateman, A. W., A. Ozgul, J. F. Nielsen, T. Coulson, and T. H. Clutton-Brock. 2013. Social structure mediates environmental effects on group size in an obligate cooperative breeder, Suricata suricatta. Ecology 94:587–597.

Besbeas, P., S. N. Freeman, B. J. T. Morgan, and E. A. Catchpole. 2002. Integrating mark-recapture-recovery and census data to estimate animal abundance and demographic parameters. Biometrics 58:540–547.

Bjørnstad, O. N., R. A. Ims, and X. Lambin. 1999. Spatial population dynamics: Analyzing patterns and processes of population synchrony. Trends in Ecology and Evolution. Volume 14. Elsevier Current Trends.

Boertje, R. D., and R. O. Stephenson. 1992. Effects of ungulate availability on wolf reproductive potential in Alaska. Canadian Journal of Zoology 70:2441–2443.

Bradley, L., J. Gude, N. Lance, K. Laudon, A. Messer, A. Nelson, G. Pauley, M. Ross, T. Smucker, and J. Steuber. 2015. Montana gray wolf conservation and management 2014 annual report. Helena, Montana.

Brainerd, S. M., H. Andrén, E. E. Bangs, E. H. Bradley, J. A. Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. A. Jozwiak, O. Liberg, C. M. Mack, T. J. Meier, C. C. Niemeyer, H. C. Pedersen, H. Sand, R. N. Schultz, D. W. Smith, P. Wabakken, and A. P. Wydeven. 2008. The effects of breeder loss on wolves. Journal of Wildlife Management 72:89–98.

Brooks, S. P. 2003. Bayesian computation: a statistical revolution. Philosophical Transactions of the Royal Society A 361:2681–2697.

Chandler, R. B., J. Hepinstall-Cymerman, S. Merker, H. Abernathy-Conners, and R. J. Cooper. 2018. Characterizing spatio-temporal variation in survival and recruitment with integrated population models. The Auk 135:409–426.

Clutton-Brock, T. 2016. Mammal societies. John Wiley & Sons, New York.

Courchamp, F., and D. W. Macdonald. 2001. Crucial importance of pack size in the African wild dog Lycaon pictus. Animal Conservation 4:169–174.

Courchamp, F., G. S. A. Rasmussen, and D. W. Macdonald. 2002. Small pack size imposes a trade-off between hunting and pup-guarding in the painted hunting dog Lycaon pictus. Behavioral Ecology 13:20–27.

Creel, S., and N. M. Creel. 1995. Communal hunting and pack size in African wild dogs, Lycaon pictus. Animal Behaviour 50:1325–1339.

Creel, S., and J. J. Rotella. 2010. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (Canis lupus). PloS one 5:e12918.

Dail, D., and L. Madsen. 2011. Models for estimating abundance from repeated counts of an open metapopulation. Biometrics 67:577–587.

ESRI. 2011. ArcGIS. Enironmental Systems Research Institute, Redlands, California.

Fuller, T. K., L. D. Mech, and J. Fitts-Cochran. 2003. Wolf population dynamics. Pages 161–191 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. University of Chicago Press, Chicago, Illinois.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–472.

Gimenez, O., E. Cam, and J.-M. Gaillard. 2018. Individual heterogeneity and capture-recapture models: what, why and how? Oikos 127:664–686.

Glen, E. S., L. N. Rich, and M. S. Mitchell. 2011. Estimating numbers of wolves, wolf packs, and breeding pairs in Montana using hunter survey data in patch occupancy model framework: final report. Helena, MT.

Gude, J. A., M. S. Mitchell, R. E. Russell, C. A. Sime, E. E. Bangs, L. D. Mech, and R. R. Ream. 2012. Wolf population dynamics in the U.S. Northern Rocky Mountains are affected by recruitment and human-caused mortality. The Journal of Wildlife Management 76:108–118.

Hanski, I. 1999. Metapopulation ecology. Oxford University Press, New York, New York.

Hayes, R. D., and A. S. Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology 78:36–48.

Heisey, D. M., T. L. Shaffer, and G. C. White. 2007. The ABCs of nest survival: theory and application from a biostatistical perspective. Studies in Avian Biology 34:13–33.

Horne, B. Van. 1983. Density as a misleading indicator of habitat quality. The Journal of Wildlife Management 47:901.

Horne, J. S., D. E. Ausband, M. A. Hurley, J. Struthers, J. E. Berg, and K. Groth. 2019. Integrated population model to improve knowledge and management of Idaho wolves. The Journal of Wildlife Management 83:32–42.

Hosmer, D. W. J., and S. Lemeshow. 2000. Applied logistic regression. 2nd edition. Wiley, New York, New York.

Inman, B., K. M. Podruzny, T. D. Smucker, A. A. Nelson, M. Ross, N. Lance, T. Parks, D. K. Boyd, and S. Wells. 2019. Montana gray wolf conservation and management 2018 annual report. Helena, Montana.

Jimenez, M. D., E. E. Bangs, D. K. Boyd, D. W. Smith, S. A. Becker, D. E. Ausband, S. P. Woodruff, E. H. Bradley, J. Holyan, and K. Laudon. 2017. Wolf dispersal in the Rocky Mountains, Western United States: 1993-2008. The Journal of Wildlife Management 81:581–592.

Kalbfleisch, J. D., and R. L. Prentice. 2011. The statistical analysis of failure time data. Volume 360. John Wiley & Sons.

Keever, A. C., C. P. McGowan, S. S. Ditchkoff, P. K. Acker, J. B. Grand, and C. H. Newbolt. 2017. Efficacy of N-mixture models for surveying and monitoring white-tailed deer populations. Mammal Research 62:413–422.

Koenig, A. 1995. Group size, composition, and reproductive success in wild common marmosets (Callithrix jacchus). American Journal of Primatology 35:311–317.

Koenig, W. D., S.-F. Shen, A. H. Krakauer, and J. Haydock. 2009. Reproductive skew in avian societies. Pages 227–264 in C. B. Jones and R. Hager, editors. Reproductive skew in vertebrates: proximate and ultimate causes. Cambridge University Press, Cambridge.

Lancia, R. A., J. W. Bishir, M. C. Conner, and C. S. Rosenberry. 1996. Use of catch-effort to estimate population size. Wildlife Society Bulletin 24:731–737.

Lindberg, M. S., J. S. Sedinger, and J.-D. Lebreton. 2013. Individual heterogeneity in black brant survival and recruitment with implications for harvest dynamics. Ecology and Evolution 3:4045–4056.

Llaneza, L., J. V. López-Bao, and V. Sazatornil. 2012. Insights into wolf presence in human-dominated landscapes: the relative role of food availability, humans and landscape attributes. Diversity and Distributions 18:459–469.

McCaffery, R., and P. M. Lukacs. 2016. A generalized integrated population model to estimate greater sage-grouse population dynamics. Ecosphere 7.

Mech, L. D. 1973. Wolf numbers in the Superior National Forest of Minnesota. Research Paper, St. Paul, MN.

Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1–34 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, Illinois.

Mech, L. D., and J. Fieberg. 2015. Growth rates and variances of unexploited wolf populations in dynamic equilibria. Wildlife Society Bulletin 39:41–48.

Mech, L. D., and R. O. Peterson. 2003. Wolf-prey relations. Pages 131–160 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, Illinois.

Miller, D. A. W., J. D. Nichols, J. A. Gude, L. N. Rich, K. M. Podruzny, J. E. Hines, and M. S. Mitchell. 2013. Determining occurrence dynamics when false positives occur: estimating the range dynamics of wolves from public survey data. PloS one 8:e65808.

Mills, L. S. 2013. Conservation of wildlife populations: demography, genetics, and management. 2nd edition. John Wiley & Sons.

Moeller, A. K., P. M. Lukacs, and J. S. Horne. 2018. Three novel methods to estimate abundance of unmarked animals using remote cameras. Ecosphere 9:e02331.

Montana Fish Wildlife and Parks. 2005. Biomedical protocol for free-ranging gray wolves (Canis lupus) in Montana: caputre, anesthesia, surgery, tagging, sampling and necropsy procedures. Helena, Montana.

Montana Fish Wildlife and Parks. 2018. Montana gray wolf conservation and management 2017 annual report. Helena, Montana.

Murray, D. L., D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, T. J. Meier, D. Stahler, J. Holyan, and V. J. Asher. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation 143:2514–2524.

Newman, K. B., S. T. Buckland, B. J. T. Morgan, R. King, D. L. Borchers, D. J. Cole, P. Besbeas, O. Gimenez, and L. Thomas. 2014. Modelling population dynamics. Springer, New York, NY.

Oakleaf, J. K., D. L. Murray, J. R. Oakleaf, E. E. Bangs, C. M. Mack, D. W. Smith, J. A. Fontaine, M. D. Jimenez, T. J. Meier, and C. C. Niemeyer. 2006. Habitat selection by recolonizing wolves in the Northern Rocky Mountains of the United States. Journal of Wildlife Management 70:554–563.

Packard, J. M. 2003. Wolf behavior: reproductive, social, and intelligent. Pages 35–65 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, Illinois.

Packer, C., R. Hilborn, A. Mosser, B. Kissui, M. Borner, G. Hopcraft, J. Wilmshurst, S. Mduma, and A. R. E. Sinclair. 2005. Ecological change, group territoriality, and population dynamics in Serengeti lions. Science 307:390–393.

Person, D. K., and A. L. Russell. 2008. Correlates of mortality in an exploited wolf population. The Journal of Wildlife Management 72:1540–1549.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.

Prentice, R. L., and L. A. Gloeckler. 1978. Regression analysis of grouped survival data with application to breast cancer. Biometrics 34:57–67.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Ream, R. R., M. W. Fairchild, D. K. Boyd, and A. J. Blakesley. 1989. First wolf den in western U.S. in recent history. Northwestern Naturalist 70:39–40.

Redmond, R. L., M. M. Hart, J. C. Winne, W. A. Williams, P. C. Thornton, Z. Ma, C. M. Tobalske, M. M. Thornton, K. P. McLaughlin, T. P. Tady, F. B. Fisher, and S. W. Running. 1998. The Montana gap analysis project:final report. Missoula, Montana.

Rich, L. N., M. S. Mitchell, J. A. Gude, and C. A. Sime. 2012. Anthropogenic mortality, intraspecific competition, and prey availability influence territory sizes of wolves in Montana. Journal of Mammalogy 93:722–731.

Rich, L. N., R. E. Russell, E. M. Glenn, M. S. Mitchell, J. A. Gude, K. M. Podruzny, C. A. Sime, K. Laudon, D. E. Ausband, and J. D. Nichols. 2013. Estimating occupancy and predicting numbers of gray wolf packs in Montana using hunter surveys. The Journal of Wildlife Management 77:1280–1289.

Rothman, R. J., and L. D. Mech. 1979. Scent-marking in lone wolves and newly formed pairs. Animal Behaviour 27:750–760.

Royle, J. A. 2004. N-mixture models for estimating population size from spatially replicated counts. Biometrics 60:108–115.

Russell, A. F., P. N. M. Brotherton, G. M. McIlrath, L. L. Sharpe, and T. H. Clutton-Brock. 2003. Breeding success in cooperative meerkats: effects of helper number and maternal state. Behavioral Ecology 14:486–492.

Rutledge, L. Y., B. R. Patterson, K. J. Mills, K. M. Loveless, D. L. Murray, and B. N. White. 2010. Protection from harvesting restores the natural social structure of eastern wolf packs.

Biological Conservation 143:332–339.

Sells, S. N. 2019. Mechanisms driving territorial and social behavior in a cooperative carnivore. Graduate Student Theses, Dissertations, & Professional Papers. University of Montana, Missoula.

Sidorovich, V. E., V. P. Stolyarov, N. N. Vorobei, N. V Ivanova, and B. Jędrzejewska. 2007. Litter size, sex ratio, and age structure of gray wolves, Canis lupus, in relation to population fluctuations in northern Belarus. Canadian Journal of Zoology 85:295–300.

Sikes, R. S., and J. A. Bryan. 2016. Guidelines of the American Society of Mammalogists for the use of wild mammals in research and education Downloaded from. Journal of Mammalogy 97:663–688.

Sjögren-Gulve, P., and I. Hanski. 2000. Metapopulation viability analysis using occupancy models. Ecological Bulletins 48:53–71.

Smith, D. W., E. E. Bangs, J. K. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D. H. Pletscher, C. C. Niemeyer, T. J. Meier, D. R. Stahler, J. Holyan, V. J. Asher, and D. L. Murray. 2010. Survival of colonizing wolves in the Northern Rocky Mountains of the United States, 1982-2004. Journal of Wildlife Management 74:620–634.

Solomon, N. G., and J. A. French, editors. 1997. Cooperative breeding in mammals. Cambridge University Press, Cambridge.

Stahler, D. R., D. R. MacNulty, R. K. Wayne, B. VonHoldt, and D. W. Smith. 2013. The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. The Journal of Animal Ecology 82:222–34.

Stenglein, J. L., J. H. Gilbert, A. P. Wydeven, and T. R. Van Deelen. 2015a. An individual-based model for southern Lake Superior wolves: A tool to explore the effect of human-caused mortality on a landscape of risk. Ecological Modelling 302:13–24.

Stenglein, J. L., A. P. Wydeven, and T. R. Van Deelen. 2018. Compensatory mortality in a recovering top carnivore: wolves in Wisconsin, USA (1979–2013). Oecologia 187:99–111.

Stenglein, J. L., J. Zhu, M. K. Clayton, and T. R. Van Deelen. 2015b. Are the numbers adding up? Exploiting discrepancies among complementary population models. Ecology and Evolution 5:368–376.

Su, Y.-S., and M. Yajima. 2015. R2jags: using R to run “JAGS.”

Thompson, W. L., editor. 2004. Sampling rare or elusive species: concepts, designs, and techniques for estimating population parameters. Island Press, London.

Tilman, D., and P. Kareiva. 2018. Spatial ecology: the role of space in population dynamics and interspecific interactions (MPB-30). Volume 89. Princeton University Press.

U.S. Fish and Wildlife Service. 1994a. The reintroduction of gray wolves to Yellowstone National Park and central Idaho. Final Environmental Impact Statement. Denver, Colorado.

U.S. Fish and Wildlife Service. 1994b. Endangered and threatened wildlife and plants; establishment of a nonessential experimental population of gray wolves in Central Idaho and Southwestern Montana. Federal Register 50(17):60266-60281.

U.S. Fish and Wildlife Service. 2009. Final rule to identify the Northern Rocky Mountain population of gray wolf as a Distinct Population Segment and to revise the list of Endangered and Threatened wildlife. Volume 74. Washington, D.C., USA.

U.S. Fish and Wildlife Service. 2011. Endangered and threatened widlife and plants; reissuance of final rule to identify the Northern Rocky Mountain population of gray wolf as a distinct population segment and to revise the list of endangered and threatened wildlife. Federal Register 76. Denver, Colorado.

U.S. Fish and Wildlife Service, Nez Perce Tribe, National Park Service, W. & P. Montana Fish, Blackfeet Nation, Confederated Salish and Kootenai Trives, Idaho Department of Fish and Game, and USDA Wildlife Services. 2010. Rocky Mountain Wolf Recovery 2009 Interagency Annual Report. Helena, MT.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press.

Wilson, G. J., and R. J. Delahay. 2001. A review of methods to estimate the abundance of terrestrial carnivores using field signs and observation. Wildlife Research 28:151–164.

Woodroffe, R., H. M. K. O’Neill, and D. Rabaiotti. 2019. Within- and between-group dynamics in an obligate cooperative breeder. Journal of Animal Ecology 1365-2656.13102.

Zhao, Q., J. A. Royle, and G. S. Boomer. 2017. Spatially explicit dynamic N-mixture models. Population Ecology 59:293–300.

TABLES

Table 2.1: Model selection results (deviance statistics) and number of parameters (K) from integrated population models to estimate recruitment of gray wolves in Montana from 2007-2018. Lower deviance suggests more model support, and we considered those within a standard deviation (SD) of the top model to have support. Explanatory variables included intrinsic factors (population and pack size) and extrinsic factors related to risk of mortality from humans, such as harvest, forest cover, and four-wheel (4WD) and two-wheel (2WD) drive road density, or prey availability, such as average daily snow depth (Snow) and elk catch-per-unit-effort (Elk).

Model	**K**	**Deviance**	**SD**
$\gamma \sim Population\ Size + \varepsilon_{Year}$	3	998	300.7
$\gamma \sim Harvest + \varepsilon_{Year}$	3	1000	313.3
$\gamma \sim Pack\ Size + \varepsilon_{Year}$	3	1200	433.3
$\gamma \sim Forest + \varepsilon_{Year}$	3	1484	314.2
$\gamma \sim 4WD + 2WD + \varepsilon_{Year}$	4	1964	309.1
$\gamma \sim Snow + Elk + \varepsilon_{Year}$[a]	4	2013.9	384.4

[a] This model failed to converge, and coefficient values are not included in final results.

Table 2.2: Mean coefficient estimates (95% CRI) of covariate effects on recruitment to 5 and 17 months of age from an integrated population model for gray wolves in Montana from 2007-2018. We calculated the probability (Pr) the coefficient estimate was > or < 0 (if the estimate was positive or negative) using the MCMC samples from the posterior distribution. The model that included an index of prey availability failed to converge and was not included in the final results.

Coefficient	5 months	Pr	17 months	Pr
Harvest	0.06 (-0.309 – 0.464)	0.62	-0.48 (-1.490 – 0.098)	0.91
2WD road density	-0.07 (-0.287 – 0.141)	0.70	0.01 (-0.747 – 0.356)	0.67
4WD road density	0.01 (-0.086 – 0.098)	0.65	-0.26 (-0.778 – 0.038)	0.95
Forest cover	0.10 (-0.076 – 0.227)	0.92	-0.41 (-0.709 – -0.055)	0.98
Abundance	0.0005 (-0.00196 – 0.00093)	0.68	-0.0025 (-0.00575 – 0.00012)	0.97
Pack size	0.06 (0.043 – 0.072)	1.00	-0.02 (-0.644 – 0.516)	0.48

FIGURES

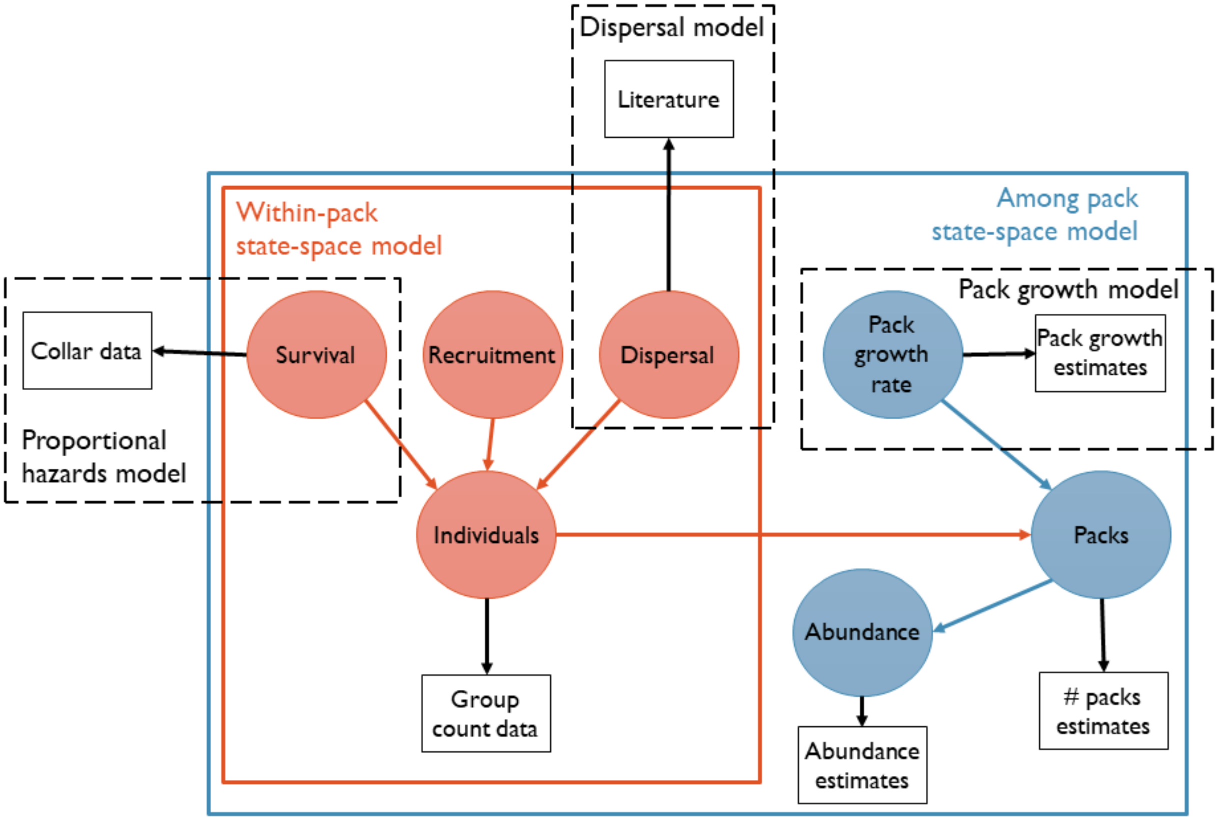

Figure 2.1: Directed acyclic graph of an integrated population model (IPM) for gray wolves in Montana from 2007-2018. The boxes represent data sources and include 1) GPS and VHF radiocollars to estimate survival using a proportional hazards, known-fate model; 2) estimates of abundance of wolves, 3) estimates of the number of packs, 4) estimates of growth rate of packs, 5) group count data to inform pack size; and 4) estimates from the literature to model wolf dispersal. The IPM explicitly accounts for hierarchical demography of a social species by modeling the processes within packs (red) and among packs (blue). The only parameter without data is recruitment and can be estimated in the integrated modeling framework.

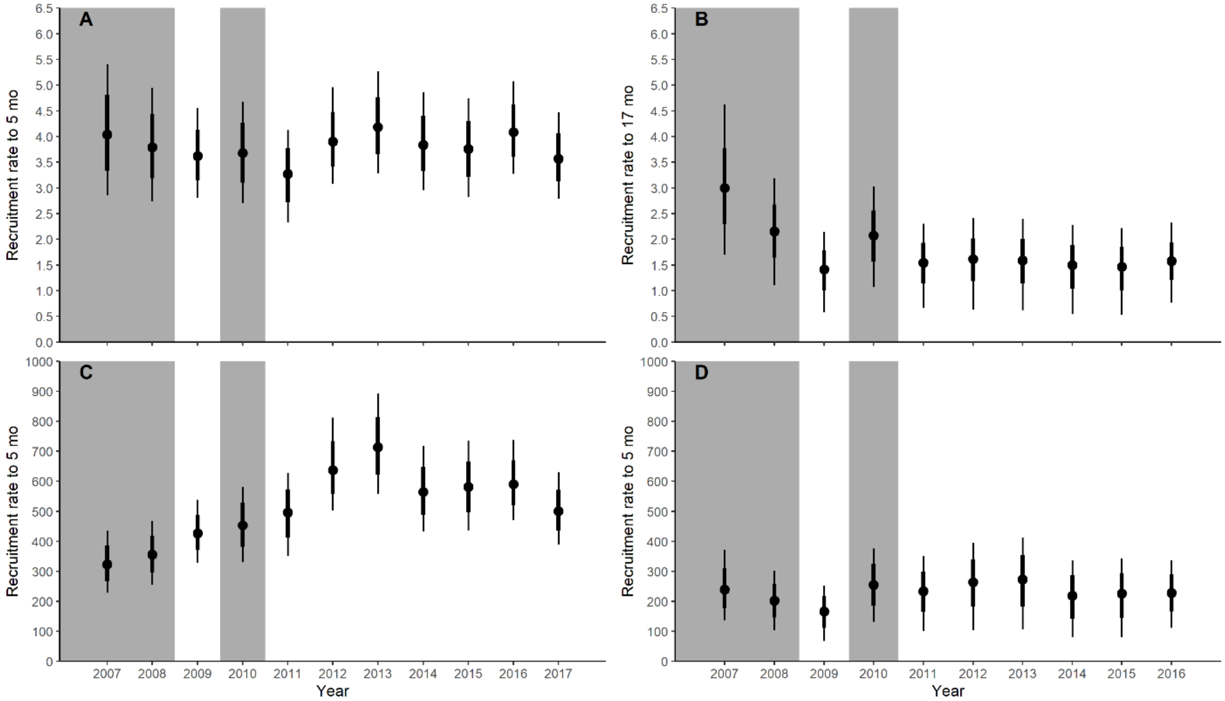

Figure 2.2: Estimates of recruitment rate (A, B; mean number of pups per pack) and total number of pups recruited (C, D) for gray wolves in Montana to 5 (A, C) and 17 months of age (B, D) estimated from an integrated population model with density dependence (population size) on recruitment from 2007-2017. Line widths represent the 66% and 95% CRI. Shaded areas represent years in which wolves were protected under the Endangered Species Act and not harvested.

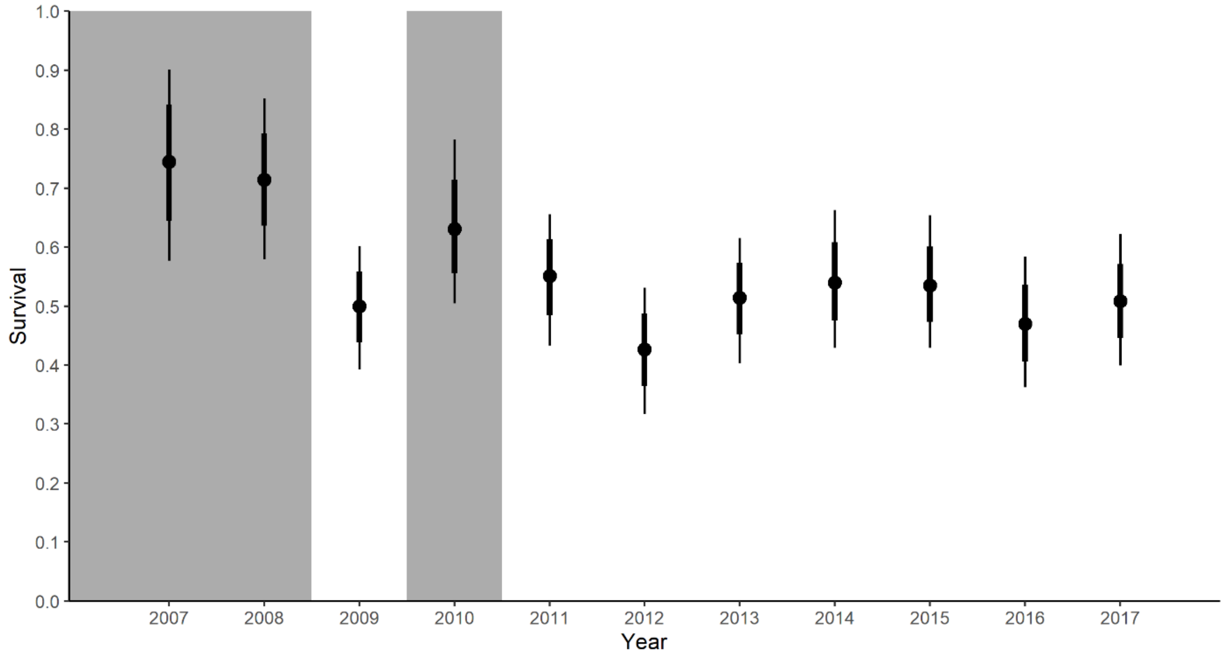

Figure 2.3: Estimates of annual survival rate and 66% and 95% credible intervals of adult gray wolves in Montana from an integrated population model (IPM) with density dependence (population size) on recruitment from 2007-2017. Shaded areas represent years in which wolves were protected under the Endangered Species Act and not harvested.

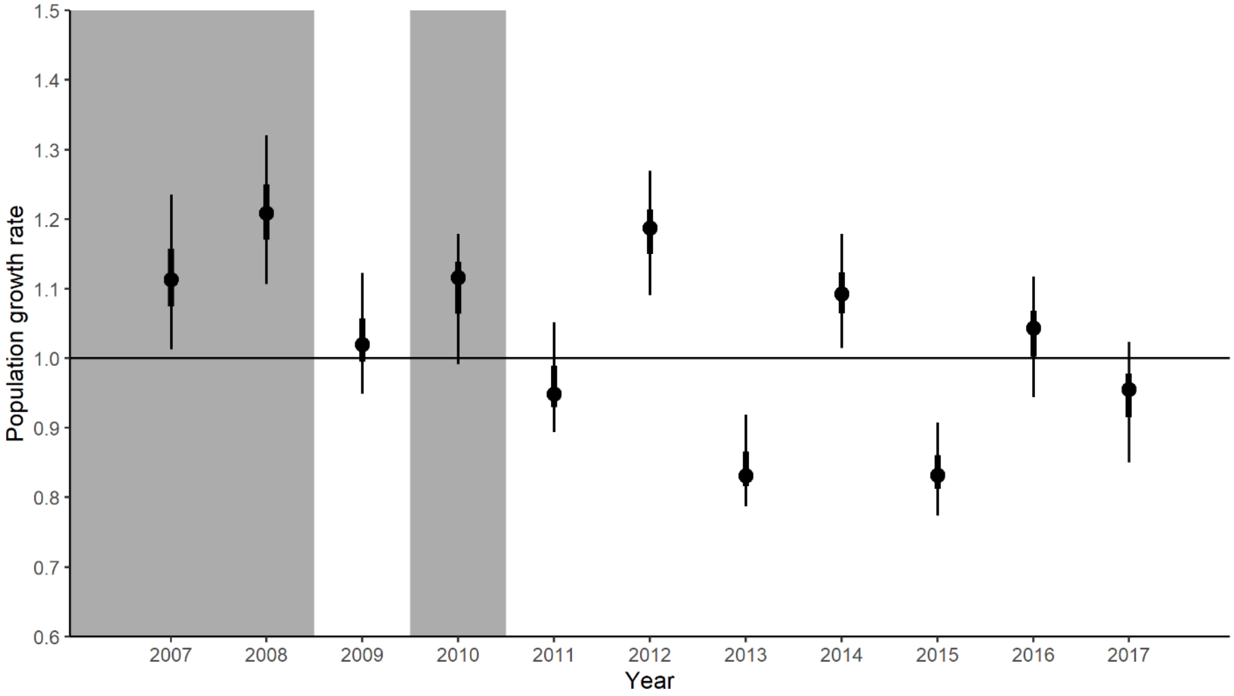

Figure 2.4: Estimates of population growth rate and 66% and 95% credible intervals of wolves in Montana from an integrated population model (IPM) with density dependence (population size) on recruitment from 2007-2017. Shaded areas represent years in which wolves were protected under the Endangered Species Act and not harvested.

CHAPTER 3:

PREDICTING RECRUITMENT IN GRAY WOLVES BASED ON INDIVIDUAL COMPONENTS OF RECRUITMENT

ABSTRACT

Recruitment is an important demographic rate that is useful for managing wildlife populations. Estimates of recruitment are particularly important for managing harvested populations to evaluate how effective management actions are at meeting population objectives. Gray wolves are harvested in parts of their range, and estimates of recruitment are needed. However, data can be costly to collect for a low-density, elusive species. We created a combined model to estimate recruitment based on the probability a pack reproduced, the probability there was more than one breeder, litter size, and pup survival to estimate recruitment. We used estimated pedigrees based on data from non-invasive genetic samples and generalized linear mixed effects models to determine the effects of prey availability, population and pack size, and harvest on multiple breeding females, litter size, and pup survival of gray wolves in Idaho. We only had data for reproductive packs in Idaho, therefore we developed four models for the probability a pack reproduced. We then used the combined model to predict recruitment of wolves in Montana as spatial and temporal validation. We found litter size varied little, yet was positively related to pack size. Survival was the most variable demographic component suggesting that factors that influence survival would have a greater effect on recruitment rate in wolves and could be targeted by management actions. We accurately predicted recruitment for wolves in Montana, suggesting this could be a viable tool.

INTRODUCTION

Recruitment is a primary driver of population dynamics for many species (Gaillard et al. 1998, 2000), and therefore is often used by managers to assess health and stability of wildlife populations and guide management recommendations (e.g. Bishop et al. 2005). To understand patterns of and variation in recruitment (offspring produced that survive to a given age), managers and researchers typically evaluate how different factors (e.g., predation or density dependence) affect the overall rate. Offspring:female ratios are commonly collected for many ungulate populations to help guide future harvest regulations (Bishop et al. 2005). Similarly, understanding effects of conservation actions on fledging or nest success is evaluated to improve population growth rate in bird populations (e.g., Cohen et al. 2016). Although recruitment is generally assessed by recruitment rate, i.e., number of offspring that survive to a certain age, it is affected by multiple demographic processes, and management decisions may differ depending on how factors affect the components of recruitment. The demographic processes depend on the life-history and mating strategy of the species, however, in general recruitment rate can be apportioned into the number of females that successfully reproduce, litter or clutch size, and offspring survival. Understanding how different factors affect the components of recruitment can better inform decisions when managing wildlife populations.

Gray wolves (*Canis lupus*) in the U.S. northern Rocky Mountains (NRM) have recovered from local extirpation and are managed with harvest in parts of their range (U.S. Fish and Wildlife Service 2011, 2017). Wolves form stable social groups, called packs, which typically consists of a breeding pair and offspring from current and past litters (Fuller et al. 2003; Mech and Boitani 2003). Wolves breed cooperatively (i.e., non-breeding pack members help raise pups; Mech and Boitani 2003), and like many other cooperative breeders, they benefit from the presence of non-breeding individuals to help raise offspring (Solomon and French 1997).

Although wolves reach sexual maturity around two years of age, the breeding pair suppresses reproduction in other pack members (Packard 2003), however some packs contain multiple breeding males and females (Ausband 2018). Recruitment in wolves is therefore a function of whether a pack successfully reproduced, the number of breeding females in a pack, litter size, and pup survival. Collecting data to estimate the components of recruitment, however, can be difficult. Data on litter size and early (<2 months) pup survival is invasive and challenging to collect given that wolf pups stay in the den for the first two months (Fuller et al. 2003; Mech and Boitani 2003). Further, it is difficult to know how many breeding females were present. Cost-effective methods to estimate the components of recruitment are thus needed to support decisions on harvest management of wolves.

Studies have evaluated patterns in pup survival and multiple breeding females for reproductive packs in harvested populations (Ausband et al. 2015, *2017a; b*). However more work is needed to understand patterns in the probability a pack reproduces and litter size to develop a combined model of recruitment based on the individual components. Ausband (2018) found that increased pack and population size were positively correlated with the probability of multiple breeding females. Harvest of wolves reduces recruitment through direct and indirect effects on pup survival (Ausband et al. 2015, 2017*a*; *b*), however increased pack size is related to increased pup survival due to greater provisioning and guarding rates of pups, and pups in larger packs have greater survival than in smaller packs (Ausband et al. 2017*a*). Similar to multiple breeding females and pup survival, factors such as food availability, pack and population characteristics, and harvest may influence the probability a pack reproduces and litter size. Packs may not produce pups every year, and successful reproduction may be affected by mortality of the breeding pair (Brainerd et al. 2008; Borg et al. 2015), pack size (Mitchell et al. 2008), and time since pack establishment and prior breeder experience (Person and Russell 2009). Available food resources may also influence whether a pack reproduces because of the positive effect of subcutaneous fat on reproduction (Boertje and Stephenson 1992). Litter size in wolves as in most canids varies little (Beja and Palma 2008; Devenish-Nelson et al. 2013), and is likely the least variable component of recruitment. Litter size and the number of females that are reproductively active, however, was positively related to prey availability in Alaska (Boertje and Stephenson 1992). However, there was only a notable decline in productivity when prey biomass declined below levels previously reported in the literature (Boertje and Stephenson 1992). Further, density dependent recruitment in wolves has been documented (Gude et al. 2012; Stenglein et al. 2015; Chapter 2), and may be due to increasing competition for food and diminishing per capita resource availability (Messier 1991) negatively affecting litter size or pup survival. There may also be a compensatory effect of harvest. In high density populations, harvest could result in increased litter size due to greater per capita food availability following harvest as demonstrated in coyotes (*Canis latrans;* Knowlton et al. 1999). Although there has been no evidence of a compensatory effect of harvest on recruitment in wolves, most studies have not evaluated the effects on litter size. The compensatory effect of harvest on litter size may be dwarfed by the negative correlation of harvest to pup survival.

Our objective was to 1) develop a component model of recruitment for wolves in Idaho based on findings by Ausband et al. (2017*a*), Ausband (2018), and our *a priori* hypotheses, and 2) test the component model by predicting recruitment for wolves in Montana. We used data from estimated pedigrees from reproductive wolf packs in Idaho from 2008-2016 (Ausband et al. 2017*a*; Ausband 2018) that included presence of multiple breeding females, litter size, and pup survival. We hypothesized that the probability a pack reproduced was 1) constant, i.e., null model, 2) was positively related to pack size because wolves are cooperative breeders (Fuller et al. 2003), 3) was negatively related to harvest because loss of a breeder can result in no reproduction (Brainerd et al. 2008; Borg et al. 2015), and 4) was related to both pack size and harvest. For litter size, we hypothesized that it 1) would be positively related to prey availability because of increased food resources for the breeding female (Boertje and Stephenson 1992), 2) would be positively related to pack size due to either greater food availability from increased hunting efficiency (Schmidt and Mech 1997; MacNulty et al. 2011) or because larger packs may have experienced breeders which is positively related to litter size (Person and Russell 2009), 3) would be negatively related to population size because recruitment may be density dependent (Gude et al. 2012; Stenglein et al. 2015), and 4) would have a compensatory response to harvest rate (Knowlton et al. 1999). We hypothesized that pup survival 1) would be positively related to prey availability due to increased food resources, and 2) would be negatively related to population size due to density dependent resource availability. We also included pack size as a predictor variable for pup survival because (Ausband et al. 2017*a*) found a positive correlation. We fitted models for multiple breeding females, litter size, and pup survival to the data from Idaho, however because the data were only for reproductive packs we developed, but did not fit, models based on our hypotheses for the probability a pack reproduced. We used the top models for multiple breeding females, litter size, and pup survival and four models for the probability a pack reproduced (based on our hypotheses) to generate predictions of recruitment under the four component models. To test the component models, we generated predictions of recruitment for wolves in Montana and compared them to counts of the number of pups recruited.

STUDY AREA

This study took place in central Idaho in the Idaho Department of Fish and Game (IDFG) Game Management Units 4, 28, 33, 34, and 35 and western Montana. The land cover was primarily comprised of mixed forests of pine (*Pinus spp*) and spruce (*Picea spp*) and sagebrush (*Artemisia tridentata*) steppe. Land ownership predominantly included public lands, private lands managed by timber companies, and private ranches (USFWS 1994). The ungulate community was comprised of elk (*Cervus canadensis*), mule deer (*Odocoileus hemionus*), white-tailed deer (*O. virginianus*), bighorn sheep (*Ovis canadensis*), mountain goats (*Oreamnos americanus*), and moose (*Alces alces*). Other predator species in the study area included grizzly bears (*Ursus arctos*), black bears (*U. americanus*), and mountain lions (*Puma concolor*).

Management of wolves in Idaho and Montana changed over this course of this study. The wolf population was delisted briefly in 2009 and again in 2011 (U.S. Fish and Wildlife Service 2011). Prior to 2011 wolves were protected (excluding 2009), however classification as experimental non-essential under the ESA in Idaho and parts of Montana allowed managing agencies and landowners to lethally remove wolves depredating or threatening livestock (USFWS 1994*b*). Following delisting, management of wolves included regulated public harvest. Annual harvest of wolves was mainly opportunistic, and harvest rates of wolves in Idaho and Montana from 2008-2016 averaged 0.24 (Ausband 2016) and 0.21 (Chapter 5), respectively. Lethal removal of wolves for livestock depredation was rare for packs in this study (Ausband et al. 2017*a*).

METHODS

Data for multiple breeding females, litter size, and pup survival

We used data from estimated pedigrees reported in Ausband et al. (2015, 2017*a*). Data were collected from annual surveys for wolves in central Idaho from 2008-2016 (Ausband et al. 2015, 2017*a*). Ausband et al. (2015) sampled known and predicted rendezvous sites (locations where pups are left and pack members congregate) and collected scat samples at occupied or recently occupied sites. They attempted to locate and sample each pack every year. They extracted DNA from scat samples using Qaigen stool kits (Qiagen Inc., Valencia, CA, USA) and identified samples by individual and sex (Stenglein et al. 2010). Ausband et al. (2017) then determined breeders and their offspring using pedigree analyses in COLONY v2.0.5.5 (Jones and Wang 2009). From the pedigree analyses they estimated group size and composition (# in each age and sex class), recruitment (pups alive at 15 months of age), and breeder turnover (change of breeder due to death, expulsion, or the position being usurped). The resulting data included number of pups present at three months of age, number of pups present at 15 months of age, number of breeders, number of adults when pups were three months of age, breeder male and female turnover, and number of adults when pups were 15 months of age for 16 unique packs totaling in 55 unique pack-years (for more details see Ausband et al. 2010, 2015, 2017*a*). Because sampling was focused on rendezvous sites packs that did not successfully reproduce were not included.

We used litter size, pup survival, and presence of multiple breeding females as response variables. We treated the number of pups at three months of age as the litter size. Any mortality of pups younger than this would bias litter size low and pup survival high, however the litter sizes were similar to those reported elsewhere for wolves (Fuller et al. 2003). We considered pup survival as the number of pups at three months of age that were still alive at 15 months of age as Ausband et al. (2017*a*) did. Similarly to Ausband (2018), we treated the presence of > 1 breeding female as a binary variable to estimate the probability of a pack containing multiple breeding females.

We included independent variables that represented prey availability, pack and population characteristics, and harvest. For the independent predictors of prey availability, we used winter severity as an index for prey vulnerability (Mech and Peterson 2003; Mech and Fieberg 2015) and catch-per-unit-effort (CPUE) of antlered deer and elk as an index of prey abundance (Lancia et al. 1996). We used the average daily snow depth for the water year (October 1 – September 30 the following year) from SNOTEL (https://www.wcc.nrcs.usda.gov/snow/) for winter severity. We estimated CPUE for antlered deer and elk in each game management unit as the number of harvested antlered deer or elk divided by the number of hunter days using harvest statistics from IDFG (idfg.idaho.gov). We used log transformed estimates of abundance of wolves from wolf monitoring by IDFG for population size (Nadeau et al. 2009; Mack et al. 2010; Holyan et al. 2011; Idaho Department of Fish and Game and Nez Perce Tribe 2012, 2013, 2014, 2015, Idaho Department of Fish and Game 2016, 2017) and the number of adults present when pups were three months of age as independent predictors representing pack and population characteristics. We used a binary variable to represent years with and without harvest and harvest rate as independent predictor variables. We estimated harvest rates for the population using abundance estimates from IDFG and reported harvest of wolves (idfg.idaho.gov).

Model fitting for multiple breeding females, litter size, and pup survival

We fit generalized linear mixed-effects models for litter size (l), pup survival (ϕ), and the probability of multiple breeding females (m). We assumed that the observed litter size at three months of age was a zero-truncated Poisson random variable, which fits litter size data for canids well (Devenish-Nelson et al. 2013), and modeled the expected litter size with a log transformation. We included a random effect of pack to account for non-independence in litter count data. We assumed that the observed number of pups that survived until 15 months of age for pack-year i was a binomial random variable. We modeled the expected number of surviving pups with a logit transformation and a random effect for pack and year to account non-independence of pup survival in littermates within a pack-year. We assumed that the observed presence of multiple breeding females was a Bernoulli random variable and modeled the expected probability of multiple breeding females using generalized linear models with a logit transformation.

We ran models based on our *a priori* hypotheses and on findings by Ausband et al. (2017*a*) and Ausband (2018) in a hierarchical framework to limit the number of total competing models in our final candidate list. We first ran five models representing prey availability (for every combination of the three predictor variables for prey availability) and three models representing population and pack characteristics (one for each population and pack size, and one with both) for litter size, pup survival, and the probability of multiple breeding females. In addition, we ran one model for harvest on pup survival. After determining which predictor variables best represented prey availability and population and pack characteristics, we used the model with most support (Supplementary Material 3.A) in the next step of model selection. We considered every combination of prey availability, population and pack characteristics, and harvest, which resulted in four competing models for litter size and multiple breeding females and eight competing models for pup survival. Additionally, we considered a model representing the hypothesis of a compensatory response to harvest for litter size and a model for pup survival representing the hypothesis that pups in larger packs are more likely to survive during years with harvest. We tested for collinearity among covariates using the Pearson correlation coefficient and excluded collinear covariates within the same model (r > |0.60|; Zuur et al. 2010) in constructing our final candidate models (Table 3.1).

We fit models in a Bayesian framework using JAGS v4.2.0 (Plummer 2003) via the R2jags package (Su and Yajima 2015) in R v3.4.1 (R Core Team 2017). We ran three Markov chains for 100,000 iterations with the first 50,000 discarded as a burn-in period and a thinning rate of five. We continued to run an additional 50,000 iterations until chains converged. We monitored convergence using visual inspection of the chains and the Gelman-Rubin diagnostic (Gelman and Rubin 1992). We used non-informative priors for all parameters. See Supplementary Material 3.B for model code for the null model. We compared models using approximate leave-one-out cross-validation score (LOO; Gabry et al. 2017; Vehtari et al. 2017) and the expected log predictive density (ELPD) using Pareto-smoothed importance-sampling in the loo package (Vehtari et al. 2019). LOO information criterion is analogous the Akaike information criterion (Vehtari et al. 2017, 2019), and has been increasing used for model selection in a Bayesian framework (Feist et al. 2017; Eisaguirre et al. 2018; Mahoney et al. 2018; Naidoo et al. 2018). We assessed model fit using the expected log predictive density for all demographic rates, Bayesian *p*-values calculated from the χ^2-discrepancy statistic (Gelman et al. 2004) for litter size, and the receiver operating characteristic (ROC) statistic and the corresponding area under the curve (AUC; Hosmer and Lemeshow 2000) for pup survival and the probability of multiple breeding females. We report all coefficient values with the mean and 95% credible interval (CRI) unless stated otherwise. When the 95% CRI contained 0 we calculated the probability the coefficient was greater than or less than 0 using the MCMC samples from the posterior distribution.

Probability a pack reproduced and a component model of recruitment

We combined results from multiple breeding females, litter size, and pup survival with hypotheses of whether a pack successfully reproduced to generate predictions of recruitment for wolf packs in Montana from 2005-2010. Group counts of wolf packs were collected by Montana Fish, Wildlife and Parks (MFWP) biologists annually. Biologists would monitor radiocollared wolves to determine pack size via aerial and ground observations in fall and winter (Mech 1973; Gude et al. 2012). Other field surveillance techniques for wolf observations were used to obtain group counts for packs that were not radiocollared (USFWS 2009; Bradley et al. 2015). Monitoring efforts increased each December to provide end-of-year counts. We used the end-of-year group counts for wolves in Montana that biologists considered of good quality (i.e., complete) and that included counts of pups. The subset of data included 184 pack counts from 82 unique packs from 2005-2010. We were predicting recruitment to 7 months whereas models for pup survival were to 15 months of age. This mismatch was an artifact of the available data, and we assumed our predictions of recruitment for wolves in Montana were optimistic. However, there was only a few wolves harvested in the 2009 hunting season (72 wolves; Inman et al. 2019), and there appears to be no seasonal difference in survival rate for wolves in the NRM (Smith et al. 2010). Therefore, the bias may be minimal. These counts also likely represent an undercount as detection of wolves in packs is imperfect and varies seasonally (Horne et al. 2019). However, these counts are from repeated visits that the biologists considered complete, and the bias may be minimal. We used the average daily snow depth for the water year from SNOTEL (https://www.wcc.nrcs.usda.gov/snow/) for winter severity in Montana. We estimated CPUE for deer for each region the pack resided in as the number of harvested antlered deer divided by the number of hunter days using harvest statistics from MFWP (fwp.mt.gov).

We used the most supported model for multiple breeding females, litter size, and pup survival to predict those components. We used four hypotheses to generate predictions of the probability a pack reproduced: 1) null model with a mean probability; 2) the probability a pack reproduced increased monotonically with pack size; 3) mortality during the breeding season reduced the probability a pack reproduced due to breeder loss; and 4) pack size and mortality during the breeding season both affect the probability a pack reproduces (Figure 3.1). We generated predictions of recruitment under the four hypotheses for the probability a pack reproduced (b) and the most supported models of multiple breeding females (m), litter size (ll), and pup survival (ϕ) in a Bayesian hierarchical model. We assumed the probability a pack reproduced was a Bernoulli random variable and modeled the probability using a logit transformation. We used informative priors to represent our hypotheses of the probability a pack reproduced and tested the sensitivity of the results to these priors. We refit the most supported models for multiple breeding females, litter size, and pup survival and estimated recruitment (γ) as $\gamma = bl\phi + mbl\phi$ using the same procedures outlined above. We compared predictions of recruitment to observed recruitment using the root mean squared error (RMSE) and the 90% credible interval coverage (coverage) of the posterior estimates (Sokal and Rohlf 1995; Walther and Moore 2005).

RESULTS

Multiple breeding females, litter size, and pup survival

All models for the probability a pack contains multiple breeding females converged with Gelman-Rubin statistics of <1.1 and had good mixing of chains indicating model convergence. There was model selection uncertainty for all initial sets of models, however the most supported model both in terms of LOO and ΔELPD representing prey availability included winter severity and the index of deer abundance (Supplementary Material 3.A Table 3). The most supported model representing population and pack characteristics included pack size (Supplementary Material 3.A Table 3). The top model for the probability of multiple breeding females included prey availability (represented as winter severity and the index of deer abundance) and pack size (Table 3.1). The model with only prey availability was also considered competitive because the SE for ΔELPD was greater than the estimated ΔELPD (Table 3.1). Both models fit the data well (all Pareto-*k* diagnostic values < 0.5; AUC ≥ 0.81; Supplementary Material 3.A Figures 12-13). Multiple breeding females had a 0.97 probability of a positive relationship with the index of deer abundance ($\beta = 38.02, CRI = -1.258 - 79.446$) and a positive relationship with winter severity ($\beta = 0.28, CRI = 0.058 - 0.542$). We found that multiple breeding females also had a positive correlation with pack size ($\beta = 0.34, CRI = 0.043 - 0.689$).

All models for litter size converged with Gelman-Rubin statistics of <1.1 and had good mixing of chains indicating model convergence. There was model selection uncertainty for all initial sets of models, however the most supported model both in terms of LOO and ΔELPD representing prey availability included the index of deer abundance (Supplementary Material 3.A Table 3). The most supported model representing population and pack characteristics included pack size (Supplementary Material 3.A Table 1). The top model for litter size included only a random effect of pack (Table 3.1). The model fitted the data marginally well (*p*-value = 0.78; all Pareto-*k* diagnostic values < 0.5; Supplementary Material 3.A Figure 1). We also considered the model with only pack size competitive because the SE for ΔELPD was greater than the estimated ΔELPD (Table 3.1). The pack size only model fitted the data slightly better than the top model (*p*-value = 0.76; all Pareto-*k* diagnostic values < 0.7; Supplementary Material 3.A Figure 2). Litter size had a 0.84 probability of a positive relationship with pack size ($\beta = 0.03, CRI =$

$-0.006 - 0.069$). We found little variation among packs for litter size ($SD\ of\ packs = 0.12, CRI = 0.006 - 0.318$).

All models for pup survival converged with Gelman-Rubin statistics of <1.1 and had good mixing of chains indicating model convergence. There was model selection uncertainty for all initial sets of models, however the most supported model both in terms of LOO and ΔELPD representing prey availability included the index of deer abundance (Supplementary Material 3.A Table 2). The most supported model representing population and pack characteristics included abundance (Supplementary Material 3.A Table 2). The top model for pup survival included prey availability (represented as the index of deer abundance), abundance, and harvest followed by the harvest only model (Table 3.1). There was considerable model selection uncertainty and all models were considered competitive (Table 3.1), however the models did not fit the data well (some Pareto-*k* diagnostic values > 0.7 for all models; AUC ~ 0.76 for all models; Supplementary Material 3.A Figures 3-11). Pup survival had 0.97 probability of a positive relationship with the index of deer abundance ($\beta = 23.86, CRI = -1.209 - 49.156$) and a 0.76 probability of a positive relationship with abundance ($\beta = 2.43, CRI = -4.335 - 7.920$). We found a 0.93 probability that pup survival was less in years with harvest compared to years without harvest ($\beta = -0.95, CRI = -2.307 - 0.484$). We found a 0.85 probability of a positive effective of pack size on pup survival ($\beta = 0.07, CRI = -0.052 - 0.192$) in the pack size only model. When we ran the interaction model with pack size and harvest we found a 0.70 probability of a negative effect of pack size on pup survival ($\beta = -0.06, CRI = -0.274 - 0.149$). There was a 0.91 probability that the interaction between harvest and pack size had a positive correlation with pup survival ($\beta = 0.16, CRI = -0.075 - 0.417$), indicating that pups may have greater survival in larger packs during years with harvest than in small packs (Figure

3.2). We found greater variation among packs ($SD\ of\ packs = 1.22, CRI = 0.575 - 2.227$) than years ($SD\ of\ years = 0.55, CRI = 0.039 - 1.521$) for pup survival.

Probability a pack reproduced and predictions of recruitment

We predicted the mean probability a pack contained > 1 breeding female was 0.02 (SD = 0.012) for a pack of 5 and 0.07 (SD = 0.052) for a pack of 10 wolves. Based on the top model, we predicted a mean litter size of 4.31 (SD = 0.046). We predicted mean pup survival to be 0.59 (SD = 0.023) during years without harvest and 0.43 (SD = 0.016) during years with harvest. Based on these components, we predicted recruitment for a pack of five wolves to be 2.83 (SD = 0.562) and 1.91 (SD = 0.419) pups per pack during years without and with harvest, respectively, under the null hypotheses for the probability a pack reproduced.

We found the null hypothesis for the probability a pack reproduced provided the best predictions of recruitment and the hypothesis with pack size and harvest effects performed worst (Figure 3.3 – 3.5). Coverage by the 95% CRI was similar for the four hypotheses when averaged across packs and years, and ranged from 82 – 84%. In general, predictions of recruitment were more accurate during years without harvest than with harvest (Figure 3.4). During years with harvest, the null model did best at predicting recruitment, with 86% of observations falling within the 95% CRI of the predictions. During years without harvest, we found that the pack size hypothesis best predicted recruitment rate, and 86% of observations were within the 95% CRI. Accuracy of estimates appeared to have increased over time, particularly for the null hypothesis (Figure 3.5). Coverage by the 95% CRI increased from 78% in 2005 to 94% in 2010 under the null hypothesis for the probability a pack reproduced.

DISCUSSION

Predictions of recruitment are helpful for managing harvested populations. Further, understanding how factors affect the components of recruitment (number of females that reproduce, litter or clutch size, and offspring survival) can be used to evaluate how effective management actions are at altering recruitment to meet population objectives. Data to estimate the components of recruitment, however, can be costly to collect. We evaluated the effects of prey availability, pack and population size, and harvest on litter size and used findings from previous studies for multiple breeding females (Ausband 2018) and pup survival (Ausband et al. 2015, 2017*a*) to develop a component model to predict recruitment in wolves in Idaho from 2008-2016. We then spatially and temporally validated the model by comparing predictions from the model to observed recruitment for wolves in Montana from 2005-2010. Contrary to prior analyses, we found that the probability a pack contained multiple breeding females was positively related to prey availability. We found that litter size varied little among packs, however was positively related to pack size. The component model, developed for wolves in Idaho, provided predictions of recruitment for wolves in Montana. The credible intervals were wide for estimates of recruitment, primarily due to the high variation in pup survival among packs. However, they provide a starting point for estimating recruitment of individual packs and can be scaled up to estimate mean recruitment rate and total pups recruited for the population while accounting for variability among packs.

We found support for our hypothesis that the presence of multiple breeding females was positively related to prey availability. We found that winter severity and the index of deer abundance was positively related to the probability of multiple breeding females, suggesting that packs are more likely to contain > 1 breeding female with greater prey availability. This is similar to the findings by Boertje and Stephenson (1992) that more females were reproductively active and had greater subcutaneous fat with greater ungulate biomass. In contrast, Ausband (2018) found no effect of elk density on the probability of multiple breeding females. Although elk are generally considered the primary prey resource of wolves (Hebblewhite et al. 2003; Mech and Peterson 2003), we found that the deer CPUE and winter severity better explained the patterns in multiple breeding females than the elk index. Similarly to Ausband (2018), we found that multiple breeding females was positively related to pack size, however contrary to Ausband (2018) we did not find that multiple breeding females was positively related to abundance of wolves. Although we did not find an effect of abundance on the probability a pack contains more than one breeding female, neighboring pack density may influence this vital rate. Ausband (2018) used wolf density in their study area instead of abundance, which may explain why our results differed. In general, the probability a pack contained multiple breeding females was low (< 0.07 for a pack of ≤ 10 wolves). In African wild dogs (*Lycaon pictus*), Marneweck et al. (2019) noted four cases out of 90 pack years (4%) of multiple litters per pack. Like wolves, African wild dogs live in packs, and mating is typically dominated by the breeding pair (Creel and Creel 2002; Packard 2003). However, sociality can lead to alternative mating strategies (Ausband 2018, 2019).

Our estimated litter size (4.31, SD = 0.046) was similar to estimates reported elsewhere. Litter size for wolves in southeast Alaska was 4.1 pups (SD = 1.7; Person and Russell 2009), however they found litter size was smaller in first-time breeders. Boertje and Stephenson (1992) examined reproductive tracts of harvested wolves in Alaska and found the average number of fetuses ranged from 6.9 to 4.6 in areas of high and low prey availability, respectively. Average litter sizes across North America ranged from 4.2 – 6.9 pups (Fuller et al. 2003). In Yellowstone National Park, average litter size at den emergence was 4.74 (SD = 0.21; Stahler et al. 2013).

Although we found support for our hypothesis that pack size was positively related to litter size, it was a small effect. Stahler et al. (2013) found a 10% increase in litter size with pack size until the pack reached eight wolves. Then, litter size decreased by 9% for each additional wolf added to the pack (Stahler et al. 2013). We only found a small effect of pack size on litter size, with a 3% increase with each additional wolf added to the pack. We may have found a stronger effect of pack size if we evaluated a quadratic relationship. However, we found little variation in litter size, and litter size was similarly explained by a mean litter size with slight variation among packs. In fact, litter size varies little in many canid species (Devenish-Nelson et al. 2013). This could indicate that biological limitations on reproduction in wolves allows for little variation in litter size. Further support for this conclusion is that we did not find support for our hypotheses that prey availability was positively related to litter size or a density dependent response in litter size. A density dependent response in litter size would indicate diminishing per capita resource availability with increasing abundance. Boertje and Stephenson (1992) found that litter size declined with declines in ungulate biomass per wolf, however they only found declines in litter size when ungulate biomass per wolf was reduced below levels previously reported in the literature. Similarly, we did not find support for the hypothesis of a compensatory effect of harvest on litter size. Contrary to our results, Sidorovich et al. (2007) found that intensive harvest of wolves in Belarus increased litter size. The maximum reported density of wolves in Belarus during their study (36 wolves/1000 km^2) was much greater than the maximum reported density of wolves in central Idaho (15 wolves/1000 km^2; Bassing 2017), and therefore reproduction of wolves in Belarus may have been limited by available food resources. These results suggest that per capita prey availability may not be a limiting factor for reproduction of wolves in our study area.

We could not reject our hypothesis that prey availability was positively correlated to pup survival. Food resources are necessary for growth and maintenance and larger pups may be less vulnerable to natural sources of mortality (e.g., disease or starvation Fuller et al. 2003). If the population was near biological carrying capacity, we would similarly expect a reduction in pup survival with diminishing per capita food availability, however we did not find support for our hypothesis that pup survival would be density dependent and found a slight positive effect of abundance of wolves on pup survival. Our results differ from those of Stahler et al. (2013) that found a slight negative effect of abundance on pup survival. We found greater variation in pup survival among packs than among years, suggesting that pack characteristics may be more important than temporal variation in food resources. For species that cooperatively breed, changes in group composition (number in different sex or age classes) can greatly affect recruitment (Whitman et al. 2004; Brainerd et al. 2008; Gobush et al. 2008; Ausband et al. 2017*a*). Loss or turnover of breeding males and females (Brainerd et al. 2008; Ausband et al. 2017*b*) and the number of non-breeding males and females can affect pup survival (Ausband et al. 2017*a*) and may explain the large variation among packs and marginal predictive ability of the models of wolf survival (Supplementary Material 3.A). Additionally, individual characteristics of the breeding female may influence pup survival (Stahler et al. 2013). Although pup survival is affected by pack composition and breeder turnover (Ausband et al. 2017*a*; *b*), data on group composition and breeder fate are difficult to collect. Including those factors in a model would limit the ability of the model to predict recruitment only when those data were available. Because our objective was to develop a model to predict recruitment without detailed data on pack composition, we included random variation among packs (i.e., random effect of pack) to account for the effects of pack characteristics on pup survival.

Generally, the component model predicted recruitment well for wolves in Montana. For our model that had a constant probability a pack successfully reproduced, credible intervals for recruitment contained > 82% of the observed recruitment values. Generally, our predictions for each pack were not biased high or low, and the number of packs where we predicted higher or lower recruitment were equivalent. Our predictions of recruitment during the year with harvest (2009), however, were less accurate than years without harvest (Figure 3.4). This effect was more pronounced under the models that included the effect of harvest on the probability a pack reproduced. This may suggest that our hypotheses for the effects of harvest on the probability a pack reproduced are unsupported, however there was little improvement in predictions of recruitment under the null hypothesis during years with harvest. The harvest rate was low in Montana in 2009 (72 harvested, ~ 9% harvest rate), and it may be that our predictions of pup survival were biased low because the model was developed for wolves in Idaho during years with much greater harvest rates (Ausband 2016). Future predictions could be improved by including harvest as a rate instead of as a binary variable and modeling natural survival. For the null hypotheses, we assumed that 95% of packs would successfully reproduce. Hayes and Harestad (2000) found that during recovery 35% of packs produced pups and increased to 93% after four years. Time since the pack established may have a positive effect the probability a pack reproduced. We were also unable to account for the effects of breeder turnover on pup survival (Ausband et al. 2017*a*) or on the probability a pack reproduced (Brainerd et al. 2008). To fully test predictions of this component model, data on which packs reproduced, litter size, the number of breeding females, and pup survival are needed.

We did not evaluate all potential factors that could affect the components of recruitment which may have affected our results. Disease may affect litter size or pup survival if the breeding female or pups are infected which can result in highly variable recruitment rates (Fuller et al. 2003; Almberg et al. 2009). Canine distemper virus (CDV) in Yellowstone National Park resulted in almost complete loss of pup recruitment in some years (Almberg et al. 2009), however CDV requires a large population of susceptible individuals to persist, and wolf populations quickly recover (Almberg et al. 2010). Density and connectivity of wolves in Idaho may not be high enough to experience a similar outbreak to Yellowstone National park, however Almberg et al. (2010) suggested that periodic (2-5 years) and unpredictable population declines were possible. We found annual variation in pup survival was less than variation among packs for the nine years of data we analyzed suggesting that if CDV were affecting pup survival, then it is limited to a few packs and not greatly affecting annual pup survival. We did not account for the effect of individual characteristics (e.g., age or body mass) on the components of recruitment. Age of first reproduction may influence litter size, and has been documented in wolves (Person and Russell 2009; Sparkman et al. 2017) and African wild dogs (Marneweck et al. 2019). First-time breeders produced smaller litters for wolves in Alaska (Person and Russell 2009), and females with greater body mass produced larger litters in Yellowstone National Park, USA (Stahler et al. 2013). We did not have detailed data on individual characteristics from mothers, however the pack random effect in litter size may have accounted for these differences.

MANAGEMENT IMPLICATIONS

Estimating recruitment of a low density, elusive species can be difficult for the agency responsible for management, however this component model may be a viable option to predict recruitment of wolves. The data required to generate predictions are readily available in most circumstances: deer CPUE, snow depth, pack size, and whether or not the population was harvested. In instances when pack sizes are not know for all packs, an estimate of mean pack size and variance could be used to impute missing pack sizes and account for uncertainty. Because the component model focuses on individual components, one component could be updated while retaining the others to generate predictions. For example, if new data on pup survival become available managers could update that portion of the model to generate predictions of recruitment. Further, litter size varied little and the probability a pack contained multiple breeding females was low, therefore managers wishing to alter recruitment may have more success when targeting successful reproduction and pup survival.

LITERATURE CITED

Almberg, E. S., P. C. Cross, and D. W. Smith. 2010. Persistence of canine distemper virus in the Greater Yellowstone Ecosystem’s carnivore community. Ecological Applications 20:2058–2074.

Almberg, E. S., L. D. Mech, D. W. Smith, J. W. Sheldon, and R. L. Crabtree. 2009. A serological survey of infectious disease in Yellowstone National Park’s canid community. PloS one 4:e7042.

Ausband, D. E. 2016. Gray wolf harvest in Idaho. Wildlife Society Bulletin 40:500–505.

Ausband, D. E. 2018. Multiple breeding individuals within groups in a social carnivore. Journal of Mammalogy 99:836–844.

Ausband, D. E. 2019. Pair bonds, reproductive success, and rise of alternate mating strategies in a social carnivore. Behavioral Ecology 30:1618–1623.

Ausband, D. E., M. S. Mitchell, K. Doherty, P. Zager, C. M. Mack, and J. Holyan. 2010. Surveying predicted rendezvous sites to monitor gray wolf populations. Journal of Wildlife Management 74:1043–1049.

Ausband, D. E., M. S. Mitchell, C. R. Stansbury, J. L. Stenglein, and L. P. Waits. 2017a. Harvest and group effects on pup survival in a cooperative breeder. Proceedings of the Royal Society of London B: Biological Sciences 284:20170580.

Ausband, D. E., M. S. Mitchell, and L. P. Waits. 2017b. Effects of breeder turnover and harvest on group composition and recruitment in a social carnivore. Journal of Animal Ecology 86:1094–1101.

Ausband, D. E., C. R. Stansbury, J. L. Stenglein, J. L. Struthers, and L. P. Waits. 2015. Recruitment in a social carnivore before and after harvest. Animal Conservation 18:415–423.

Bassing, S. 2017. Harvest and persistence of wolf populations: variable effects of harvest on wolf packs in the Rocky Mountains. University of Montana.

Beja, P., and L. Palma. 2008. Limitations of methods to test density-dependent fecundity hypothesis. Journal of Animal Ecology 77:335–340.

Bishop, C. J., G. C. White, D. J. Freddy, and B. E. Watkins. 2005. Effect of limited antlered harvest on mule deer sex and age ratios. Wildlife Society Bulletin 33:662–668.

Boertje, R. D., and R. O. Stephenson. 1992. Effects of ungulate availability on wolf reproductive potential in Alaska. Canadian Journal of Zoology 70:2441–2443.

Borg, B. L., S. M. Brainerd, T. J. Meier, and L. R. Prugh. 2015. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. The Journal of Animal Ecology 84:177–187.

Bradley, L., J. Gude, N. Lance, K. Laudon, A. Messer, A. Nelson, G. Pauley, M. Ross, T. Smucker, and J. Steuber. 2015. Montana gray wolf conservation and management 2014 annual report. Helena, Montana.

Brainerd, S. M., H. Andrén, E. E. Bangs, E. H. Bradley, J. A. Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. A. Jozwiak, O. Liberg, C. M. Mack, T. J. Meier, C. C. Niemeyer, H. C. Pedersen, H. Sand, R. N. Schultz, D. W. Smith, P. Wabakken, and A. P. Wydeven. 2008. The effects of breeder loss on wolves. Journal of Wildlife Management 72:89–98.

Cohen, J. B., A. Hecht, K. F. Robinson, E. E. Osnas, A. J. Tyre, C. Davis, A. Kocek, B. Maslo, and S. M. Melvin. 2016. To exclose nests or not: structured decision making for the conservation of a threatened species. Ecosphere 7:e01499.

Creel, S., and N. M. Creel. 2002. The African wild dog: behavior, ecology, and conservation. Volume 65. Princeton University Press.

Devenish-Nelson, E. S., P. A. Stephens, S. Harris, C. Soulsbury, and S. A. Richards. 2013. Does litter size variation affect models of terrestrial carnivore extinction risk and management? PLoS ONE 8:e58060.

Eisaguirre, J. M., T. L. Booms, C. P. Barger, C. L. Mcintyre, S. B. Lewis, and G. A. Breed. 2018. Local meteorological conditions reroute a migration. Proceedings of the Royal Society B 285:20181779.

Feist, B. E., E. R. Buhle, D. H. Baldwin, J. A. Spromberg, S. E. Damm, J. W. Davis, and N. L. Scholz. 2017. Roads to ruin: conservation threats to a sentinel species across an urban gradient. Ecological Applications 27:2382–2396.

Fuller, T. K., L. D. Mech, and J. Fitts-Cochran. 2003. Wolf population dynamics. Pages 161–191 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. University of Chicago Press, Chicago, Illinois.

Gabry, J., D. Simpson, A. Vehtari, M. Betancourt, and A. Gelman. 2019. Visualization in Bayesian workflow. Journal of the Royal Statistical Soceity A 182:389–402.

Gaillard, J.-M., M. Festa-Bianchet, and N. G. Yoccoz. 1998. Population dynamics of large herbivores: variable recruitment with constant adult survival. Trends in Ecology & Evolution 13:58–63.

Gaillard, J.-M., M. Festa-Bianchet, N. G. Yoccoz, A. Loison, and C. Toïgo. 2000. Temporal variation in fitness components and population dynamics of large herbivores. Annual Review of Ecology and Systematics 31:367–393.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis. Second edition. Chapman and Hall/CRC Press.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–472.

Gobush, K. S., B. M. Mutayoba, and S. K. Wasser. 2008. Long-term impacts of poaching on relatedness, stress physiology, and reproductive output of adult female African elephants. Conservation Biology 22:1590–1599.

Gude, J. A., M. S. Mitchell, R. E. Russell, C. A. Sime, E. E. Bangs, L. D. Mech, and R. R. Ream. 2012. Wolf population dynamics in the U.S. Northern Rocky Mountains are affected by recruitment and human-caused mortality. The Journal of Wildlife Management 76:108–118.

Hayes, R. D., and A. S. Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology 78:36–48.

Hebblewhite, M., P. C. Paquet, D. H. Pletscher, R. B. Lessard, and C. J. Callaghan. 2003. Development and application of a ratio estimator to estimate wolf kill rates and variance in a multiple-prey system. Wildlife Society Bulletin 31:933–946.

Holyan, J., K. Holder, J. Cronce, and C. M. Mack. 2011. Wolf conservation and management in Idaho progress report 2010. Lapwaii, Idaho.

Horne, J. S., D. E. Ausband, M. A. Hurley, J. Struthers, J. E. Berg, and K. Groth. 2019. Integrated population model to improve knowledge and management of Idaho wolves. The Journal of Wildlife Management 83:32–42.

Hosmer, D. W. J., and S. Lemeshow. 2000. Applied logistic regression. 2nd edition. Wiley, New York, New York.

Idaho Department of Fish and Game. 2016. 2015 Idaho wolf monitoring progress report. Boise, Idaho.

Idaho Department of Fish and Game. 2017. 2016 Idaho wolf management report. Boise, Idaho.

Idaho Department of Fish and Game, and Nez Perce Tribe. 2012. 2011 Idaho wolf monitoring progress report. Boise, Idaho.

Idaho Department of Fish and Game, and Nez Perce Tribe. 2013. 2012 Idaho wolf monitoring progress report. Boise, Idaho.

Idaho Department of Fish and Game, and Nez Perce Tribe. 2014. Idaho wolf monitoring progress report.

Idaho Department of Fish and Game, and Nez Perce Tribe. 2015. 2014 Idaho wolf monitoring progress report. Boise, Idaho.

Inman, B., K. M. Podruzny, T. D. Smucker, A. A. Nelson, M. Ross, N. Lance, T. Parks, D. K. Boyd, and S. Wells. 2019. Montana gray wolf conservation and management 2018 annual report. Helena, Montana.

Jones, O., and J. Wang. 2009. COLONY: a program for parentage and sibship inference from multilocus genotype data. Mol. Ecol. Resour.

Knowlton, F. F., E. M. Gese, and M. M. Jaeger. 1999. Coyote depredation control: an interface between biology and management. Journal of Range Management 52:398–412.

Lancia, R. A., J. W. Bishir, M. C. Conner, and C. S. Rosenberry. 1996. Use of catch-effort to estimate population size. Wildlife Society Bulletin 24:731–737.

Mack, C. M., J. Rachael, J. Holyan, J. Husseman, M. Lucid, and B. Thomas. 2010. Wolf conservation and management in Idaho progress report 2009. Boise, Idaho.

MacNulty, D. R., D. W. Smith, L. D. Mech, J. A. Vucetich, and C. Packer. 2011. Nonlinear effects of group size on the success of wolves hunting elk. Behavioral Ecology 23:75–82.

Mahoney, P. J., J. K. Young, K. R. Hersey, R. T. Larsen, B. R. McMillan, and D. C. Stoner. 2018. Spatial processes decouple management from objectives in a heterogeneous landscape: predator control as a case study. Ecological Applications 28:786–797.

Marneweck, D. G., D. J. Druce, and M. J. Somers. 2019. Food, family and female age affect reproduction and pup survival of African wild dogs. Behavioral Ecology and Sociobiology 73:1–15.

Mech, L. D. 1973. Wolf numbers in the Superior National Forest of Minnesota. Research Paper, St. Paul, MN.

Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1–34 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, Illinois.

Mech, L. D., and J. Fieberg. 2015. Growth rates and variances of unexploited wolf populations in dynamic equilibria. Wildlife Society Bulletin 39:41–48.

Mech, L. D., and R. O. Peterson. 2003. Wolf-prey relations. Pages 131–160 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, Illinois.

Messier, F. 1991. The significance of limiting and regulating factors on the demography of moose and white-tailed deer. The Journal of Animal Ecology 60:377–393.

Mitchell, M. S., D. E. Ausband, C. A. Sime, E. E. Bangs, J. A. Gude, M. D. Jimenez, C. M. Mack, T. J. Meier, M. S. Nadeau, and D. W. Smith. 2008. Estimation of successful breeding pairs for wolves in the Northern Rocky Mountains, USA. Journal of Wildlife Management 72:881–891.

Nadeau, M. S., Mack, Curt M, J. Holyan, J. Husseman, M. Lucid, D. Spicer, and B. Thomas. 2009. Wolf conservation and management plan in Idaho progress report 2008. Boise, Idaho.

Naidoo, R., J. W. Kilian, P. Du Preez, P. Beytell, O. Aschenborn, R. D. Taylor, and G. Stuart-Hill. 2018. Evaluating the effectiveness of local- and regional-scale wildlife corridors using quantitative metrics of functional connectivity. Biological Conservation 217:96–103.

Packard, J. M. 2003. Wolf behavior: reproductive, social, and intelligent. Pages 35–65 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, Illinois.

Person, D. K., and A. L. Russell. 2009. Reproduction and den site selection by wolves in a disturbed landscape. Northwest Science 83:211–224.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Schmidt, P. A., and L. D. Mech. 1997. Wolf pack size and food acquisition. The American Naturalist 150:513–517.

Sidorovich, V. E., V. P. Stolyarov, N. N. Vorobei, N. V Ivanova, and B. Jędrzejewska. 2007. Litter size, sex ratio, and age structure of gray wolves, Canis lupus, in relation to population fluctuations in northern Belarus. Canadian Journal of Zoology 85:295–300.

Smith, D. W., E. E. Bangs, J. K. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D. H. Pletscher, C. C. Niemeyer, T. J. Meier, D. R. Stahler, J. Holyan, V. J. Asher, and D. L. Murray. 2010. Survival of colonizing wolves in the Northern Rocky Mountains of the United States, 1982-2004. Journal of Wildlife Management 74:620–634.

Sokal, R. R., and F. J. Rohlf. 1995. Biometry: the principles and practice of statistics in biological research. Freeman.

Solomon, N. G., and J. A. French, editors. 1997. Cooperative breeding in mammals. Cambridge University Press, Cambridge.

Sparkman, A. M., M. Blois, J. Adams, L. Waits, D. A. W. Miller, and D. L. Murray. 2017. Evidence for sex-specific reproductive senescence in monogamous cooperatively breeding red wolves. Behavioral Ecology and Sociobiology 71:1–11.

Stahler, D. R., D. R. MacNulty, R. K. Wayne, B. VonHoldt, and D. W. Smith. 2013. The adaptive value of morphological, behavioural and life-history traits in reproductive female wolves. The Journal of Animal Ecology 82:222–34.

Stenglein, J. L., L. P. Waits, D. E. Ausband, P. Zager, and C. M. Mack. 2010. Efficient, noninvasive genetic sampling for monitoring reintroduced wolves. Journal of Wildlife Management 74:1050–1058.

Stenglein, J. L., J. Zhu, M. K. Clayton, and T. R. Van Deelen. 2015. Are the numbers adding up? Exploiting discrepancies among complementary population models. Ecology and Evolution 5:368–376.

Su, Y.-S., and M. Yajima. 2015. R2jags: using R to run "JAGS."

U.S. Fish and Wildlife Service. 1994a. The reintroduction of gray wolves to Yellowstone National Park and central Idaho. Final Environmental Impact Statement. Denver, Colorado.

U.S. Fish and Wildlife Service. 1994b. Endangered and threatened wildlife and plants; establishment of a nonessential experimental population of gray wolves in Central Idaho and Southwestern Montana. Federal Register 50(17):60266-60281.

U.S. Fish and Wildlife Service. 2009. Final rule to identify the Northern Rocky Mountain population of gray wolf as a Distinct Population Segment and to revise the list of Endangered and Threatened wildlife. Volume 74. Washington, D.C., USA.

U.S. Fish and Wildlife Service. 2011. Endangered and threatened widlife and plants; reissuance of final rule to identify the Northern Rocky Mountain population of gray wolf as a distinct population segment and to revise the list of endangered and threatened wildlife. Federal Register 76. Denver, Colorado.

U.S. Fish and Wildlife Service. 2017. Endangered and threatened wildlife and plants; reinstatement of removal of federal protections for gray wolves in Wyoming. Federal Register 82(82) 20284-20285.

Vehtari, A., J. Gabry, Y. Yao, and A. Gelman. 2019. loo: efficient leave-one-out cross-validation and WAIC for Bayesian models.

Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing 27:1413–1432.

Walther, B. A., and J. L. Moore. 2005. The concepts of bias, precision and accuracy, and their use in testing the performance of species richness estimators, with a literature review of estimator performance. Ecography 28:815–829.

Whitman, K., A. M. Starfield, H. S. Quadling, and C. Packer. 2004. Sustainable trophy hunting of African lions. Nature 428:175–178.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

TABLES

Table 3.1: Candidate models and model selection for litter size (l), pup survival (ϕ), and multiple breeding females (m) for wolves in Idaho from 2008-2016 using leave-one-out cross-validation information criteria (LOO) and mean and standard error of the difference in the expected log predictive density (ΔELPD). Independent variables included pack size (PS), abundance of wolves (PA), winter severity (WS), index of deer abundance (DR), elk index (E), harvest as a binary variable (H), harvest rate (HR), a random effect of pack (α_p), and a random effect of year (ε_t).

Demographic rate	Model	K	LOO	ΔLOO	ΔELPD (SE)
Litter size	$l = \beta_0 + \alpha_p$	2	228.50	0	0 (0)
	$l = \beta_0 + PS + \alpha_p$	3	229.35	0.85	0.43 (0.707)
	$l = \beta_0 + DR + \alpha_p$	3	229.96	1.46	0.73 (0.394)
	$l = \beta_0 + DR + PS + \alpha_p$	4	230.99	2.49	1.25 (0.923)
	$l = \beta_0 + HR + PA + HR * PA + \alpha_p$	5	232.11	3.61	1.81 (0.466)
Pup Survival	$\phi = \beta_0 + DR + PA + H + \alpha_p + \varepsilon_t$	6	177.55	0	0 (0)
	$\phi = \beta_0 + H + \alpha_p + \varepsilon_t$	4	177.57	0.02	0.01 (1.957)
	$\phi = \beta_0 + DR + H + \alpha_p + \varepsilon_t$	5	177.60	0.05	0.03 (0.675)
	$\phi = \beta_0 + DR + \alpha_p + \varepsilon_t$	4	177.86	0.31	0.16 (0.998)
	$\phi = \beta_0 + PA + H + \alpha_p + \varepsilon_t$	5	178.23	0.68	0.34 (1.986)
	$\phi = \beta_0 + DR + PA + \alpha_p + \varepsilon_t$	5	178.23	0.68	0.37 (1.070)
	$\phi = \beta_0 + PA + \alpha_p + \varepsilon_t$	4	178.41	0.86	0.43 (2.180)

	$\phi = \beta_0 + \alpha_p + \varepsilon_t$	3	179.45	1.90	0.95 (2.100)
	$\phi = \beta_0 + H + PS + H * PS + \alpha_p + \varepsilon_t$	6	180.70	3.15	1.58 (2.639)
Multiple breeding females	$m = \beta_0 + PS + WS + DR$	4	34.89	0	0 (0)
	$m = \beta_0 + WS + DR$	3	37.30	2.41	1.21 (1.881)
	$m = \beta_0 + PS$	2	42.42	7.53	3.76 (2.929)
	$m = \beta_0$	1	44.12	9.23	4.62 (3.126)

FIGURES

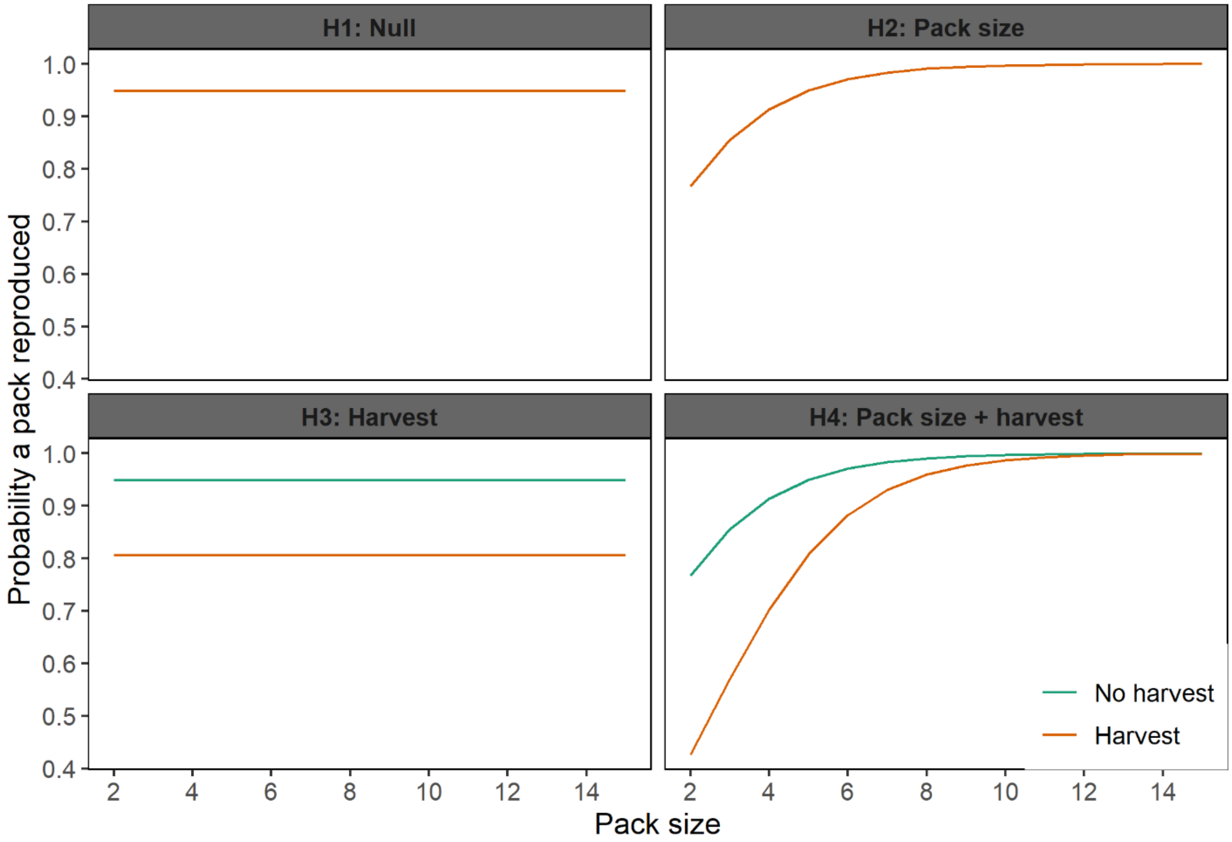

Figure 3.1: Hypothesized relationships between the probability a pack reproduced and pack size and harvest for gray wolves under four hypotheses: the null hypothesis (i.e., constant probability), the pack size hypothesis with a positive relationship between pack size and the probability a pack reproduced, the harvest hypothesis where harvest reduced the probability a pack reproduced, and the pack size + harvest hypothesis.

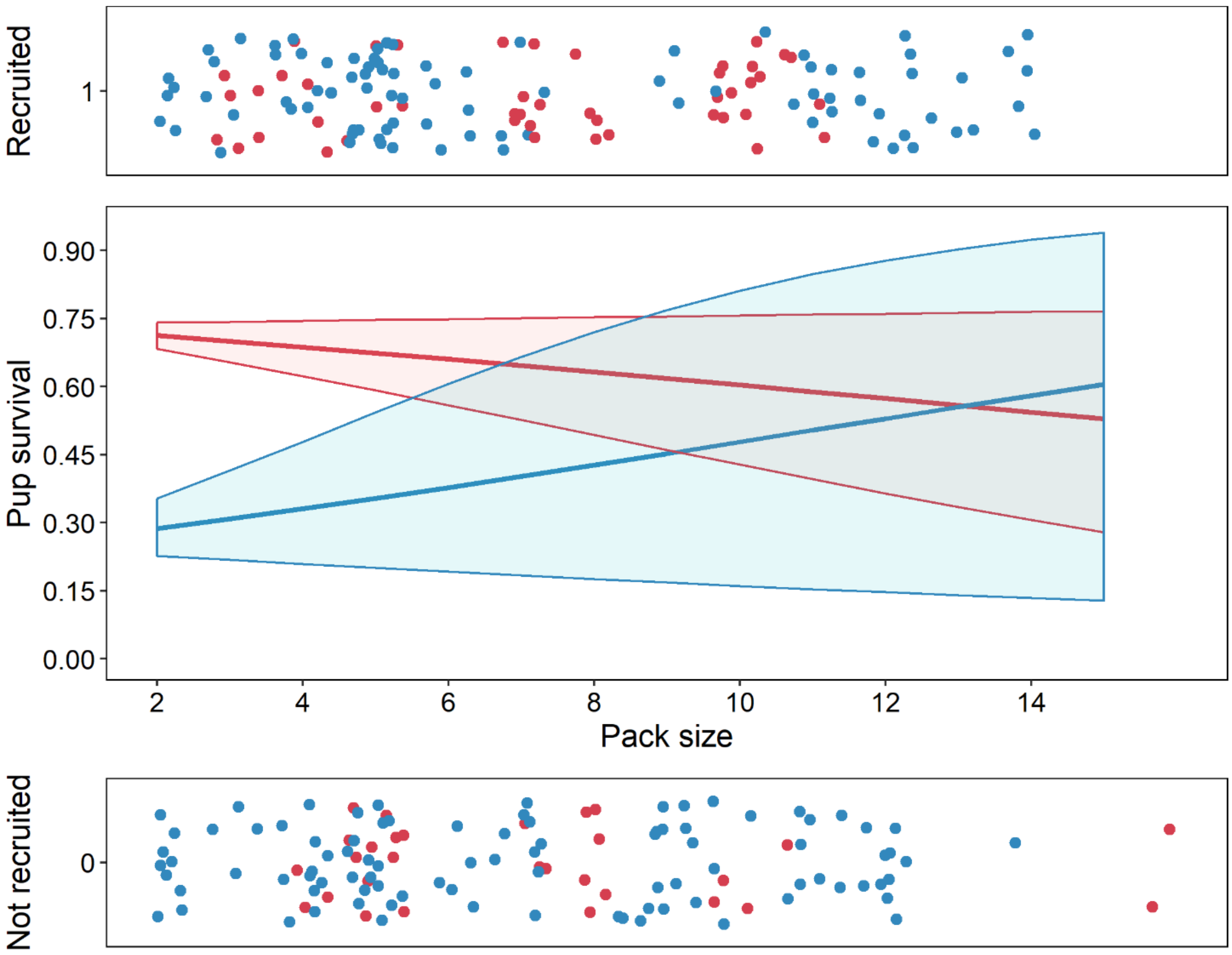

Figure 3.2: Predicted effects and 95% credible intervals of pack size on pup survival during years with (blue) and without (red) harvest from an interaction model fitted to data from gray wolves in Idaho from 2008-2016. The model included an interaction between harvest and pack size. Observed data of pups recruited (i.e., survived; 1) and not recruited (i.e., died; 0) are displayed above and below the figure of pup survival, respectively.

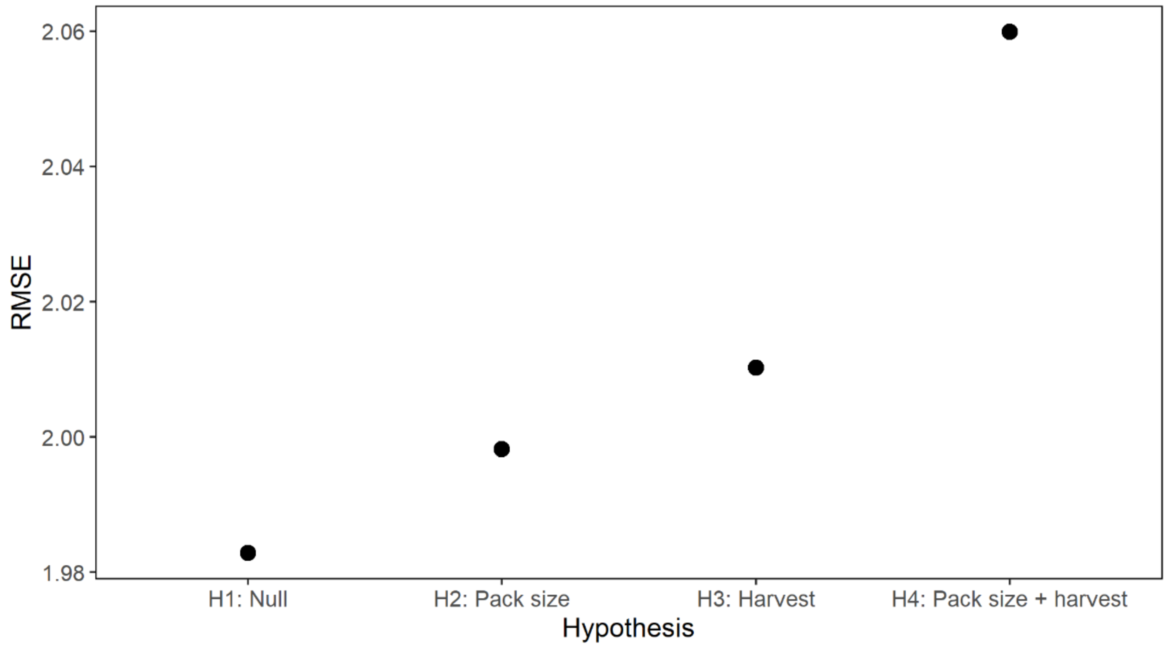

Figure 3.3: Root mean squared error (RMSE) of mean posterior predictions of recruitment for gray wolves in Montana from 2005 – 2010. The model to estimate recruitment was developed for wolves in Idaho from 2008-2016 and tested in Montana by comparing predictions to observed number of pups recruited. RMSE was averaged across packs, pack sizes, and years. Predictions were generated under four hypotheses for the probability a pack reproduced: 1) the null hypothesis was a constant probability, 2) the pack size hypothesis was increased probability with increasing pack size, 3) the harvest hypothesis was a greater probability during years without harvest, and 4) the pack size and harvest hypothesis combined the two previous hypotheses.

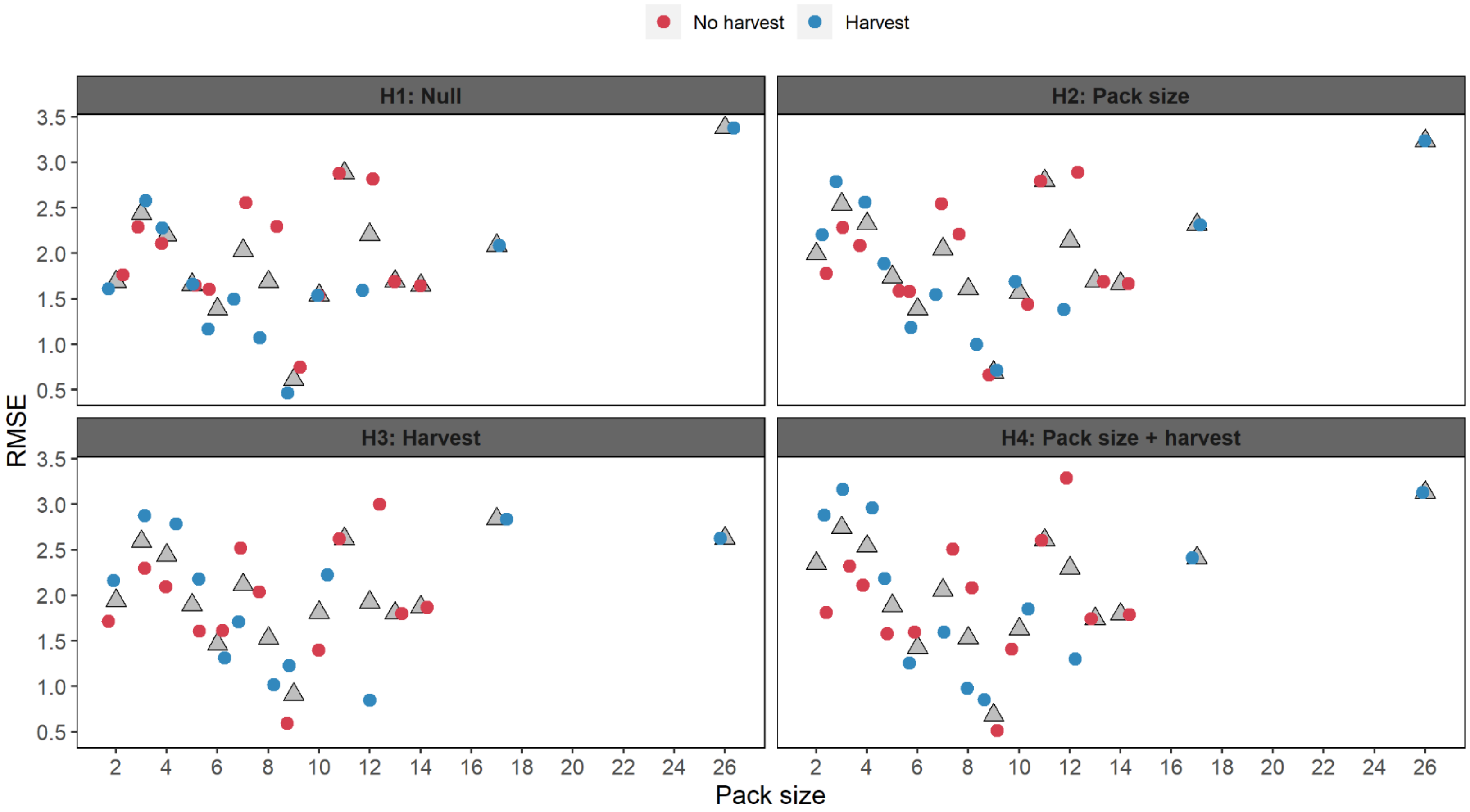

Figure 3.4: Root mean squared error (RMSE) of mean posterior predictions of recruitment during years with and without harvest for gray wolves in Montana from 2005 – 2010. The model to estimate recruitment was developed for wolves in Idaho from 2008-2016 and tested in Montana by comparing predictions to observed number of pups recruited. RMSE was averaged across packs and years, and the triangles represent an average across years with and without harvest. Predictions were generated under four hypotheses for the

probability a pack reproduced: 1) the null hypothesis was a constant probability, 2) the pack size hypothesis was increased probability with increasing pack size, 3) the harvest hypothesis was a greater probability during years without harvest, and 4) the pack size and harvest hypothesis combined the two previous hypotheses.

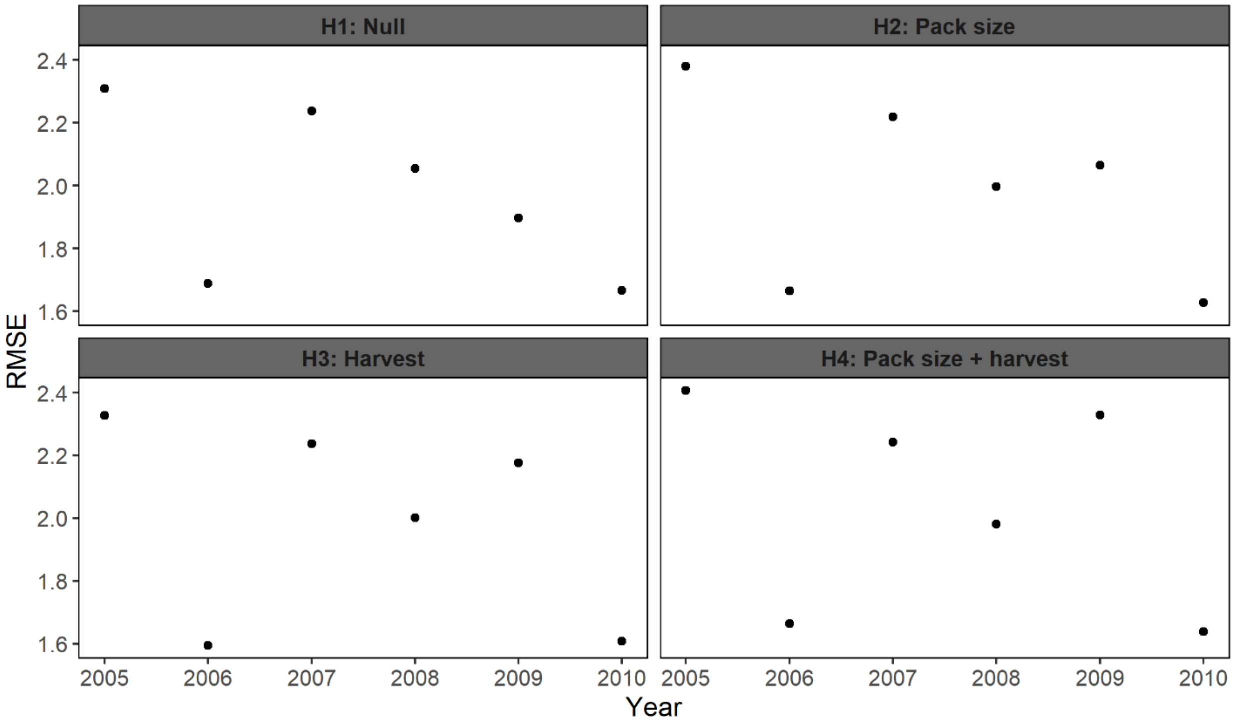

Figure 3.5: Root mean squared error (RMSE) of mean posterior predictions of recruitment for gray wolves in Montana from 2005 – 2010. The model to estimate recruitment was developed for wolves in Idaho from 2008-2016 and tested in Montana by comparing predictions to observed number of pups recruited. RMSE was averaged across packs and pack sizes. Predictions were generated under four hypotheses for the probability a pack reproduced: 1) the null hypothesis was a constant probability, 2) the pack size hypothesis was increased probability with increasing pack size, 3) the harvest hypothesis was a greater probability during years without harvest, and 4) the pack size and harvest hypothesis combined the two previous hypotheses.

CHAPTER 4:

ADDITIVE HARVEST MORTALITY, DENSITY DEPENDENT RECRUITMENT, AND HIERARCHICAL DEMOGRAPHY INFLUENCE WOLF POPULATION DYNAMICS

ABSTRACT

For species that form stable social groups, population dynamics depends on hierarchical demography where dynamics within groups (e.g., survival or dispersal) influence the dynamics among groups (e.g., group formation or persistence). Population dynamics of gray wolves (*Canis lupus*) are still debated, particularly the role of recruitment and harvest mortality. Understanding hierarchical demography may be important for managing harvested populations and evaluating the role of recruitment and harvest mortality in dynamics of wolf populations. We evaluated competing hypotheses to describe population dynamics in gray wolves and tested for evidence of additive or compensatory harvest mortality and density dependent recruitment. Additionally, we determined whether simple per capita models or complex models that account for hierarchical demography were able to accurately predict population dynamics in wolves. We used time series estimates of abundance for wolves in Montana from 2007-2018 to compare to predictions from competing models of wolf population dynamics using Bayesian model weight updating. We found that the model that explicitly incorporated social structure and also included additive harvest mortality and density dependent recruitment best predicted the observed estimates of abundance. We were able to detect similar evidence for additive harvest mortality and density dependent recruitment with simpler models. We found support for the hypotheses that harvest mortality is additive in wolves and that recruitment is density dependent. Our results suggest that explicit consideration for social structure will be key to predicting changes in wolf populations,

however simpler models can be useful to determine patterns in dynamics of wolf populations (e.g., density dependent recruitment).

INTRODUCTION

Dynamics of social, group-living species are complex because the population is hierarchically structured. The population consists of groups, which themselves consists of individuals. Thus, dynamics of a group-living species depends on group formation and persistence, which, in turn, partially depends on survival, recruitment, and dispersal of individuals within groups. For example, in meerkats (*Suricata surricatta*) larger groups produce more dispersers than smaller groups and increase group formation rates, which increases population growth rates (Bateman et al. 2018). Small meerkat groups, however, have greater per capita recruitment and growth rates than larger groups (Bateman et al. 2018). Growth rates in populations with hierarchical demography (Al-Khafaji et al. 2009) can differ due to differences in survival and recruitment of individuals or due to differences in group formation or persistence. Ignoring hierarchical demography in group-living species could bias estimates of population trends (Brault and Caswell 1993) and factors driving population dynamics (Bateman et al. 2011).

Gray wolves (*Canis lupus*) are an example of a group-living species with complex population dynamics. Wolves form family-based groups called packs that generally consist of a breeding pair, non-breeding adults from past litters, and pups (Mech and Boitani 2003). Dynamics of wolf populations therefore depend on hierarchical demography because populations are structured into packs. Within a pack, typically only the breeding pair reproduces (but see Ausband 2018), and reproduction is suppressed in other, sexually mature, adults (Packard 2003). Juveniles reach sexual maturity between one and three years of age, and typically disperse from their natal pack within three years (Mech and Boitani 2003; Packard 2003; Jimenez et al. 2017).

Wolves that dispersed from their natal pack will either find a mate and form a new pack or join an existing pack (Fuller et al. 2003; Jimenez et al. 2017). Pack formation thus depends on dispersal. Similarly, pack persistence depends on dynamics within a pack. Loss of the breeding male or female can lead to pack dissolution (Brainerd et al. 2008; Borg et al. 2015). Understanding hierarchical demography may be important to estimate dynamics in wolf populations, and failure to account for it may result in misinformed management decisions.

Wolves in the northern Rocky Mountains (NRM) have been harvested consistently since 2011 in parts of their range, and a better understanding of the effects of regulated public harvest and the influence of recruitment on wolf population dynamics is needed. Previous analyses of mortality rates of wolves in the NRM found conflicting results of partial compensation, additivity, and super-additivity of human-caused mortality (Creel and Rotella 2010; Murray et al. 2010; Horne et al. 2019); however, a majority of these studies took place prior to regulated harvest of wolves. Prior to regulated harvest, lethal removal of wolves for livestock depredation (control removals) was a main source of human-caused mortality (Murray et al. 2010; Inman et al. 2019). Control removals likely have a different effect than non-targeted harvest on dynamics of wolf populations, behavior, and social structure (Haber 1996; Webb et al. 2011). Since harvest was implemented, there has been few studies evaluating whether harvest mortality was an additive or compensatory source of mortality. However, harvest was found to be an additive source of mortality for pups (Ausband et al. 2015, 2017) in Idaho following implantation of regulated harvest. Whether harvest mortality is additive or compensatory can influence the level of harvest a population can sustain, and a better understanding of how regulated harvest mortality influences the population is needed. Variation in recruitment can also influence the level of harvest mortality a wolf population could sustain (Creel and Rotella 2010; Gude et al.

2012). Prior studies in Montana also found evidence of density dependent recruitment (Gude et al. 2012, Chapter 2). Therefore, understanding how harvest mortality and recruitment influences dynamics of wolf populations will be important for harvest management.

Population models are a useful tool to inform management decisions by evaluating the effects of alternative actions (Starfield 1997; Haight et al. 2002; Stringham and Robinson 2015). Population models range from simple models that describe patterns (i.e., phenomenological), to more complex models that consider the mechanisms (e.g., birth or survival) and structure of the population (e.g., stage-structured matrix models; Lefkovitch 1965). Phenomenological models sometimes fail to accurately describe dynamics (Clutton–Brock and Coulson 2002; Bateman et al. 2011), however the models can describe patterns in population size well (Lande et al. 2002). Although more complex models may better capture dynamics of structured populations (Brault and Caswell 1993; Coulson et al. 2001), the models require data or estimates of the demographic rates that may be difficult to obtain (Gimenez et al. 2012). It is therefore necessary to balance the complexity needed to accurately describe the dynamics of the population with the availability of empirical data or estimates of demographic rates. This can be particularly challenging for group-living species because of their hierarchical demography. Wolves are elusive and occur at low densities (Fuller et al. 2003), and it can be difficult to collect data for all the demographic rates (e.g., dispersal, group formation, or recruitment). Consequently, although simple models that match the available data may be better suited to project wolf populations, models that fail to account for hierarchical demography may perform poorly.

Our objective was to evaluate the role of hierarchical demography, harvest mortality, and recruitment in wolf population dynamics. We compared a candidate set of models to describe population dynamics in wolves, and tested for evidence of additive or compensatory harvest mortality and density dependent recruitment. Further, we evaluated whether simple per capita models or more complex models that account for hierarchical demography were able to accurately predict wolf population dynamics. The candidate set of models varied in population structure, density dependent recruitment, and the effect of harvest mortality on survival. We compared each model to estimates of abundance for wolves in Montana from 2007-2018 using Bayesian model weight updating (McGowan 2015) to determine which hypotheses (i.e., models) of wolf population dynamics had most support. Because survival of adult wolves in absence of harvest is high (Fuller et al. 2003; Stenglein et al. 2015*b*), we hypothesized that harvest was an additive source of mortality for wolves in Montana. Conversely, because the wolf population in Montana is larger than during previous studies and thus had greater capacity for compensation, we hypothesized harvest may be a compensatory source of mortality. In addition to the effects of harvest on totally mortality, we evaluated the role of density dependent recruitment. Because previous research supports density dependent recruitment, we hypothesized that recruitment was density dependent and expected models with density dependent recruitment to gain more support than those without.

METHODS

Candidate Population Models

Our candidate model set included 10 models of wolf population dynamics ranging from simple (no structure) to more complex (hierarchical demography; Table 4.1). The first two models did not include population structure and were more phenomenological. The first model was the geometric growth model, and population growth rate was density independent. This represents the simplest model structure with only one parameter, population growth rate (λ). The second model was the discrete-time logistic growth model (i.e., Ricker model; Ricker 1954). This model structure allowed population growth rate to decrease linearly with population size, and had two parameters including carrying capacity (K) and maximum growth rate (r_0). We considered theta-logistic growth that allowed population rate to decrease non-linearly with population size, however these models are difficult to fit without perfect data and unexplained environmental stochasticity (Clark et al. 2010).

The next four models were per capita models where population size changed based on survival and recruitment as

$$N_{t+1} \sim Binomial(N_t, \phi_t) + Poisson(N_t \rho_t),$$

where ϕ_t was survival rate and ρ_t was per capita recruitment rate in year t. We included density dependent recruitment and additive and compensatory harvest mortality in two models each. Therefore, we had density dependent and independent recruitment each with additive and compensatory harvest mortality. We modeled density dependent recruitment rate as a linear relationship with abundance as

$$\rho_t = \exp(\rho max_t + \alpha_1 N_{t-1})$$

where ρmax_t was the maximum recruitment rate in absence of density dependence and α_1 was the slope of the effect of density on recruitment on the log scale. Although a quadratic relationship between recruitment and density representing an Allee effect has been reported (Stenglein et al. 2015*b*; Stenglein and Van Deelen 2016), we did not expect recruitment to first increase with abundance because the wolf population in Montana was already well established by 2007. We used a mean recruitment rate ($\rho mean_t$) for density independent recruitment. We modeled additive or compensatory harvest mortality as a function of non-harvest survival rate (S_t), harvest rate (hr_t), and a slope coefficient (β):

$$\phi_t = S_t(1 - \beta hr_t).$$

When $\beta = 1$, harvest mortality was additive, and when $\beta < 1$ harvest mortality was partially compensatory. Harvest mortality could only compensate up to the level of non-harvest mortality (i.e., $(1 - S_t)$); therefore after this threshold we modeled all harvest mortality as additive.

The last four models explicitly incorporated hierarchical demography. These models were based on those presented in Chapters 1 and 2, where we explicitly accounted for the hierarchical demography of wolf populations by modeling the processes that occur within packs (i.e., recruitment of pups, and dispersal, immigration, and survival of individuals) and the processes that occur among packs (i.e., pack formation and persistence). We adjusted the models presented in Chapters 1 and 2 to model the number of wolves in packs as well as lone wolves.

We modeled changes in pack size as a function of survival (ϕ_t), dispersal (δ_t), immigration/adoption of unrelated adults (ε_t), and number of pups recruited per pack (γ_t) as

$$G_{t+1,g} \sim Binomial\big(G_{tg}, \phi_t(1 - \delta_t)\big) + Poisson(\gamma_t) + Binomial(D_t, \varepsilon_t),$$

where D_t was the number of lone wolves and G_{tg} was the number of individuals in pack g and year t. We modeled immigration rate into the pack (ε_t) by multiplying the probability that dispersal was successful (Pe_t), the proportion of successful dispersers that did not form a new pack $(1 - f_t)$, and the probability a wolf was adopted into that specific pack $(1/Z_t)$, where Z_t was the number of packs in year t. We modeled the lone wolves using binomial distributions as

$$D_{t+1} \sim Binomial\big(G_{tg}, \phi_t \delta_t\big) + Binomial(D_t, \omega_t),$$

where $\phi_{D,t}$ was survival rate of lone wolves and ω_t was immigration into the population. Lone wolves that survived but were unsuccessful at joining or forming a pack were regarded as emigrants having left the population. We modeled the number of new packs that formed (F_t) as a function of the probability that dispersal was successful (Pe_t), the proportion of successful dispersers that formed a new pack (f_t), and survival of lone wolves ($\phi_{D,t}$) as a binomial random variable with the number of lone wolves as the number of trials:

$$\eta.F_t \sim Binomial(D_{t-1}, \phi_{D,t-1} Pe_{t-1} f_{t-1}),$$

$$F_t = \frac{\eta.F_t}{2}.$$

We divided by two because a pair of wolves was needed to form a new pack. For simplicity, we assumed that packs with less than two individuals would not persist, and also included random pack persistence (ψ_t) modeled using a binomial distribution. The number of packs in the population was then

$$\eta.Z_t \sim Binomial(Z_{t-1}, \psi_{t-1}),$$

$$Z_t = F_t + \eta.Z_t.$$

Similar to the per capita models, we included density dependent recruitment in two of the models, and additive and compensatory harvest mortality in two models each. We modeled density dependence in recruitment and additive or compensatory harvest mortality as detailed above.

Model Fitting and Parameterization

For parameter values, we either fitted the models to data from wolves in Montana, used estimates of the parameters from Chapter 2, or used estimates from the literature. We fitted the geometric growth model and the logistic growth model to abundance estimates of wolves in Montana (Inman et al. 2019) to get parameter values for those models. We transformed both equations to the log scale, and provided abundance estimates on the log scale for model fitting. We followed the model fitting procedure outlined in Pedersen et al. (2011) for both models. Further, to help inform the parameters of interest for the logistic model, we regressed the log-transformed observed population growth rate (i.e., $r_{OBS} = \log(N_{t+1}/N_t)$) against N_t, which allows K and r_0

to be estimated (Sibly et al. 2005). We used non-informative priors and ran the model in program JAGS v4.2.0 (Plummer 2003) via the R2jags package (Su and Yajima 2015) in R v3.6.1 (R Core Team 2017). See Supplementary Material 4.A for code to fit the models. We ran three chains for 500,000 iterations with 100,000 burn-in to estimate the posterior distribution of the parameter values. We used the median estimate and standard deviation in a normal distribution to incorporate parametric uncertainty.

We used survival and recruitment rates for wolves in Montana (Chapter 2; Smith et al. 2010) and the literature as the parameter values for the per capita and hierarchical demography models (Table 4.2). For non-harvest survival rates for wolves in packs, we used the mean and variance of estimates of survival for years without harvest (mean = 0.73, variance = 0.003; Chapter 2; Smith et al. 2010). We incorporated environmental stochasticity by drawing annual survival rates from a beta distribution, and calculated alpha and beta shape parameters based on the mean and variance of survival using the method of moments. Lone wolves appear to have lower survival rates than those in packs (Peterson et al. 1984; Chapron et al. 2003). Jimenez et al. (2017) found that of the 297 wolves that dispersed during their study, 166 (56%) survived dispersal. Because we were uncertain of the survival rate for lone wolves, we drew a mean survival rate from a uniform distribution (0.45 – 0.65) for each iteration that was then used as the mean estimate for a beta distribution (with a variance of 0.003) to draw annual survival rates. Therefore, we included parametric uncertainty for survival of lone wolves similarly to steps outlined by McGowan et al. (2011). We estimated annual survival rates for the per capita models as a weighted average (with 12.5% of weight for survival of lone wolves) of the annual survival rates for wolves in packs and dispersed wolves for each iteration. We used 12.5% because that is the assumed percentage of lone wolves (Inman et al. 2019). We drew the slope coefficient for the effect of additive or compensatory harvest mortality from a uniform distribution set to 0.5-0.99 for compensatory harvest mortality to incorporate parametric uncertainty with a mean near the slope coefficient reported by Murray et al. (2010). When harvest mortality was additive, we set the slope coefficient to one.

We used the mean estimates of recruitment for years with (1.5 pups per pack) and without harvest (2.6 pups per pack; Chapter 2), and incorporated environmental stochasticity by drawing annual recruitment from a Poisson distribution. For density dependent recruitment, we used the coefficient values for the maximum recruitment rate and the slope of the effect of density on recruitment found in Chapter 2 (Table 4.2). We included uncertainty by drawing annual coefficient values from a normal distribution based on the mean and standard deviation.

We used the literature to set the parameter values for movement and pack persistence rates (Table 4.2). We accounted for parametric uncertainty for all movement and persistence parameters by drawing a mean value for each iteration from a uniform distribution. We used that mean value and a coefficient of variation of 20% to calculate the shape parameters for a beta distribution to draw annual rates from. For dispersal probability we used a range of 0.10 to 0.30 (Fuller et al. 2003; Marescot et al. 2012; Jimenez et al. 2017; Horne et al. 2019). We used a range of 0.85 to 0.99 for the probability that dispersal was successful given the wolf survived, and 0.45 to 0.75 for the proportion of successful dispersers that form a new pack (Adams et al. 2008; Jimenez et al. 2017). Jimenez et al. (2017) found that of the 166 wolves that survived dispersal, all of them either formed a new pack (58%) or joined an existing pack (42%). Similarly, Adams et al. (2008) found that most dispersers that survived were successful at establishing a new pack (75%). Therefore, we assumed that if a wolf survived dispersal it would most likely be successful in either forming or joining a pack. Although immigration into a population is thought to be an infrequent occurrence (Adams et al. 2008; Bassing et al. 2020), studies have suggested that immigration may be important for harvested populations where territories may become vacant (Ballard et al. 1987; Hayes and Harestad 2000; Larivière et al. 2000). However, immigration into the population is difficult to estimate, and most studies assume immigration is negligible (e.g., Chapron et al. 2003; Marescot et al. 2012; Stenglein et al. 2015; Horne et al. 2019). The proportion of long-distance immigrants (i.e., immigrants from outside of the study area) into existing packs was 0.01 – 0.02 in a study in Idaho (Bassing et al. 2020). This included immigration into the population and adoption into an existing pack. Immigrants into the population may also form new packs (Hayes and Harestad 2000). Therefore, immigration into the population may be greater than rates reported by Bassing et al. (2020). Hayes and Harestad (2000) found a mean of 0.07 wolves annually were part of a colonizing pack (i.e., had immigrated from outside the study area). Therefore, we used a range of 0.01 to 0.1. Pack persistence in a harvested population in Alberta was high, with only one documented full pack turnover (Bassing et al. 2019). Other studies have documented pack dissolution rates of 0 – 35% (Brainerd et al. 2008; Borg et al. 2015). Because we already assumed all packs with < 2 wolves dissolved, we included an additional pack dissolution rate of 0 – 25%. Therefore, pack persistence ranged from 0.75 – 1.00.

We set the initial population size for each of the models to the estimate of abundance for wolves in Montana for 2007 (Inman et al. 2019). For the hierarchical demography models, we set the number of lone wolves to 12.5% of the total population, which is an average of the documented proportion of the population that was considered lone wolves (Fuller et al. 2003; Inman et al. 2019). The remaining wolves were divided into the estimated number of packs in Montana for 2007, with a mean pack size of seven wolves (Inman et al. 2019). We used reported total harvest and estimates of abundance from Montana Fish, Wildlife and Parks (MFWP) to determine annual harvest rates (Inman et al. 2019; fwp.mt.gov)

Bayesian Model Weight Updating

We used the predicted population size from the 10 models to compare with observed estimates of abundance for each year from 2007-2018. Estimates of abundance were from monitoring data collected by Montana Fish, Wildlife and Parks (Inman et al. 2019). We projected the wolf population under each model for 12 years, and we replicated each model projection for 10000 iterations. Similarly to Robinson et al. (2017), we projected the models in parallel to limit the effects of stochasticity so the models were directly comparable. Therefore, each parameter drawn from the statistical distribution for each year and iteration was used for all models for that year and iteration.

We assigned weights to the 10 population models based on how well each predicted annual abundance of wolves (McGowan 2015; Robinson et al. 2017). Each model was assigned equal weight for the initial time-step, and model weights in subsequent time-steps were updated using Bayes' theorem such that

$$P(model_i|data_{t+1}) = \frac{P(model_i)P(data_{t+1}|model_i)}{\sum_i P(model_i)P(data_{t+1}|model_i)},$$

where $P(model_i|data_{t+1})$ was the posterior model probability or the weight for model i in year $t+1$, $P(model_i)$ was the prior model probability for model i, and $P(data_{t+1}|model_i)$ was the normal likelihood of the observed abundance estimates given model i. We resampled the observed data (i.e., abundance estimates) 1000 times for each time-step and iteration by sampling the observed data from a normal distribution using the mean and standard deviation to account for error in estimates of abundance (Robinson et al. 2017). Therefore, each model had 12 years of evolving model weights for each of the 10000 iterations and 1000 data resampling runs. We took the mean model weight for each iteration and resampling run to get the annual weight for each model. Population projection and Bayesian model weight updating were implemented in program R v.3.6.1 (R Core Team 2017).

RESULTS

Both the geometric and logistic growth models converged with Gelman-Rubin statistics of <1.01 and had good mixing of chains upon visual inspection indicating that models converged. For geometric growth, we found that λ was estimated as 1.03 (1.019 – 1.063 95% CRI). For logistic growth, we estimated the maximum intrinsic growth rate to be 0.50 (0.123 – 0.773 95% CRI), which expressed as λ was approximately 1.65. Last, we estimated the median carrying capacity to be 915 (mean = 1000; 830 – 2238 95% CRI).

Mean population trajectories varied across models (Figure 4.1). We found that geometric growth in the wolf population resulted in a 60% increase in population size, with the final population size in 2018 projected to be 1007 wolves (Figure 4.1A). Under logistic growth, the projected size of the wolf population increased by 69% over 12 years (Figure 4.1B). The per capita model with partially compensatory mortality and density independent recruitment was projected to have the greatest population size with a mean population trajectory increasing by 167% (Figure 4.1C). Conversely, under the per capita model with density dependent recruitment and additive harvest mortality the population trajectory increased by 44% after 12 years and was more similar to observed abundance (Figure 4.1C). Models that included hierarchical demography had similar patterns to the per capita models, however population trajectories were more similar to observed estimates of abundance for all model types (Figure 4.1D).

Model weights varied over time for the 10 competing models (Figure 4.2). Weight for the geometric growth model declined to <1% by 2009 (Figure 4.2A). We found that the weight for the logistic model initially fluctuated around 10% and then decreased to a final model weight of <1% by 2018 (Figure 4.2B). We found that model weights for all per capita models decreased over time (Figure 4.2C). The per capita model with most weight by 2018 was the density dependent recruitment with additive harvest mortality at a weight of 0.006% (Figure 4.2C). Weight for the models with hierarchical demography and density dependent recruitment were relatively stationary at first and then gained support (Figure 4.2D). By 2018, the hierarchical demography models with density dependent recruitment had the most weight, with 56% and 40% for additive and compensatory harvest mortality, respectively (Figure 4.2D). When we considered only the per capita models and the models of hierarchical demography, we found support for density dependent recruitment (Figure 4.3A) with 97% weight. We also found support for additive harvest mortality, but with only 58% weight (Figure 4.3B). In general, models that explicitly included hierarchical demography had greater weight than the per capita models with similar structure for survival and recruitment (Figure 4.2).

DISCUSSION

We evaluated the role of harvest mortality, density dependent recruitment, and hierarchical demography in wolf population dynamics by comparing predicted population size under different models to observed estimates of abundance. We found that the population model that best fits observed estimates of abundance included hierarchical demography, density dependent recruitment, and additive harvest mortality. We found evidence that harvest was an additive source of mortality. We also found support for models with density dependent recruitment. Last, we found more support for models that included hierarchical demography than per capita models.

We found some support for our hypothesis that harvest is an additive source of mortality. While not fully conclusive, these results are consistent with results from Idaho during the same time period (Horne et al. 2019). Survival of adult and yearling wolves is quite high in absence of harvest (Stenglein et al. 2015*b*), and leaves little ability for harvest mortality to be compensated for through decreased natural mortality. Contrary to our findings, other studies have found evidence of partial compensation of harvest mortality (Murray et al. 2010; Stenglein et al. 2018). In theory, the potential for compensation is greater for populations near carrying capacity (Sinclair and Pech 1996; Péron 2013). Stenglein et al. (2018) found partial compensation in mortality sources in later years of wolf recovery as the population grew, which supports this theory. However, estimates of human-caused mortality rates from (Stenglein et al. 2018) were lower than estimates of reported harvest rates from our study (0.114 – 0.176 and 0.17 – 0.36, respectively). Therefore, it is likely that a greater portion of harvest mortality in our study would be additive even if compensation were occurring. Compensation can only occur up to a certain threshold, i.e. the level of non-harvest mortality, and after the threshold harvest mortality is additive (Mills 2013). Mortality during years without harvest was 0.27 (adult survival was 0.73; Chapter 2), whereas harvest rates in Montana ranged from 0.17 to 0.36 from 2011-2018. Therefore, when harvest mortality exceeded 0.27 a portion of the mortality would be additive. When harvest mortality is additive, survival rate can be altered through changes in harvest rate. Additionally, survival of adult wolves had a greater effect on population growth rate than recruitment of pups to 17 months of age in Montana (Chapter 2), therefore this suggest that harvest can be an effective tool for managing wolf populations in Montana.

We did not find support for our hypothesis that harvest mortality was compensatory. We used a uniform distribution between 0.5 and 0.99, therefore our mean estimate was 0.75. It may be that a model of compensatory harvest mortality with a greater slope coefficient would have better predicted observed abundance than a model with a lower slope coefficient, and may have been more similar or better than models with additive harvest mortality. Evaluation of additive or compensatory harvest mortality could be greatly improved with additional years of monitoring data (i.e., abundance estimates) and further Bayesian model weight updating, and perhaps with additional models with a greater slope coefficient estimate for compensatory harvest mortality. Uncertainty in the slope coefficient estimate could be reduced in an adaptive management framework.

We found support for our hypothesis that recruitment in wolves was density dependent. All models with density dependent recruitment had greater model weight than density independent models (Figure 4.3A). This result was somewhat expected because in Chapter 2 we found a negative correlation between population size and recruitment empirically for wolves in Montana from 2007-2018. However, this finding demonstrates the utility of using Bayesian model weight updating to show support for one hypothesis over another (i.e., density dependent over independent recruitment) because our results using model weights also supports the hypothesis that recruitment is density dependent. Our results suggest that wolves in Montana may have saturated the available habitat and reached some carrying capacity (Oakleaf et al. 2006; Gude et al. 2012; Chapter 2). This carrying capacity could be due to per capita food availability (Boertje and Stephenson 1992; Sidorovich et al. 2007), intraspecific aggression and conflict among packs (Cubaynes et al. 2014), or human tolerance (Murray et al. 2010). Our estimated carrying capacity for wolves in Montana (mean = 1000 wolves) was greater than that for Wisconsin (650 wolves), yet lower than the estimated carrying capacity for the whole southern Lake Superior population (1321 wolves; Wydeven et al. 2009). In simulations of an unharvested population, Stenglein et al. (2015*a*) found the carrying capacity for wolves in Wisconsin was 1242. Our estimated carrying capacity may also be lower than expected in absence of human-caused mortality. Thus, our carrying capacity may represent a socially mediated (i.e., human tolerance) threshold where wolves have saturated prime habitat and expanded into marginal habitat with more human activity and greater risk of mortality from humans (Murray et al. 2010; Stenglein et al. 2018).

Our results suggest that accounting for hierarchical demography is important for predicting dynamics of wolf populations, however both types of models can similarly detect density dependence and additive vs compensatory harvest mortality. All models that incorporated hierarchical demography had greater weights than per capita models, suggesting that they better predicted changes in the wolf population over time. Per capita recruitment rates can easily over- or underestimate recruitment in wolf populations because wolves are social and the pack is the reproductive unit (Fuller et al. 2003). Wolf populations can increase due to either an increase in the number of packs, the number of individuals in a pack, or both. How abundance changes can have different effects on demographic rates and future population size. Although models that included hierarchical demography had greater weights, we were able to draw the same conclusions from both model types. Both per capita models and models of hierarchical demography suggest that recruitment is density dependent and that harvest is an additive source of mortality. Under both model types, the models with density dependent recruitment and additive harvest mortality had greater weight. Therefore, the best type of modeling framework to adopt depends on the objectives of the study and the data available. Both per capita and hierarchical demography models were sufficient for understanding patterns, however the hierarchical demography models better predicted dynamics. Our models that included hierarchical demography, however, required more than twice the number of parameters (Table 4.1) than per capita models, and these parameters values would likely be more difficult to collect (e.g., pack formation rates). Although we were able to use information from the literature and incorporate parametric uncertainty, projected population trends would have likely improved if we were able to obtain more accurate estimates from our population.

Our analysis relied on several important assumptions. First, we assumed that the estimates of abundance we used as observed data were unbiased. The abundance estimates for wolves in Montana hinge on the assumption of average territory size (Glen et al. 2011; Rich et al. 2013; Inman et al. 2019; Sells 2019). MFWP first estimates area occupied by wolves using a dynamic, false-positive occupancy model (Miller et al. 2013; Rich et al. 2013; Inman et al. 2019). They then divide by average territory size to calculate how many packs fit in the area occupied, and then multiple by average pack size (Rich et al. 2013; Inman et al. 2019). Territory size, however, is quite variable and following harvest implementation the average territory size used to estimate abundance may be inaccurate (Sells 2019). Therefore, estimates of abundance may be biased. We did, however, account for uncertainty in estimates of abundance by resampling the data. Although our estimated population dynamics may still be accurate if all the estimates of abundance were systematically biased, our estimated carrying capacity would be biased. All individuals except pups had the same demographic rates and could not be differentiated. Dispersal rates likely differ by age class and sex (Fuller et al. 2003; Jimenez et al. 2017). Some studies found survival differed by age class (Marucco et al. 2009; Smith et al. 2010) whereas others found no difference (Wydeven et al. 2009; Cubaynes et al. 2014). Undoubtedly, it would be more realistic to consider demographic rates that varied by age. However, we compared predictions of population size from the models to reported estimates of abundance that did not differentiate by age or sex. Therefore, we did not differentiate individuals by age or sex. This also served to limit the number of parameters in the models. For the per capita models we assumed that immigration and emigration summed to zero and were not included. Many studies assumed that immigration and emigration sum to zero (Schmidt et al. 2015; Stenglein et al. 2015*b*; Horne et al. 2019) or that different ages classes had equal demographic rates (Chapron et al. 2003; Schmidt et al. 2015; Stenglein et al. 2015*b*; Horne et al. 2019). Last, we assumed that dispersal and survival rates were density independent. Dispersal from a pack may increase with pack size, and may decrease with surrounding pack density (Jimenez et al. 2017). Additionally, survival of adults may decrease with density, either due to increased intraspecific aggression (Cubaynes et al. 2014) or more wolves being located near human activity (Murray et al. 2010; Stenglein et al. 2018). Density dependence in survival or dispersal could be accounted for similar to density dependence in recruitment.

MANAGEMENT IMPLICATIONS

Results from this analysis can be used in an adaptive harvest management plan for wolves to predict effects of harvest on the wolf population. In an adaptive management framework, multiple models can be used to generate predictions weighted by the model support to determine optimal management strategies that best meet objectives (Williams et al. 2002, 2009; Conroy and Peterson 2013). Over time, monitoring data are used to compare how the population responds to management with predictions from the competing models to update model weights with Bayes' theorem (Williams et al. 2002; Conroy and Peterson 2013) as we did in this analysis. It may be prudent to include models of high and low rates of immigration to understand its role in wolf population dynamics. This type of analysis can be used to evaluate the effects of different harvest rates under multiple hypotheses of wolf population dynamics. Bayesian model weight updating can be a useful tool to evaluate competing hypotheses for any species with time series count data and could be an alternative to traditional model selection methods (e.g., Akaike information criterion or Watanabe-Akaike information criterion; Burnham and Anderson 2002; Vehtari et al. 2017).

LITERATURE CITED

Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. Wildlife Monographs 170:1–25.

Al-Khafaji, K., S. Tuljapurkar, J. R. Carey, and R. E. Page. 2009. Hierarchical demography: a general approach with an application to honey bees. Ecology 90:556–566.

Ausband, D. E. 2018. Multiple breeding individuals within groups in a social carnivore. Journal of Mammalogy 99:836–844.

Ausband, D. E., M. S. Mitchell, C. R. Stansbury, J. L. Stenglein, and L. P. Waits. 2017. Harvest and group effects on pup survival in a cooperative breeder. Proceedings of the Royal Society of London B: Biological Sciences 284:20170580.

Ausband, D. E., C. R. Stansbury, J. L. Stenglein, J. L. Struthers, and L. P. Waits. 2015. Recruitment in a social carnivore before and after harvest. Animal Conservation 18:415–423.

Ballard, W. B., J. S. Whitman, and C. L. Gardner. 1987. Ecology of an exploited wolf population in south-central Alaska. Wildlife Monographs 98:3–54.

Bassing, S. B., D. E. Ausband, M. S. Mitchell, P. Lukacs, A. C. Keever, G. Hale, and L. Waits. 2019. Stable pack abundance and distribution in a harvested wolf population. The Journal of Wildlife Management 83:577–590.

Bassing, S. B., D. E. Ausband, M. S. Mitchell, M. K. Schwartz, J. J. Nowak, G. C. Hale, and L. P. Waits. 2020. Immigration does not offset harvest mortality in groups of a cooperatively breeding carnivore. Animal Conservation acv.12593.

Bateman, A. W., T. Coulson, and T. H. Clutton-Brock. 2011. What do simple models reveal about the population dynamics of a cooperatively breeding species? Oikos 120:787–794.

Bateman, A. W., A. Ozgul, M. Krkošek, and T. H. Clutton-Brock. 2018. Matrix models of hierarchical demography: linking group- and population-level dynamics in cooperative breeders. The American Naturalist 192:188–203.

Boertje, R. D., and R. O. Stephenson. 1992. Effects of ungulate availability on wolf reproductive potential in Alaska. Canadian Journal of Zoology 70:2441–2443.

Borg, B. L., S. M. Brainerd, T. J. Meier, and L. R. Prugh. 2015. Impacts of breeder loss on social structure, reproduction and population growth in a social canid. The Journal of Animal Ecology 84:177–187.

Brainerd, S. M., H. Andrén, E. E. Bangs, E. H. Bradley, J. A. Fontaine, W. Hall, Y. Iliopoulos, M. D. Jimenez, E. A. Jozwiak, O. Liberg, C. M. Mack, T. J. Meier, C. C. Niemeyer, H. C. Pedersen, H. Sand, R. N. Schultz, D. W. Smith, P. Wabakken, and A. P. Wydeven. 2008. The effects of breeder loss on wolves. Journal of Wildlife Management 72:89–98.

Brault, S., and H. Caswell. 1993. Pod-specific demography of killer whales (Orcinus Orca). Ecology 74:1444–1454.

Burnham, K. P., and D. R. Anderson. 2002. Model selection and multimodel inference: a practical information-theoretic approach. 2nd edition. Springer-Verlag, New York, New York.

Chapron, G., S. Legendre, R. Ferrière, J. Clobert, and R. G. Haight. 2003. Conservation and control strategies for the wolf (Canis lupus) in western Europe based on demographic models. Comptes Rendus Biologies 326:575–587.

Clark, F., B. W. Brook, S. Delean, H. Reşit Akçakaya, and C. J. A. Bradshaw. 2010. The theta-logistic is unreliable for modelling most census data. Methods in Ecology and Evolution 1:253–262.

Clutton–Brock, T. H., and T. Coulson. 2002. Comparative ungulate dynamics: the devil is in the detail. Philosophical Transactions of the Royal Society of London. Series B: Biological Sciences 357:1285–1298.

Conroy, M. J., and J. T. Peterson. 2013. Decision making in natural resource management: a structured, adaptive approach. John Wiley & Sons.

Coulson, T., E. A. Catchpole, S. D. Albon, B. J. Morgan, J. M. Pemberton, T. H. Clutton-Brock, M. J. Crawley, and B. T. Grenfell. 2001. Age, sex, density, winter weather, and population crashes in Soay sheep. Science 292:1528–1531.

Creel, S., and J. J. Rotella. 2010. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (Canis lupus). PloS one 5:e12918.

Cubaynes, S., D. R. MacNulty, D. R. Stahler, K. A. Quimby, D. W. Smith, and T. Coulson. 2014. Density-dependent intraspecific aggression regulates survival in northern Yellowstone wolves (Canis lupus). The Journal of Animal Ecology 83:1344–1356.

Fuller, T. K., L. D. Mech, and J. Fitts-Cochran. 2003. Wolf population dynamics. Pages 161–191 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. University of Chicago Press, Chicago, Illinois.

Gimenez, O., J.-D. Lebreton, J.-M. Gaillard, R. Choquet, and R. Pradel. 2012. Estimating demographic parameters using hidden process dynamic models. Theoretical Population Biology 82:307–316.

Glen, E. S., L. N. Rich, and M. S. Mitchell. 2011. Estimating numbers of wolves, wolf packs, and breeding pairs in Montana using hunter survey data in patch occupancy model framework: final report. Helena, MT.

Gude, J. A., M. S. Mitchell, R. E. Russell, C. A. Sime, E. E. Bangs, L. D. Mech, and R. R. Ream. 2012. Wolf population dynamics in the U.S. Northern Rocky Mountains are affected by recruitment and human-caused mortality. The Journal of Wildlife Management 76:108–118.

Haber, G. C. 1996. Biological, conservation, and ethical implications of exploiting and controlling wolves. Conservation Biology 10:1068–1081.

Haight, R. G., E. Travis, Laurel, K. Nimerfro, and L. D. Mech. 2002. Computer simulation of wolf-removal strategies for animal damage control. Wildlife Society Bulletin 30:844–852.

Hayes, R. D., and A. S. Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology 78:36–48.

Horne, J. S., D. E. Ausband, M. A. Hurley, J. Struthers, J. E. Berg, and K. Groth. 2019. Integrated population model to improve knowledge and management of Idaho wolves. The Journal of Wildlife Management 83:32–42.

Inman, B., K. M. Podruzny, T. D. Smucker, A. A. Nelson, M. Ross, N. Lance, T. Parks, D. K. Boyd, and S. Wells. 2019. Montana gray wolf conservation and management 2018 annual report. Helena, Montana.

Jimenez, M. D., E. E. Bangs, D. K. Boyd, D. W. Smith, S. A. Becker, D. E. Ausband, S. P. Woodruff, E. H. Bradley, J. Holyan, and K. Laudon. 2017. Wolf dispersal in the Rocky Mountains, Western United States: 1993-2008. The Journal of Wildlife Management 81:581–592.

Lande, R., S. Engen, B.-E. Saether, F. Filli, E. Matthysen, and H. Weimerskirch. 2002. Estimating density dependence from population time series using demographic theory and life-history data. The American Naturalist 159:321–337.

Larivière, S., H. Jolicoeur, and M. Crête. 2000. Status and conservation of the gray wolf (Canis lupus) in wildlife reserves of Québec. Biological Conservation 94:143–151.

Lefkovitch, L. P. 1965. The study of population growth in organisms grouped by stages. Biometrics 21:1–18.

Marescot, L., O. Gimenez, C. Duchamp, E. Marboutin, and G. Chapron. 2012. Reducing matrix population models with application to social animal species. Ecological Modelling 232:91–96.

Marucco, F., D. H. Pletscher, L. Boitani, M. K. Schwartz, K. L. Pilgrim, and J.-D. Lebreton. 2009. Wolf survival and population trend using non-invasive capture-recapture techniques in the Western Alps. Journal of Applied Ecology 46:1003–1010.

McGowan, C. P. 2015. Comparing models of red knot population dynamics. The Condor 117:494–502.

McGowan, C. P., M. C. Runge, and M. A. Larson. 2011. Incorporating parametric uncertainty into population viability analysis models. Biological Conservation 144:1400–1408.

Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1–34 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, Illinois.

Miller, D. A. W., J. D. Nichols, J. A. Gude, L. N. Rich, K. M. Podruzny, J. E. Hines, and M. S. Mitchell. 2013. Determining occurrence dynamics when false positives occur: estimating the range dynamics of wolves from public survey data. PloS one 8:e65808.

Mills, L. S. 2013. Conservation of wildlife populations: demography, genetics, and management. 2nd edition. John Wiley & Sons.

Murray, D. L., D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, T. J. Meier, D. Stahler, J. Holyan, and V. J. Asher. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation 143:2514–2524.

Oakleaf, J. K., D. L. Murray, J. R. Oakleaf, E. E. Bangs, C. M. Mack, D. W. Smith, J. A. Fontaine, M. D. Jimenez, T. J. Meier, and C. C. Niemeyer. 2006. Habitat selection by recolonizing wolves in the Northern Rocky Mountains of the United States. Journal of Wildlife Management 70:554–563.

Packard, J. M. 2003. Wolf behavior: reproductive, social, and intelligent. Pages 35–65 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, Illinois.

Pedersen, M. W., C. W. Berg, U. H. Thygesen, A. Nielsen, and H. Madsen. 2011. Estimation methods for nonlinear state-space models in ecology. Ecological Modelling 222:1394–1400.

Péron, G. 2013. Compensation and additivity of anthropogenic mortality: life-history effects and review of methods. Journal of Animal Ecology 82:408–417.

Peterson, R. O., J. D. Woolington, and T. N. Bailey. 1984. Wolves of the Kenai Peninsula, Alaska. Wildlife Monographs 88:3–52.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rich, L. N., R. E. Russell, E. M. Glenn, M. S. Mitchell, J. A. Gude, K. M. Podruzny, C. A. Sime, K. Laudon, D. E. Ausband, and J. D. Nichols. 2013. Estimating occupancy and predicting numbers of gray wolf packs in Montana using hunter surveys. The Journal of Wildlife Management 77:1280–1289.

Ricker, W. E. 1954. Stock and recruitment. Journal of the Fisheries Board of Canada 11:559–623.

Robinson, O. J., C. P. McGowan, and P. K. Devers. 2017. Disentangling density-dependent dynamics using full annual cycle models and Bayesian model weight updating. Journal of Applied Ecology 54:670–678.

Schmidt, J. H., D. S. Johnson, M. S. Lindberg, and L. G. Adams. 2015. Estimating demographic parameters using a combination of known-fate and open N-mixture models. Ecology 96:2583–2589.

Sells, S. N. 2019. Mechanisms driving territorial and social behavior in a cooperative carnivore. Graduate Student Theses, Dissertations, & Professional Papers. University of Montana, Missoula.

Sibly, R. M., D. Barker, M. C. Denham, J. Hone, and M. Pagel. 2005. On the regulation of populations of mammals, birds, fish, and insects. Science 309:607–610.

Sidorovich, V. E., V. P. Stolyarov, N. N. Vorobei, N. V Ivanova, and B. Jędrzejewska. 2007. Litter size, sex ratio, and age structure of gray wolves, Canis lupus, in relation to population fluctuations in northern Belarus. Canadian Journal of Zoology 85:295–300.

Sinclair, A. R. E., and R. P. Pech. 1996. Density dependence, stochasticity, compensation and predator regulation. Oikos 75:164–173.

Smith, D. W., E. E. Bangs, J. K. Oakleaf, C. Mack, J. Fontaine, D. Boyd, M. Jimenez, D. H. Pletscher, C. C. Niemeyer, T. J. Meier, D. R. Stahler, J. Holyan, V. J. Asher, and D. L. Murray. 2010. Survival of colonizing wolves in the Northern Rocky Mountains of the United States, 1982-2004. Journal of Wildlife Management 74:620–634.

Starfield, A. M. 1997. A pragmatic approach to modeling for wildlife management. The Journal of Wildlife Management 61:261–270.

Stenglein, J. L., and T. R. Van Deelen. 2016. Demographic and component Allee effects in Southern Lake Superior gray wolves. PloS one 11:e0150535.

Stenglein, J. L., J. H. Gilbert, A. P. Wydeven, and T. R. Van Deelen. 2015a. An individual-based model for southern Lake Superior wolves: A tool to explore the effect of human-caused mortality on a landscape of risk. Ecological Modelling 302:13–24.

Stenglein, J. L., A. P. Wydeven, and T. R. Van Deelen. 2018. Compensatory mortality in a recovering top carnivore: wolves in Wisconsin, USA (1979–2013). Oecologia 187:99–111.

Stenglein, J. L., J. Zhu, M. K. Clayton, and T. R. Van Deelen. 2015b. Are the numbers adding up? Exploiting discrepancies among complementary population models. Ecology and Evolution 5:368–376.

Stringham, O. C., and O. J. Robinson. 2015. A modeling methodology to evaluate the efficacy of predator exclosures versus predator control. Animal Conservation 18:451–460.

Su, Y.-S., and M. Yajima. 2015. R2jags: using R to run "JAGS."

Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing 27:1413–1432.

Webb, N. F., J. R. Allen, and E. H. Merrill. 2011. Demography of a harvested population of wolves (Canis lupus) in west-central Alberta, Canada. Canadian Journal of Zoology 89:744–752.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press.

Williams, B. K., R. C. Szaro, and C. D. Shapiro. 2009. Adaptive management: the U.S. Department of the Interior technical guide. Adaptive Management Working Group, U.S. Department of the Interior, Washington, DC.

Wydeven, A. P., T. R. van Deelen, and E. Heske, editors. 2009. Recovery of gray wolves in the Great Lakes region of the United States: an endangered species success story. Springer.

TABLES

Table 4.1: List of population models to project population dynamics of gray wolves in Montana from 2007-2018. Models varied in complexity and the number of parameters (K), whether or not recruitment was density dependent, and whether or not harvest mortality was additive or compensatory to total mortality. The per capita models were modeled with survival and recruitment rate. The last four models modeled the hierarchical demography (HD) of the wolf population. Recruitment was either density dependent (DD) or density independent (ND) and harvest mortality was either compensatory (C) or additive (A).

Model	K	Density dependent recruitment?	Compensatory or additive harvest mortality?
Geometric growth	1	No	NA
Logistic growth	3	Yes*	NA
Per capita model: NDC	3	No	Compensatory
Per capita model: NDA	3	No	Additive
Per capita model: DDC	4	Yes	Compensatory
Per capita model: DDA	4	Yes	Additive
HD model: NDC	8	No	Compensatory
HD model: NDA	8	No	Additive
HD model: DDC	9	Yes	Compensatory
HD model: DDA	9	Yes	Additive

*Population growth rate is assumed to be density dependent

Table 4.2: Demographic parameters used for models of gray wolf population dynamics.

Parameter	Value [a]
S – Non-harvest survival of wolves in packs	0.73
S_D – Non-harvest survival of lone wolves	0.45 – 0.65
β – Slope coefficient for compensatory harvest mortality	0.50 – 0.99
$\gamma mean$ – Mean number of pups per pack	2.6 or 1.5 [b]
γmax – Max number of pups per pack	3.1 [c]
α_γ – Slope coefficient for density dependence in pups per pack	-0.00247 [c]
$\rho mean$ – Mean per capita recruitment	0.50 or 0.42 [b]
ρmax – Max per capita recruitment	0.05 [c]
α_ρ – Slope coefficient for density dependence in per capita recruitment rate	-0.00114 [c]
Pe – Probability of successful dispersal	0.85 – 0.99
f – Proportion of successful dispersing wolves that form new pack	0.45 – 0.75
δ – Dispersal rate from pack	0.10 – 0.30
ω – Immigration rate into population	0.01 – 0.10
ψ – Pack persistence rate	0.75 – 1.00

[a] Single values represent mean parameter values whereas two values represents the range used to draw mean parameter values from.

[b] The first recruitment parameter was for years without harvest followed by the recruitment parameter for years with harvest.

[c] These values are on the log scale.

FIGURES

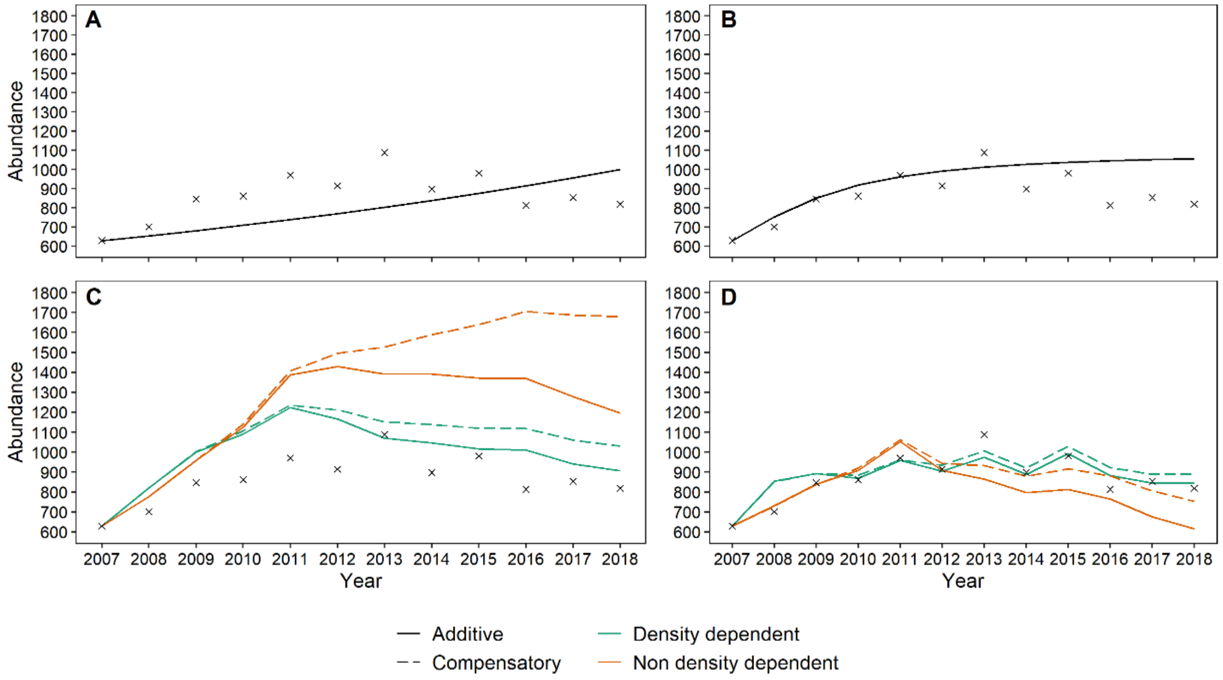

Figure 4.1: Observed estimates of abundance of wolves in Montana (X) from 2007-2018 and projected mean population size based on A) geometric growth model, B) logistic growth model, C) per capita models where harvest mortality was either additive or compensatory and recruitment was either density dependent or density independent, and D) models that included population structure and explicitly incorporated hierarchical demography where harvest mortality was either additive or compensatory and recruitment was either density dependent or density independent.

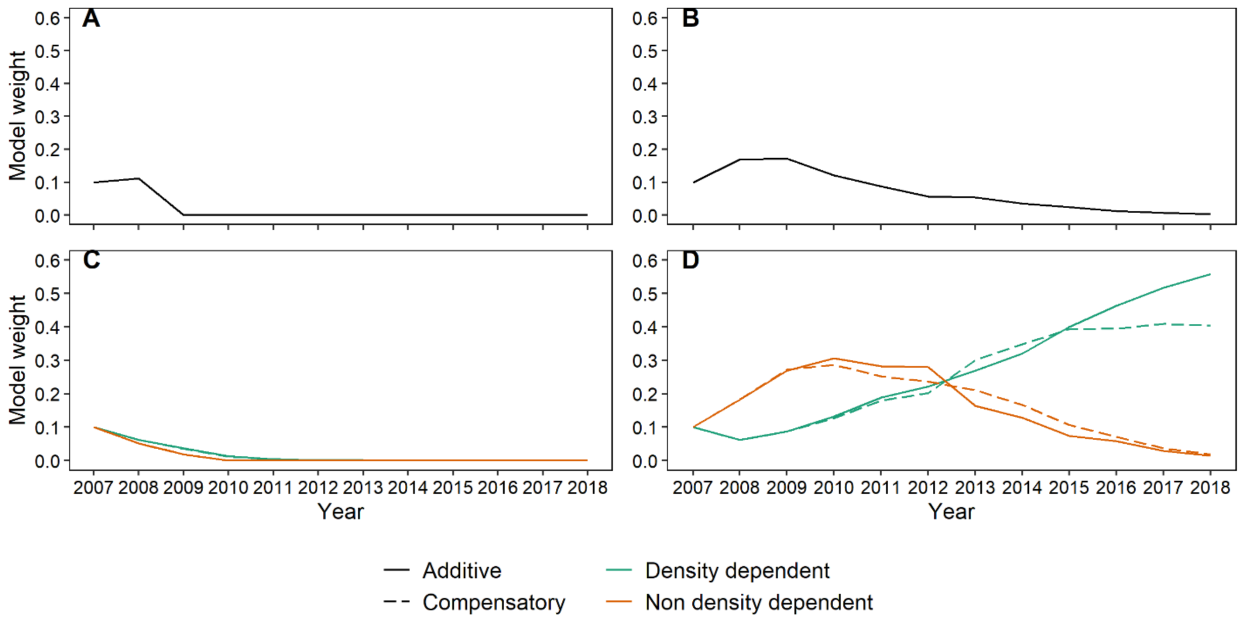

Figure 4.2: Evolving model weights of 10 competing models for population dynamics of wolves in Montana from 2007-2018. All models began with equal weight and were updated annually using Bayes' theorem. The population models included A) geometric growth model, B) logistic growth model, C) per capita models where harvest mortality was either additive or compensatory and recruitment was either density dependent or density independent, and D) models that included population structure and explicitly incorporated hierarchical demography where harvest mortality was either additive or compensatory and recruitment was either density dependent or density independent.

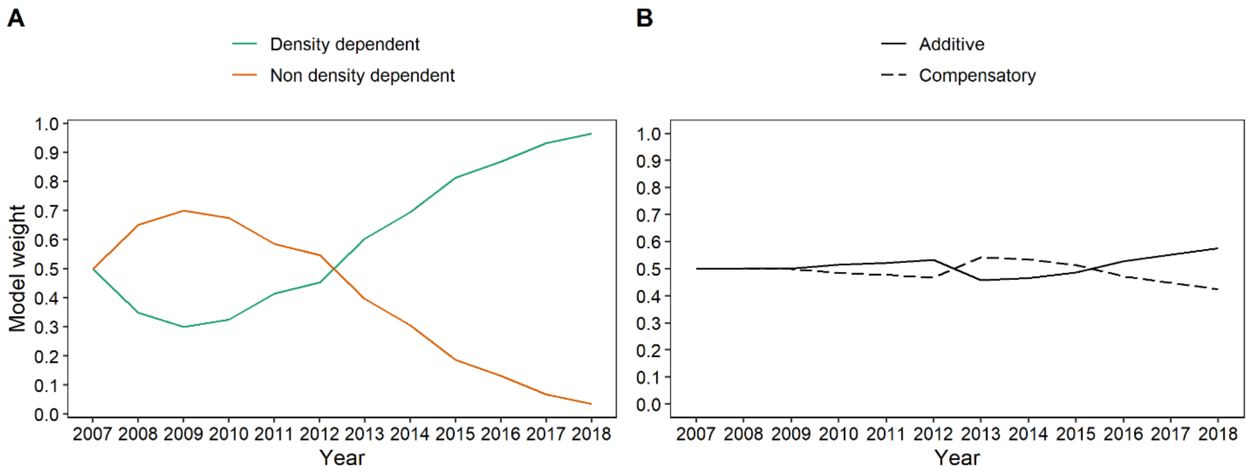

Figure 4.3: Evolving model weights for A) density dependent or independent recruitment, and B) additive or compensatory harvest mortality, based on eight competing models for population dynamics of wolves in Montana from 2007-2018. All models began with equal weight and were updated annually using Bayes' theorem. The population models included per capita models and models that included population structure and explicitly incorporated hierarchical demography where harvest mortality was either additive or compensatory and recruitment was either density dependent or density independent.

CHAPTER 5:

ADAPTIVE HARVEST MANAGEMENT OF WOLVES: INCORPORATING BIOLOGICAL AND SOCIETAL VALUES

ABSTRACT

Management of large carnivore populations with harvest is contentious, and has been criticized for failing to account for relevant uncertainty in the effects of harvest, not including socio-economic values, and not having explicit objectives. Adaptive management (AM) incorporates scientific information and associated uncertainty in a transparent process that relates alternative management actions to explicit, quantifiable objectives to guide decisions making. Through monitoring, uncertainty can be reduced over time to improve future decisions. Our objectives were to develop a flexible decision tool for wolf management that included biological and societal values in a transparent process, and to incorporate and potentially reduce uncertainty in the effects of harvest on gray wolf (*Canis lupus*) populations. We developed an AM framework to guide decisions for harvest regulations for wolves in Montana. We used stochastic dynamic programing and passive adaptive learning to determine optimal management actions, given the biological and socio-political objectives we used and uncertainty about the effects of harvest on wolf population dynamics. Specifically, using AM we tested the hypothesis that net immigration into Montana was positive and partially compensated for harvest mortality. We found the optimal management actions were 1) no harvest when the population was below 170 wolves, 2) restricted harvest (bag limit = 1, hunting season length = 4 weeks, trapping season length = 4 weeks) when the population was between 170 and 280, 3) status quo harvest (bag limit = 5, hunting season length = 28 weeks, trapping season length = 11 weeks) when the population was

between 280 and 1330, and 4) liberal harvest (bag limit = 10, hunting season length = 40 weeks, trapping season length = 17 weeks) when the population was greater than 1330 wolves. Simulations that implemented the optimal, state-dependent management actions indicated that the wolf population became relatively stable at 650 wolves. This suggests that maintaining the wolf population at this size best meets management objectives for wolves. We found no support for the hypothesis that net immigration into Montana was positive. This suggests that net immigration into Montana is zero. Further use of passive AM can continue to reduce uncertainty and refine predictive models to improve decisions for harvest regulations of wolves. In scenarios where stakeholder opinions are divisive, such as with carnivore populations that come into conflict with humans, AM can be used to include multiple, often conflicting objectives to guide management decisions in a transparent process.

INTRODUCTION

Managing populations of large carnivores can be challenging not only because of their need for large tracts of suitable habitat, but also because of conflicts with humans. Predation on livestock and competition for ungulates are the main sources of conflict between humans and large carnivores (Muhly and Musiani 2009; Laporte et al. 2010; Macdonald and Loveridge 2010; Treves et al. 2013). Livestock losses and non-lethal effects of carnivores on livestock have a negative socioeconomic impact (Muhly and Musiani 2009; Laporte et al. 2010), and disproportionately affect rural communities. Hunters may also have concerns that carnivores will negatively affect prey populations and reduce opportunities for hunting ungulates (Ericsson and Heberlein 2003). Conversely, large carnivores can generate interest and revenues due to ecotourism (Tortato et al. 2017) or positive attitudes due to perceived ecosystem services and their role in wildlife communities (Ritchie et al. 2012; Treves et al. 2013). Further, many carnivore populations are considered threated or endangered (Di Marco et al. 2014), and managing agencies are required to maintain a sustainable population. Therefore, balancing a viable carnivore population with addressing the often-divisive opinions of stakeholders regarding carnivore management can be challenging.

Management of gray wolves (*Canis lupus*) in Montana is subject to many of the challenges faced by carnivore management. The wolf population in Montana recovered from extirpation following successful natural recolonization and reintroductions into central Idaho and the Greater Yellowstone Area (Ream et al. 1989; Bangs and Fritts 1996; Bangs et al. 1998). Wolves were delisted in 2011 by congressional action (U.S. Fish and Wildlife Service 2011), and since delisting, regulated public harvest has been used to manage the wolf population. The commission-approved Montana Wolf Conservation Strategy (MFWP 2002) stipulates that Montana Fish, Wildlife and Parks (MFWP) will maintain a minimum of 15 breeding pairs (a male and female wolf with ≥ 2 pups that survive until December 31) and 150 wolves to have a regulated, public harvest season. Harvest decisions, however, are challenging due to conflicting values and objectives from various stakeholder groups. The stakeholders for wolf management, including federal and state agencies, hunters, general public, wildlife enthusiasts, and livestock producers, have conflicting values due to MFWP's mandate to conserve wildlife resources for future generations and provide opportunity for public enjoyment and human-wolf conflicts. The number of annual livestock depredation events steadily increased with the growing wolf population, and peaked at 117 depredation events in 2010 then declined to < 75 depredation events since 2012 (DeCesare et al. 2018; Inman et al. 2019). Management of wolf-livestock conflicts in Montana have included non-lethal practices, lethal removal of wolves by public agencies, permitted landowner take, and public harvest (Bradley et al. 2015; DeCesare et al.

2018; Inman et al. 2019). Despite these management practices, a greater percentage of Montanans feel that wolves negatively affect the economy, likely due to livestock losses and the perceived or realized loss of hunting revenues from decreased elk populations (Berry et al. 2016). Potentially as a result of these beliefs, private landowners and people that identify as a ungulate hunters have more positive opinions and are more tolerant of wolf hunting and trapping (Lewis et al. 2012, 2018; Berry et al. 2016). Conversely, some Montanans feel wolves positively affect tourism (Berry et al. 2016). Duffield et al. (2006) found that wolves and grizzly bears (*Ursus arctos*) were the top species that visitors to Yellowstone National Park wanted to view. Respondents to a general household survey of Montanans tended to agree that wolves helped maintain balance in nature (Lewis et al. 2018), and a slightly greater percentage of Montanans had a positive opinion of maintaining wolves on the landscape than not (Berry et al. 2016).

Another challenge with wolf management in Montana is general uncertainty in the effects of harvest on population dynamics of wolves. First, managers cannot directly control harvest rate, because changes in harvest regulations do not necessarily change harvest rates (Bischof et al. 2012). Harvest rates can vary based on many factors, including weather, hunter and trapper effort, hunter and trapper success, regulations, and prey availability (Kapfer and Potts 2012). Second, there is uncertainty in the effects of harvest on demography. There is no consensus for how harvest affects wolves (Fuller et al. 2003; Adams et al. 2008; Creel and Rotella 2010; Gude et al. 2012). Substantial variation is estimated in the level of harvest wolf populations can sustain before growth rate decreases (Fuller et al. 2003; Adams et al. 2008; Creel and Rotella 2010; Gude et al. 2012), which could result in management actions not reaching objectives. Harvest appears to be mostly an additive source of mortality for yearlings and adults (Chapter 4, Creel and Rotella 2010; Murray et al. 2010; Horne et al. 2019) and to reduce pup survival and recruitment (Chapter 2, Ausband et al. 2015, 2017). Despite the negative effects of harvest on survival and recruitment, however, wolves in Montana have sustained harvest rates from 0.17 to 0.36 and remained relatively stationary (Inman et al. 2019). This may be due to increased immigration into Montana or decreased dispersal from Montana (i.e., positive net immigration). Because wolves can travel great distances, immigration and dispersal can be important processes in dynamics of wolf populations (Hayes and Harestad 2000; Fuller et al. 2003; Adams et al. 2008; Bassing 2017). Decreased dispersal rates of wolves in Alaska partially compensated for harvest mortality and resulted in stationary densities. It is unclear, however, how net immigration into Montana affects wolf population dynamics.

Structured decision making (SDM) can help managers address the conflicting objectives surrounding management of wolves. SDM is a value-focused approach that provides a transparent process to relate objectives of management to alternative actions while accounting for uncertainty (Gregory and Keeney 2002; Gregory and Long 2009). SDM is increasingly used to address a variety of decisions in wildlife and natural resource management (McGowan et al. 2011; Cohen et al. 2016; Robinson et al. 2016; O'Donnell et al. 2017). Objectives for wolf management in Montana were developed by MFWP representatives, including regional managers, biologists, and wolf specialists, during a SDM workshop in 2010 (see Runge et al. 2013 pg. 65-68 for details). The working group focused on including objectives of the different stakeholders, and developed a set of six fundamental objectives, two process objectives, and two strategic objectives (Runge et al. 2013 pg. 66). Although MFWP representatives attempted to anticipate objectives from the stakeholder groups, it is important to note that the objectives may not include the full range of societal values. Regardless, these objectives were adopted by the Montana Fish and Wildlife Commission and have guided management decisions for wolves since 2010. Although the 2010 SDM workshop provided objectives for management, the original intent was to set the number and location of wolf management units, and formal, mathematical models relating changes in harvest regulations to how well those regulations met objectives were not developed. Given the multiple, conflicting objectives of wolf management, a decision model is needed to evaluate how well different management actions (i.e., harvest regulations) meet objectives for wolf management. Further, a decision model that incorporates and can potentially reduce uncertainty is critical to making informed harvest regulation decisions because there is uncertainty in the effects of harvest on wolf population dynamics.

Adaptive management (AM) is a special case of SDM when decisions are iterated over time or space and outcomes uncertain, and can be a useful decision tool for management of wolves in Montana. Because decisions are iterated, AM can be used to learn and reduce uncertainty to improve future decisions (Figure 5.1). There are generally two phases to AM (Williams et al. 2009). First, the deliberative or set-up phase is when the components of AM and SDM are developed: 1) clearly defined objectives, 2) alternative management actions, 3) models to predict outcomes of actions, 4) evaluation of tradeoffs, and, in the case of AM, 5) a monitoring program to determine the current system state (e.g., population size), reduce uncertainty, and learn over time (Figure 5.1). Objectives are most important and help determine whether or not management was successful. Objectives are generally translated into a quantitative statement to evaluate outcomes of management actions (McGowan et al. 2011; Conroy and Peterson 2013). Management actions are a set of alternatives available for the decision maker to select from to meet objectives. Models are used to predict consequences or outcomes of different management actions. These outcomes must include predictions of metrics used to quantify objectives, and thereby provide a link between actions and objectives. In situations where there is uncertainty in how the system (e.g., population) functions, multiple models can be used to represent competing hypotheses. These competing models each have a corresponding model weight, which specifies measures of support or confidence in each model (hypothesis). The decision model is then solved by using the objectives, actions, and predictive models to select the management action that best meets objectives, i.e., provides the highest value as measured by objectives. Last, monitoring provides an estimate of the current system state (e.g., population size) to make decisions based on current system state, evaluate effectiveness of management, and facilitate learning during the second phase of AM. The second phase of AM is the iterative phase, which is the implementation of management and monitoring based on the AM framework developed during the deliberative phase. The iterative phase consists of determining the optimal management action based on objectives, available management actions, model-based predictions, and the estimates of the current system state (Williams et al. 2009). After management is implemented, the change in system state is estimated via monitoring. Comparison of predictions from the competing models to monitoring data provides support for some models (i.e., hypotheses) over others, and leads to increased model weight or support for the models that predict well. The new model weights and population size are used with the objectives, available management actions, and model predictions to determine the optimal management action, and the iterative phase continues. Learning is the reduction of uncertainty, and reflected in an increase in model weight or support. Model weights are incorporated in the model-based predictions, thus learning at each step improves future decisions. There are two types of learning in AM, passive and active. In active AM, learning is anticipated, and if future management will be greatly improved by reducing uncertainty then a management action may be selected that will accelerate learning and result in greater long-term gain (Walters and Hilborn 1978; Conroy and Peterson 2013). In passive AM, optimal actions are chosen based on long-term gain in objectives without consideration for how a reduction in uncertainty could improve future management (Conroy and Peterson 2013). Learning is still incorporated in passive, AM, but not as part of the optimization. Because the iterative phase is based on the components developed during the deliberative phase, optimal decisions and reduction of uncertainty all depend on how objectives were quantified, the candidate set of management actions considered, and the models used to predict consequences. An AM framework can help guide harvest regulation decisions for wolf management while reducing uncertainty in the role of immigration in wolf population dynamics to improve future decisions.

Our objectives were to develop a flexible decision tool for wolf management that included biological and societal values in a transparent process, and to incorporate and potentially reduce uncertainty in the effects of harvest on wolf populations. Using the objectives from the 2010 SDM workshop, we simulated AM based on harvest management decisions for gray wolves in Montana from 2011–2018 to reduce uncertainty over time. We used the fundamental objectives and one strategic objective that was previously deemed critical to the decision (Runge et al. 2013 pg. 66): 1) reduce wolf impacts on ungulate (i.e., elk [*Cervus canadensis*] and deer [*Odocoileus spp.*]) populations; 2) reduce wolf impacts on livestock; 3) maintain hunter opportunity for ungulates; 4) maintain a viable and connected wolf population in Montana; 5) maintain hunter opportunity for wolves; 6) increase broad public acceptance of harvest and hunter opportunity as part of wolf conservation; and 7) maintain positive and effective working relationships with livestock producers, hunters, and other stakeholders. We used population models to describe changes in abundance of wolves and formalized the relationships between population size of wolves, recruitment, depredation events, impacts of wolves on ungulates, and the harvest regulations and management objectives. We considered two alternative models of wolf population dynamics based the uncertainty in the role of immigration in wolf population dynamics. The first model assumed net immigration of wolves into Montana was zero and was not partially compensating for harvest. The second model assumed net immigration into Montana was positive and was partially compensating for harvest. We used estimates from the literature to estimate livestock depredation events from wolf abundance (DeCesare et al. 2018) and estimate public acceptance of wolf harvest from harvest regulations (Lewis et al. 2012, 2018). We used an optimization method, stochastic dynamic programing (SDP; Bellman 1957; Williams et al. 2002), to determine sequences of harvest regulation decisions (i.e., policies) that were optimal with respect to objectives for wolf management in Montana. Finally, we considered passive AM as a tool to reduce uncertainty in wolf population dynamics.

METHODS

We developed an AM framework to guide decisions regarding harvest regulations for wolves in Montana and reduce uncertainty in the role of immigration in wolf population dynamics. Based on the objectives developed during the 2010 SDM workshop, we developed metrics and utility functions for each objective. Further, we developed alternative harvest regulations to evaluate, models to predict harvest from regulations, and a model of wolf population dynamics. Using this AM framework, we determined the optimal, state-dependent (i.e., population size) management actions for wolves using SDP.

Objectives and Utility Functions

With multiple objectives, the values for each objective can be combined into a single value using a reward (or objective) function to determine how well a management action meets all objectives

(Conroy and Peterson 2013). When the objectives are measured in different units (e.g., number of animals and dollars), the values for each objective must first be converted into common units and combined using utility functions. To evaluate how well management actions met objectives listed above, we converted the values of each objective into a common scale using utilities that ranged from 0 (worst) to 1 (best) outcome. We then combined the utility values into a single value using a reward function that took into account the weights (relative importance) of each objective. We elicited utility functions and weights for objectives from MFWP representatives, including wildlife managers and wolf specialists, to incorporate their values and knowledge. We also determined their risk attitudes as either risk adverse, risk neutral, or risk tolerant (Conroy and Peterson 2013). For the reward function, we used the weighted-sum method (Conroy and Peterson 2013) to combine the utility values into a single reward value as:

$$Reward = w_i U_i + \cdots w_I U_I,$$

where w_i is the weight and U_i the utility value for objective i. Weights for objectives were averaged from the responses by MFWP representatives (Table 5.1). We described the metrics, utility functions, and risk attitude for each objective below.

Reduce Impacts of Wolves on Ungulate Populations.— We measured the impact of wolves on ungulates using a scale from 0 (no impact) to 1 (wolves are reducing ungulate populations). For simplicity, we assumed that the impact of wolves on ungulates was only a function of the statewide number of wolves. We assumed if there were no wolves, then there was no impact on ungulates (utility value of 1). Second, we assumed that an increase in the wolf population was associated with a greater impact on ungulates and lower utility values. We used a combination of value elicitation and function elicitation (Conroy and Peterson 2013) to determine the relationship between wolf population size and the impact on ungulates. The most frequently selected risk attitude was risk tolerant, i.e., a line that decreases at an increasing rate (Figure 5.2A).

Reduce Impacts of Wolves on Livestock.— The metric we used for the objective to reduce wolf impacts on livestock (i.e., cattle and sheep) was the number of depredation events each year. We estimated the number of depredation events per year using the mean and variance of the per-wolf depredation rates for before and after harvest reported in DeCesare et al. (2018) and multiplying by wolf population size. We assumed that zero depredation events had a utility value of one and an increase in the number of depredation events was associated with smaller utility values. MFWP representatives selected a risk tolerant attitude (Figure 5.2B).

Maintain Hunter Opportunity for Ungulates.— We did not consider a utility function for maintaining hunter opportunity for ungulates. Maintaining hunter opportunity for ungulate species is integral to MFWP's mission for providing opportunity for public enjoyment and honoring the tradition and heritage of hunting as part of Montana's culture (fwp.mt.gov). However, we assumed the main effect of wolves on maintaining hunter opportunity for ungulates was through an impact on ungulate populations. Wolves likely had little effect on other factors associated with maintaining hunter opportunity for ungulates, such as public access, and would likely not be influenced by decisions for wolf harvest regulations. Therefore, we assumed that reducing impacts of wolves on ungulates would maintain sufficient hunter opportunity with how management of wolves affect ungulate populations.

Maintain Viable Wolf Population.— We measured maintaining a viable and connected wolf population by the number of wolves and pups recruited. We assumed that 1) if there were fewer than the legally required minimum of 150 wolves or 30 pups recruited, then the utility value was zero (i.e., a penalty function), and 2) an increase in the number of wolves or pups recruited above the minimum was associated with greater utility values. We created a utility function for wolf abundance and recruitment separately, then combined them by multiplying the utility values together (Figure 5.3). Therefore, if either abundance of wolves or the number of pups recruited was below the required minimum then the combined utility value was zero. MFWP representatives were risk averse for abundance and risk neutral for recruitment (Figure 5.3).

Maintain Hunter Opportunity for Wolves.— We used abundance of wolves, bag limit, and hunting and trapping season lengths as a metric for hunter opportunity for wolves. We assumed if abundance of wolves or the number of pups recruited fell below the required minimum then there was no hunter opportunity and the utility value was zero. We also assumed that an increase in abundance of wolves was associated with an increase in hunter opportunity. To convert from abundance to utilities, MFWP representatives were risk tolerant, and risk neutral for bag limit and season length (Figure 5.4). We combined the components by multiplying the utility values for abundance, bag limit, and season length together.

Increase Public Acceptance of Wolf Harvest.— We used the percent Montanans satisfied with season length and bag limit as the metric for acceptance of wolf harvest. We used survey data to predict the percent Montanans satisfied with regulations for hunting season length, trapping season length, and bag limit (Lewis et al. 2012, 2018). Survey data were categorized as resident private landowners, resident wolf hunting license holders, resident deer/elk license holders, and general household (Lewis et al. 2018). We developed utility functions for satisfaction with hunting season length, trapping season length, and bag limit separately for the four stakeholder groups. Survey data included 1) the percent of respondents that thought the season or bag limit was too short/low, suggesting they would be more satisfied with a longer/greater season or bag limit and thus a positive relationship with season length or bag limit, and 2) the percent of respondents that thought the season or bag limit was too long/high, suggesting they would be more satisfied with a shorter/smaller season or bag limit and thus a decreasing line. We used these relationships to convert the percent Montanans satisfied with hunting season length, trapping season length, and bag limits into utility values for each respondent group. To create the utility function we assumed that 1) if no Montanans were satisfied with the regulations (0%), then the utility value was zero, and 2) an increase in the percent of Montanans satisfied was associated with an increase in utility values. MFWP representatives were risk neutral, therefore we used a linear relationship between percent Montanans satisfied and utility (Figure 5.5A). For each regulation (e.g., hunting season length) and survey group (e.g., private landowner), we combined the utility values for the increasing and decreasing utility values using the negative squared-error loss function (Figure 5.5A; Williams and Kendall 2017). The negative squared-error loss function had small values when the utility for the increasing and decreasing utility values were far apart, and large values when the utility values were equal (i.e., the percent Montanans that thought the season was too long and too short were equal). Therefore, the negative squared-error loss function balances the competing interests of the respondents that want a shorter or longer season. We then combined the utility values of the four survey groups for each regulation type using the weighted sum method with equal weights for each group (i.e., 0.25; Figure 5.5). To combine the three regulation types into one utility value, we used a weighted-sum with equal weights (i.e., 1/3). Therefore, we created the utility value for the objective (U_{Public}) as

$$U_{r,g} = -\left(U.short_{r,g} - U.long_{r,g}\right)^2$$

$$U_r = 0.25 * \left(U_{r,landower} + U_{r,wolf} + U_{r,deer} + U_{r,household}\right)$$

$$U_{Public} = \frac{1}{3} * \left(U_{bag} + U_{hunting} + U_{trapping}\right)$$

where $U.short$ was the utility value for the percent of respondents that thought the season or bag limit was too short/low, $U.long$ was the utility value for the percent of respondents that thought the season or bag limit was too long/high, U was the utility value for hunting regulation r (bag limit, hunting season length, trapping season length) and survey group g (landowner, wolf license holder, deer/elk license holder, household).

Maintain Positive Working Relationships.— We did not consider a utility function for maintaining positive working relationships with stakeholders because we assumed that increasing acceptance of wolf harvest would also be positively related to positive relationships with stakeholders. Further, maintaining positive working relationships may require alternative management actions outside of harvest regulations (e.g., public outreach) that we did not consider.

Management Actions

We considered four different management actions that were different combinations of bag limits hunting season length, and trapping season length. First, we considered the no harvest management action, which was included if the population fell below established minimums for a regulated wolf harvest season. Second, the status quo management action included the 2018-2019 harvest regulations for wolves, which have been consistent since the 2013-2014 license year. This included a bag limit of five wolves per year, two weeks of archery, 26 weeks of firearm, and 11 weeks of trapping. For the remaining two management actions, we asked MFWP representatives what combination of bag limits and season lengths to include in a restricted management action and a liberal management action. Based on an average of responses, the restricted management action included a bag limit of one per year, two weeks of archery, two weeks of firearm, and four weeks of trapping. The liberal management action was a bag limit of 10 wolves per year, two weeks of archery, 38 weeks of firearm, and 17 weeks of trapping.

We predicted the total number of wolves harvested for each license-year under the four different management actions and incorporated stochasticity using posterior predictive distributions (distribution of possible values; Gelman et al. 2004). We fitted negative binomial mixed-effects models of the relationship between harvest regulations, social factors (e.g., hunting and trapping effort from harvest statistics and licenses sold), and environmental/ecological factors (e.g., winter severity or wolf density) and the total number of wolves harvested, and used top models to develop the posterior predictive distribution (Supplementary Material 5.A). These posterior predictive distributions were based on season length, method of hunting (archery or firearm), and the type of season (i.e., archery, general, trapping, and post-trapping) for the number of wolves hunted. For the number of wolves trapped the posterior predictive distribution was a function of trapping season length. We then used the mean and standard deviation of the posterior predictive distribution in a normal distribution to draw values of the total wolves harvested for each year for each management action.

Models of Population Dynamics

We used two alternative population models to estimate future population size and then calculate the probability of transition from one system state to any other, given an action. The population model was a per capita model, and we predicted future population size for the following year (i.e., annual time-step). To limit the number of system states, we then discretized population size (N_t) into states from 0, 10, 20 … 2000 wolves by rounding values to the nearest 10 wolves. We chose 200 states because it exceeded the assumed carrying capacity of 1000 wolves (Chapter 4).

We then used the frequencies of the predicted future states to derive the probability mass function to calculate the probability of transition from one state to any other.

The two alternative models shared a common form, which predicted changes in wolf population size based on annual survival rates, per capita reproductive rates, and harvest:

$$N.adult_t \sim Binomial(N_{t-1}, \phi_{t-1})$$

$$N.pup_t \sim Poisson(N_{t-1}\rho_{t-1})$$

$$N_t = N.adult_t + N.pup_t - H_t,$$

where ϕ_t was annual survival rate, ρ_t was the per capita recruitment rate, and H_t was the number of wolves harvested. Similarly to Stenglein et al. (2015), we did not include age or sex structure because monitoring data could not distinguish between sexes and age classes. Therefore, we assumed that yearlings and adults of both sexes had equal survival rates, and modeled changes in total abundance over time. Many studies on wolves assumed equal survival rates between age classes (Marescot et al. 2012; Schmidt et al. 2015; Stenglein et al. 2015; Horne et al. 2019), and Wydeven et al. (2009) found no difference in survival of yearling and adult wolves in Wisconsin. We also assumed that harvest mortality was additive based other studies supporting additive harvest mortality (Chapter 4; Horne et al. 2019). In the first competing model, we assumed that net immigration into Montana was zero. The alternative hypothesis was that net immigration into Montana was positive. We included a term for net immigration (δ_t), and adjusted the above equation for adults to

$$N.imm_t \sim Poisson(N_{t-1} * (1 + \delta_{t-1}))$$

$$N.adult_t \sim Binomial(N.imm_t, \phi_{t-1}).$$

We used estimates of survival and recruitment for wolves in Montana to parameterize the population models (Chapter 2; Chapter 4; Smith et al. 2010). Because we assumed additive harvest mortality, we used the mean and variance of non-harvest survival rates (mean = 0.73, variance = 0.003; Chapter 2; Chapter 4; Smith et al. 2010). We included stochasticity in survival by drawing random values from a beta distribution based on the mean and variance. For recruitment rate, we included density dependence (Chapter 2; Chapter 4). We used a maximum recruitment rate of 0.05 and a slope coefficient for the effect of density of -0.00114 in a generalized linear model with a log-link function as:

$$\rho_t = \exp(0.05 - 0.00114 \times N_{t-1})$$

We included stochasticity in recruitment by drawing random values for the intercept and slope coefficient from a gamma distribution based on the mean and variance. We assumed a mean of 0.10 and a variance of 0.005 for net immigration, and drew random values from a beta distribution to incorporate stochasticity. We included partial controllability in harvest by drawing the annual total number of wolves harvested from the posterior predictive distribution described above.

We calculated utility values using the future predicted population size (N_t) prior to discretization. We adjusted the predicted number of pups recruited ($N.pup_t$) using harvest rate ($hr_t = H_t/N_t$) and a binomial distribution because we subtracted total harvest (H_t) from total population size:

$$Rec_t \sim Binomial(N.pup_t, hr_t),$$

where Rec_t is the expected number of pups recruited used to calculate utility values. This assumes that pups are not more vulnerable to harvest than adults, which appears to be supported from wolf harvest data in Idaho (Ausband. 2016).

To estimate the probability of transitioning from one population state to another, given the management action, we first initiated population size randomly within each discretized population state for 50,000 iterations. Then, we used the two population models and their respective model weights to predict abundance the following year. We discretized population size by rounding to the nearest 10 wolves, and then used the frequencies of predicted population size to create state transition matrices. Thus, for any system state and management action, we derived the probability mass function describing the probability of transitioning from one system state to any other. We discretized model weights in increments of 0.1, from 0.1 to 0.9. Therefore, we had 10,000,000 simulations (200 population states * 50,000 iterations) for each of the four harvest management actions under each model weight state.

Optimization and Simulation

We used SDP to compute the optimal set of management actions (Bellman 1957; Williams et al. 2002; Puterman 2014). We solved the problem for an infinite time horizon by using policy iteration in R v3.6.1 (R Core Team 2017) using package MDPtoolbox (Chadès et al. 2017). The problem is solved by maximizing the expected cumulative reward value over the infinite time horizon. We assumed a discount factor close to 1 (i.e., 0.99999; Puterman 2014). A discount factor close to one indicates the value of a resource in the future is the same as the value now. The optimal management actions were state-dependent, i.e., the optimal action depended on population size and model weight. Therefore, uncertainty could be reduced by implementing the optimal management actions and then updating model weights.

We used a passive adaptive framework and updated model weights using Bayes' theorem in two different types of simulations to understand the consequences of following the optimal management actions and to simulate following passive AM. First, we simulated a population through time following the optimal management actions to predict the median annual population size, number of pups recruited, number of depredation events, and the reward value for how well each management action met objectives. We ran 1,000 replications of each simulation for 100 years. Each year, the optimal management action dependent on the current population size and model weights was selected and enacted, and the population and model weight states were updated. We updated model weights assuming model 1 was correct, and then model 2 was correct. For example, when we assumed model 1 was correct, we used abundance estimates from model 1 as the mean in a normal distribution with a standard deviation of 20% to draw an estimate for the observed data. Then we determined the normal likelihoods of the observed data given the estimates of abundance for each model again with a standard deviation of 20%. Second, we simulated the wolf population in Montana from 2011-2018, however, instead of using the optimal management actions, we used the management actions enacted by MFWP. We used the status quo management action for 2012-2018, and the restricted management action for 2011-2012 because the harvest regulations for that season (four weeks of archery and ten weeks of firearm) were more similar to the restricted management action than the status quo. The optimal action, given the estimated population size, was the status quo. We ran 1,000 replications of each simulation. To update model weights, we compared predictions from the competing models to the estimated abundance of wolves in Montana from monitoring data (Inman et al. 2019). To account for uncertainty in the estimates of abundance, we resampled the estimates 1000 times for each year and replication by sampling from a Normal distribution using the reported mean and standard deviation (Inman et al. 2019) similarly to Robinson et al. (2017). We took the mean model weight for each replication and resampling run to get the annual weight for both models. Again, we recorded predictions for median population size, number of pups recruited, number of depredation events, and the reward value for each replication and resampling run.

Sensitivity Analyses

We evaluated model performance and sensitivity of results to uncertainty in parameter values, construction of utility functions, and weights of objectives (Supplementary Material 5.B). We changed each parameter value in turn to the lower and upper 95% quantile or credible intervals to test sensitivity of the reward value of the optimal decision to uncertainty in parameter estimates (i.e., one-way sensitivity analysis; Conroy and Peterson 2013). Additionally, we conducted a response profile sensitivity analysis (Conroy and Peterson 2013), where each parameter value was varied over the range of possible values and the expected reward value was recorded for each management action to identify how the optimal decision changed across a range of parameter values. To assess sensitivity of results to the construction of utility functions and risk attitude, we compared the reward values for a risk averse, risk neutral, and risk tolerant attitude. We evaluated sensitivity of the expected reward values to weights for objectives using indifference curves by varying the weight on a single objective from 0-1 while holding the remaining objective weights at their original values. Last, we evaluated the sensitivity of evolving model weights to bias in abundance estimates of wolves. Estimates of abundance of wolves in Montana hinge on assumptions of an average territory size (Rich et al. 2013; Inman et al. 2019). Territory size, however, varies both spatially and temporally, which may bias estimates of abundance (Sells 2019). Therefore, we tested the sensitivity of model weights over time to a 15% increase or decrease in annual estimates of abundance (Supplementary Material 5.B).

RESULTS

Expected annual performance metrics (i.e., median population size, number of pups recruited, number of depredation events, and the reward value) differed for the four management actions (no harvest, restricted harvest, status quo, and liberal harvest) when the weights of the two population models were equal. No harvest had greater median number of depredation events per year for all initial population states (Figure 5.6). Restricted harvest was expected to have slightly more depredation events than the status quo or liberal harvest actions (Figure 5.6). Total number of pups recruited was expected to be greatest under more restrictive harvest management actions (Figure 5.6). Total harvest different under the four management actions, with a median of 66 wolves harvested under restricted harvest, 225 wolves under status quo, and 253 wolves under liberal harvest (Figure 5.6). Generally, the no harvest or restricted harvest management actions resulted in greater expected future population size whereas the status quo and liberal management actions resulted in a smaller expected future population size (Figure 5.6).

We chose to evaluate the expected annual (i.e., based on one time-step) utility values instead of the cumulative reward value that is maximized over an infinite time horizon in SDP. Therefore, all results are the expected utilities based on one time-step. More liberal harvest regulations had greater utility than no or restricted harvest for the objectives to reduce impacts of wolves on ungulates, reduce impacts of wolves on livestock, maintain hunter opportunity for wolves, and increase public acceptance of wolf harvest (Figure 5.7). Conversely, the utility values for maintaining a viable wolf population were greatest with the no or restricted harvest management action (Figure 5.7). The median reward using the weighted sum reward function for each management action differed across the population states (Figure 5.7).

Policy plots are used to depict the optimal management actions for each system state (i.e., the optimal policy). The optimal management action varied little with different model weights (varied by ~ 150 wolves for 0.1 and 0.9 model weight; Figure 5.8). In general, the optimal management action was no harvest when population size was less than 170 wolves, restricted harvest when the population was between 170 and 280 wolves, status quo harvest when population size was between 280 and 1330 wolves, and liberal harvest when population size was greater than 1330 wolves (Figure 5.8).

We found the expected annual performance of passive adaptive management was similar when we assumed model one and model two were true. When we simulated a population under the optimal management actions, wolf population size fluctuated around 650 wolves under both scenarios (Figure 5.9). The expected number of depredations was ~60 events per year, and the annual number of pups recruited was 256. Under both scenarios, weight for model one increased over 100 years. When we simulated passive adaptive management for the wolf population in Montana from 2011 to 2018, we found that expected wolf population size, number of pups recruited, and depredation events declined (Figure 5.10). This follows general patterns for estimates of abundance of wolves and the number of verified depredation events in Montana (Inman et al. 2019). Over the eight year period, weight for model one (net immigration = 0) increased from 0.50 to 0.67, and weight for model two (net immigration > 0) decreased from 0.50 to 0.33 (Figure 5.10).

Sensitivity Analyses

The expected reward for meeting objectives was most sensitive to the depredations per wolf, mean recruitment of offspring, and harvest (Figure 5.B.1 in Supplementary Material 5.B). The model was least sensitive to uncertainty in immigration rate or the change in coefficient values for the effect of harvest regulations on the percent Montanans satisfied with the regulations. As the mean recruitment rate decreased the management action with most support became more restricted. For example, when wolf abundance was 350 the optimal management action changed from the status quo to restricted harvest as recruitment rate decreased (Figure 5.B.3 in Supplementary Material 5.B). As current wolf abundance increased, however, this relationship become less pronounced (Figures 5.B.2-5 in Supplementary Material 5.B). Uncertainty in adult survival also altered the optimal management action, but only when the population was small (Figures 5.B.2-5 in Supplementary Material 5.B). Uncertainty in total harvest under the four management actions and the depredation per wolf rate also affected the optimal management action, however this was only when the population was around 350 wolves (Figures 5.B.2-5 in Supplementary Material 5.B).

We also evaluated the sensitivity of the decisions to construction of utility functions. We found that the optimal management action was most sensitive to the construction of the utility function for the objectives to maintain a viable wolf population and reduce the impact of wolves on livestock. However, this effect was only observed when abundance was around 350 wolves (Figures 5.B.6-8 in Supplementary Material 5.B). To convert to utility values, we assumed there was a maximum threshold beyond which the utility value was one (highest utility) for an increasing function or zero (lowest utility) for a decreasing function. For example, for the objective to maintain a viable wolf population we assumed that beyond the threshold of 700 wolves the population was viable and utility was one (Figure 5.3A). When the maximum threshold for the viable wolf population decreased, more conservative regulations performed better at meeting objectives (Figure 5.B.7 in Supplementary Material 5.B).

The expected reward for meeting objectives was most sensitive to the objective weights for reducing impacts on ungulates, reducing impacts on livestock, and increasing public acceptance of wolf harvest (Figure 5.B.12-15 in Supplementary Material 5.B). However, changes in weights for these objectives did not alter the optimal management action. The optimal management action was most sensitive to objective weights for the maintaining a viable wolf population and increasing public acceptance of harvest opportunity (Figure 5.B.13 in

Supplementary Material 5.B). Although changing the weights of the other objectives resulted in slight changes in the recommended management action, the overall reward values for the different management actions remained close, suggesting that changes in weights would not result in a clearly superior decision.

We found that reduction of uncertainty in the role of immigration to wolf population dynamics was not sensitive to a systematic bias in estimates of abundance. We found similar change in model support over time with a 15% increase or decrease in estimates of abundance (Figure 5.B.16 in Supplementary Material 5.B). When the estimates were biased low, support for no immigration into Montana increased to 0.67 compared to 0.66 when the estimates were biased high.

DISCUSSION

Management of large carnivore populations can be particularly challenging due to conflicting values of stakeholders, debated science, and their ecological complexity. Managing large carnivores with harvest has been criticized for 1) not including uncertainty in harvest or population estimates, 2) failing to reduce conflicts (i.e., livestock loss or competition for ungulates), 3) not including social, political, and cultural values, and 4) not having clearly defined, quantitative objectives (Treves 2009; Bruskotter and Shelby 2010; Bischof et al. 2012; Creel et al. 2015). We developed an AM framework to guide decisions of harvest regulations of wolves using 1) objectives from a previous SDM workshop in 2010, 2) a set of four alternative management actions, 3) two competing models of wolf population dynamics where net immigration was assumed to partially compensate or not compensate for harvest, 4) SDP to determine optimal harvest management actions, and 5) monitoring data for wolves in Montana to facilitate learning. The AM framework explicitly incorporated uncertainty in estimates of harvest, biological and sociopolitical values, and quantitative objectives in a transparent framework. Given this framework, we were able to identify optimal management actions that reduced the impacts of wolves on ungulates and livestock, maintained a viable wolf population and hunting opportunity for wolves, and maximized public acceptance of harvest and hunting opportunity for wolves. When we simulated passive AM for wolves in Montana, we found similar patterns in expected performance characteristics (wolf population size, depredation events, and total harvest) to those observed in Montana. Using AM, we found support for the hypothesis that net immigration rate into Montana was zero.

We found that the optimal management actions became more liberal as the population grew (Figure 5.8), and the management actions differed in the expected change to wolf population size, number of livestock depredations, and total harvest (Figure 5.6). When the population was between 170 and 280 wolves, the optimal management action was restricted harvest, which was expected to increase population size given the initial population state (Figure 5.8). When the population was greater than 1330 wolves, the optimal management action was liberal harvest, which was expected to result in the greatest population decline (Figure 5.8). Therefore, the optimal management actions lead to wolf population sizes being managed above 280 wolves and below 1330 wolves. When we simulated a population under the optimal management actions for 100 years, the wolf population size remained relatively stationary around 650 wolves. This suggests that maintaining the wolf population at this size, or at least between 280 to 1330 wolves, with status quo harvest regulations best meets our objectives for wolf management, given how we quantified objectives. Setting a numerical population objective (i.e., 800 animals) can be controversial for large carnivores because of the divisive values of stakeholders. Those that value large carnivores on the landscape may think the numerical target is too low, and those that have or could be affected by livestock depredation may think the numerical target is too high. Basing the population objective solely on the ecological or behavioral aspects of the species biology ignores the social, political, and cultural aspects of wildlife management (Bruskotter and Shelby 2010). In SDM and AM the focus is on how best to meet objectives, not what population size to maintain. The stationary population size of 650 wolves when following the optimal management actions is an emergent property of managing the population to best meet all objectives.

AM can easily account for many sources of uncertainty, including structural or model uncertainty. Using AM, we were able to find support for the hypothesis that net immigration of wolves into Montana was zero. We considered two competing models of wolf population dynamics. One model assumed that there was not net immigration into Montana, whereas the second model assumed that net immigration into Montana was positive. By simulating the wolf population in Montana with passive AM, we found that model uncertainty could be reduced (Figure 5.10D). From 2011 to 2018, the first model gained support increasing from 0.5 to 0.67. This supports the hypothesis that net immigration of wolves into Montana is zero. Many population models of wolf dynamics assumed that immigration and emigration sum to zero (Schmidt et al. 2015; Stenglein et al. 2015*b*; Horne et al. 2019), and this assumption may be valid. A study in Idaho found that immigration into their study site was low and did not change following harvest implementation and density of wolves declined, which suggests that immigration does not compensate for harvest (Bassing et al. 2020). The wolf population in Montana is well established, and wolves may have saturated much of the prime available habitat (Chapter 2). Immigration may be more important for colonizing or isolated, small sub-populations (Bull et al. 2009).

Learning, or the reduction of uncertainty, in AM is contingent on the accuracy of the monitoring data. Estimates of abundance of wolves in Montana is dependent on accurate estimates of territory size and group size (Inman et al. 2019). The estimate of territory size used to estimate the number of wolf packs, however, is from before harvest implementation, and may not reflect current territory sizes (Sells 2019). Using a more accurate estimate of territory size may alter the abundance estimates used for monitoring data and change in model weights of the two competing models. Therefore, model support, and the reduction of uncertainty, is contingent on the accuracy of monitoring data we used in our AM framework. Although we found model support was insensitive to a 15% increase or decrease in abundance estimates (Supplementary Material 5.B), if there was a trend of increasing bias over time that could influence results. An assumption in many optimization methods is that the state, in our case population size, is observed without error (Williams 2009; Conroy and Peterson 2013). This is clearly violated in most ecological applications. We attempted to account for uncertainty in abundance estimates by resampling the abundance estimates (Robinson et al. 2017). The observed abundance estimates we compared to predictions was drawn from a normal distribution with mean and standard deviation of the reported estimates.

We evaluated objectives and considered management actions at a statewide scale. However, metrics used to evaluate the objectives may vary spatially. For example, a majority of livestock depredation events (95%) occur in only 22% of the state (DeCesare et al. 2018). Harvest may also vary spatially. We predicted total statewide harvest, however, most harvest (60%) occurs in the northwestern part of the state. Lastly, public attitudes or values may vary across the state. Montanans in the western half of the state were less likely to hold a positive opinion of trapping, but more likely to hold a positive opinion of hunting (Berry et al. 2016).

Spatial variation in depredation events, harvest, ungulate populations, and public attitudes and opinions would likely influence weight of objectives as well as the expected performance metrics (e.g., number of depredation events). Therefore, this framework could be improved by determining optimal management actions at a finer spatial scale (e.g., by MFWP administrative regions).

Our results are completely dependent on the components we used in the AM framework we established during the deliberative phase. Specifically, the optimal harvest regulations are dependent on the objectives we used, how we quantified objectives, and the set of alternative management actions we considered. Because SDM and AM are value focused, accurately translating objectives into mathematical functions to provide a reward value may be the most important component. As a metric for the objective to reduce impacts of wolves on ungulates we used a scale from 0 (no impact) to 1 (wolves reducing ungulate populations) based on expert opinion. This is a simplification of the effects of wolves on ungulates that ignores functional and numerical responses of wolves to ungulates (Mech and Peterson 2003; Hebblewhite 2013; Zimmermann et al. 2015), the confounding effects of other predators on ungulates (e.g., the effects of mountain lions on elk; Rotella et al. 2018), and the non-lethal effects (e.g., behavioral) of wolves on ungulates (Creel et al. 2005; Say-Sallaz et al. 2019). However, this simplification allowed us to easily quantify the objective in terms of wolf abundance, which was predicted from the model. For the objective to increase broad public acceptance of wolf harvest and harvest opportunity, we used survey data (Lewis et al. 2018) to relate hunting season length, trapping season length, and bag limit to the percent Montanans satisfied. There are other metrics or considerations we could have included, such as overall tolerance of wolves in Montana (Lewis et al. 2018), however there was not a clear way of predicting how tolerance changed with metrics of the wolf population or harvest regulations. Wildlife value orientations can be useful for understanding differences in support for management actions (Teel and Manfredo 2010; Teel et al. 2010; Manfredo et al. 2011). Wildlife value orientations are clusters of basic beliefs about wildlife that give meaning to more basic values (Teel and Manfredo 2010), and can be used to predict acceptability of management actions (Straka et al. 2020). Future work could incorporate wildlife value orientations to better predict stakeholder acceptance for wolf management in Montana.

One way to determine how quantification of objectives or uncertainty in parameter values influenced optimal decisions is with sensitivity analyses. Our sensitivity analyses revealed that the optimal management actions were most sensitive to uncertainty in recruitment rate, adult survival, depredation events per wolf, and harvest (Supplementary Material 5.B). However, uncertainty in these parameters only influenced the optimal decision when the population was small (≤350 wolves). The optimal management actions were not sensitive to the parameter value for immigration rate. Although we found no support for the hypothesis that net immigration into Montana was positive, reducing this uncertainty had little effect on the optimal management actions (Figure 5.8). When there was little to no support for the zero net immigration hypothesis (model 1 weight of 0.1) the population size at which to implement the liberal management action occurred at 1280 compared to 1420 when there was most support for the hypothesis (model 1 weight of 0.9). Therefore, this uncertainty does not influence optimal decisions for harvest management of wolves. Our results were most sensitive to objective weights for maintaining a viable wolf population and for increasing public acceptance of harvest as part of wolf management. Therefore, in an applied setting of AM for wolf management, managers should carefully consider objective weights to ensure they accurately reflect values of stakeholders.

The objectives we used were elicited from MFWP representatives during the 2010 SDM workshop, and may not be representative of the stakeholder groups. Ideally, objectives, metrics, and utility values would be crafted with input from representatives of all stakeholder groups. Stakeholder groups for wolf management in Montana include hunters, general public, wildlife enthusiasts, wildlife conservation groups, and livestock producers. While wildlife enthusiasts and conservation groups may value, and thus assign greater weight, to the objective for maintaining a viable wolf population, livestock producers that suffer economic losses would likely assign greater weight to the objective for reducing impact of wolves on livestock. There can be significant differences in wildlife value orientations between wildlife managers/agency staff and the general public (Gigliotti and Harmoning 2003; Rogers 2018), and this may be particularly true for large carnivores. For example, sheep farmers in Norway hold similar values toward nature as wildlife managers, however their views differed towards large carnivores (Bjerke and Kaltenborn 1999). Based on a survey of western U.S. residents, a majority of Montanans were classified as traditionalists with domination value orientation that prioritizes human well-being over wildlife and is generally more utilitarian (Teel and Manfredo 2010). Although wildlife managers are thought to hold more traditionalist values (Gill 1996; Peyton 2000), future revisions of objectives would benefit from inclusion of public input.

We considered a specific carnivore management scenario, however this approach can be useful for management of other carnivores or hunted populations in general. When there are diverse stakeholder opinions, as in carnivore management, AM can be used to include multiple, often conflicting objectives to manage a population or system. We believe that a formal SDM or AM process would be useful for managing carnivore populations, particularly those that come into conflict with humans. Objectives for minimizing conflict and maintaining a viable carnivore population are conflicting, yet can both be included in a SDM-AM approach. Further, the effectiveness of lethal responses to livestock depredation and non-lethal deterrents are debated (Wielgus and Peebles 2014; Bradley et al. 2015; Miller et al. 2016; Poudyal et al. 2016; DeCesare et al. 2018). The uncertainty in the effectiveness of lethal control actions and other, non-lethal preventative actions, can be included and potentially reduced in an AM framework for carnivore management. Additionally, SDM or AM can incorporate survey data from stakeholders to rigorously include sociopolitical objectives. Our AM framework included recent survey data related to Montanans values and opinions on harvest regulations for wolves (Lewis et al. 2018). Public opinion is an influential component in wildlife management, yet it is rarely explicitly incorporated into the decision process (McCool and Guthrie 2001). When there is a transparent link between public input and management decisions, satisfaction with management also increases (McCool and Guthrie 2001). When uncertainty impedes effective decision making, AM can facilitate learning and reduce uncertainty (Williams et al. 2002; Conroy and Peterson 2013). Not only does learning improve understanding of ecology and effectiveness of management, but through AM we can improve future decisions to manage populations more effectively.

LITERATURE CITED

Adams, L. G., R. O. Stephenson, B. W. Dale, R. T. Ahgook, and D. J. Demma. 2008. Population dynamics and harvest characteristics of wolves in the Central Brooks Range, Alaska. Wildlife Monographs 170:1–25.

Al-Khafaji, K., S. Tuljapurkar, J. R. Carey, and R. E. Page. 2009. Hierarchical demography: a general approach with an application to honey bees. Ecology 90:556–566.

Ausband, D. E., M. S. Mitchell, C. R. Stansbury, J. L. Stenglein, and L. P. Waits. 2017. Harvest and group effects on pup survival in a cooperative breeder. Proceedings of the Royal Society of London B: Biological Sciences 284:20170580.

Ausband, D. E., C. R. Stansbury, J. L. Stenglein, J. L. Struthers, and L. P. Waits. 2015. Recruitment in a social carnivore before and after harvest. Animal Conservation 18:415–423.

Bassing, S. 2017. Harvest and persistence of wolf populations: variable effects of harvest on wolf packs in the Rocky Mountains. University of Montana.

Bassing, S. B., D. E. Ausband, M. S. Mitchell, M. K. Schwartz, J. J. Nowak, G. C. Hale, and L. P. Waits. 2020. Immigration does not offset harvest mortality in groups of a cooperatively breeding carnivore. Animal Conservation acv.12593.

Bateman, A. W., A. Ozgul, M. Krkošek, and T. H. Clutton-Brock. 2018. Matrix models of hierarchical demography: linking group- and population-level dynamics in cooperative breeders. The American Naturalist 192:188–203.

Bellman, R. E. 1957. Dynamic programming. Princeton University Press, Princeton.

Berry, M. S., N. P. Nickerson, and E. C. Metcalf. 2016. Using spatial, economic, and ecological opinion data to inform gray wolf conservation. Wildlife Society Bulletin 40:554–563.

Bischof, R., E. B. Nilsen, H. Brøseth, P. Männil, J. Ozoliņš, J. D. C. Linnell, and M. Bode. 2012. Implementation uncertainty when using recreational hunting to manage carnivores. The Journal of applied ecology 49:824–832.

Bjerke, T., and B. P. Kaltenborn. 1999. The relationship of ecocentric and anthropocentric motives to atttudes toward large carnivores. Journal of Environmental Psychology 19:415–421.

Bradley, E. H., H. S. Robinson, E. E. Bangs, K. Kunkel, M. D. Jimenez, J. A. Gude, and T. Grimm. 2015. Effects of wolf removal on livestock depredation recurrence and wolf recovery in Montana, Idaho, and Wyoming. The Journal of Wildlife Management 79:1337–1346.

Bruskotter, J. T., and L. B. Shelby. 2010. Human dimensions of large carnivore conservation and management: introduction to the special issue. Human Dimensions of Wildlife 15:311–314.

Bull, J., E. B. Nilsen, A. Mysterud, and E. J. Milner-Gulland. 2009. Survival on the border: a population model to evaluate management options for Norway's wolves Canis lupus. Wildlife Biology 15:412–424.

Chadès, I., G. Chapron, M.-J. Cros, F. Garcia, and R. Sabbadin. 2017. MDPtoolbox: Markov decision processes toolbox.

Clutton-Brock, T. 2016. Mammal societies. John Wiley & Sons, New York.

Cohen, J. B., A. Hecht, K. F. Robinson, E. E. Osnas, A. J. Tyre, C. Davis, A. Kocek, B. Maslo, and S. M. Melvin. 2016. To exclose nests or not: structured decision making for the conservation of a threatened species. Ecosphere 7:e01499.

Conroy, M. J., and J. T. Peterson. 2013. Decision making in natural resource management: a structured, adaptive approach. John Wiley & Sons.

Creel, S., M. Becker, D. Christianson, E. Dröge, N. Hammerschlag, M. W. Hayward, U. Karanth, A. Loveridge, D. W. Macdonald, W. Matandiko, J. M'Soka, D. Murray, E. Rosenblatt, and P. Schuette. 2015. Questionable policy for large carnivore hunting : U.S. wolf-hunting policies do not align with ecological theory or data. Science 350:1473–1475.

Creel, S., and J. J. Rotella. 2010. Meta-analysis of relationships between human offtake, total mortality and population dynamics of gray wolves (Canis lupus). PloS one 5:e12918.

Creel, S., J. Winnie, B. Maxwell, K. Hamlin, and M. Creel. 2005. Elk alter habitat selection as an antipredator response to wolves. Ecology 86:3387–3397.

DeCesare, N. J., S. M. Wilson, E. H. Bradley, J. A. Gude, R. M. Inman, N. J. Lance, K. Laudon, A. A. Nelson, M. S. Ross, and T. D. Smucker. 2018. Wolf-livestock conflict and the effects of wolf management. The Journal of Wildlife Management 82:711–722.

Duffield, J., C. Neher, and D. Patterson. 2006. Wolves and people in Yellowstone: impacts on the regional economy.

Ericsson, G., and T. A. Heberlein. 2003. Attitudes of hunters, locals, and the general public in Sweden now that the wolves are back. Biological Conservation 111:149–159.

Fuller, T. K., L. D. Mech, and J. Fitts-Cochran. 2003. Wolf population dynamics. Pages 161–191 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. University of Chicago Press, Chicago, Illinois.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis. Second edition. Chapman and Hall/CRC Press.

Gigliotti, L. M., and A. Harmoning. 2003. Evaluation of the North Dakota Game and Fish Department: Internal assessment. Project report for the North Dakota Game and Fish Department. Human Dimensions Consulting, Pierre, South Dakota, USA.

Gill, R. B. 1996. The wildlife professional subculture: The case of the crazy aunt. Human Dimensions of Wildlife 1:60–69.

Gregory, R., and G. Long. 2009. Using structured decision making to help implement a precautionary approach to endangered species management. Risk analysis : an official publication of the Society for Risk Analysis 29:518–32.

Gregory, R. S., and R. L. Keeney. 2002. Making smarter environmental management decisions. Journal of the American Water Resources Association 38:1601–1612.

Gude, J. A., M. S. Mitchell, R. E. Russell, C. A. Sime, E. E. Bangs, L. D. Mech, and R. R. Ream. 2012. Wolf population dynamics in the U.S. Northern Rocky Mountains are affected by recruitment and human-caused mortality. The Journal of Wildlife Management 76:108–118.

Hayes, R. D., and A. S. Harestad. 2000. Demography of a recovering wolf population in the Yukon. Canadian Journal of Zoology 78:36–48.

Hebblewhite, M. 2013. Consequences of ratio-dependent predation by wolves for elk population dynamics. Population Ecology 55:511–522.

Horne, J. S., D. E. Ausband, M. A. Hurley, J. Struthers, J. E. Berg, and K. Groth. 2019. Integrated population model to improve knowledge and management of Idaho wolves. The Journal of Wildlife Management 83:32–42.

Inman, B., K. M. Podruzny, T. D. Smucker, A. A. Nelson, M. Ross, N. Lance, T. Parks, D. K. Boyd, and S. Wells. 2019. Montana gray wolf conservation and management 2018 annual report. Helena, Montana.

Jimenez, M. D., E. E. Bangs, D. K. Boyd, D. W. Smith, S. A. Becker, D. E. Ausband, S. P. Woodruff, E. H. Bradley, J. Holyan, and K. Laudon. 2017. Wolf dispersal in the Rocky Mountains, Western United States: 1993-2008. The Journal of Wildlife Management 81:581–592.

Kapfer, P. M., and K. B. Potts. 2012. Socioeconomic and ecological correlates of bobcat harvest in Minnesota. The Journal of Wildlife Management 76:237–242.

Laporte, I., T. B. Muhly, J. A. Pitt, M. Alexander, and M. Musiani. 2010. Effects of wolves on elk and cattle behaviors: implications for livestock production and wolf conservation. PloS one 5:e11954.

Lewis, M. S., A. L. Metcalf, E. C. Metcalf, C. Phelan, J. A. Gude, Q. Kujala, and B. Inman. 2018. Better understanding Montanans thoughts regarding wolves and wolf management in Montana. Helena, Montana.

Lewis, M. S., G. Pauley, Q. Kujala, J. A. Gude, Z. King, and K. Skogen. 2012. Selected results from four separate surveys of resident Montanans regarding Montana’s wolf hunt. Helena, Montana.

Macdonald, D., and A. Loveridge, editors. 2010. The biology and conservation of wild felids. Volume 2. Oxford University Press.

Manfredo, M., T. Teel, and A. Bright. 2011. Human Dimensions of Wildlife An International Journal Why Are Public Values Toward Wildlife Changing?

Di Marco, M., L. Boitani, D. Mallon, M. Hoffmann, A. Iacucci, E. Meijaard, P. Visconti, J. Schipper, and C. Rondinini. 2014. A retrospective evaluation of the global decline of carnivores and ungulates. Conservation Biology 28:1109–1118.

Marescot, L., O. Gimenez, C. Duchamp, E. Marboutin, and G. Chapron. 2012. Reducing matrix population models with application to social animal species. Ecological Modelling 232:91–96.

McCool, S. F., and K. Guthrie. 2001. Mapping the dimensions of successful public participation in messy natural resources management situations. Society and Natural Resources 14:309–323.

McGowan, C. P., D. R. Smith, J. A. Sweka, J. Martin, J. D. Nichols, R. Wong, J. E. Lyons, L. J. Niles, K. Kalasz, J. Brust, M. Klopfer, and B. Spear. 2011. Multispecies modeling for adaptive management of horseshoe crabs and red knots in the Delaware Bay. Natural Resource Modeling 24:117–156.

Mech, L. D., and L. Boitani. 2003. Wolf social ecology. Pages 1–34 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, Illinois.

Mech, L. D., and R. O. Peterson. 2003. Wolf-prey relations. Pages 131–160 in L. D. Mech and L. Boitani, editors. Wolves: behavior, ecology and conservation. The University of Chicago Press, Chicago, Illinois.

Miller, J. R. B., K. J. Stoner, M. R. Cejtin, T. K. Meyer, A. D. Middleton, and O. J. Schmitz. 2016. Effectiveness of contemporary techniques for reducing livestock depredations by large carnivores. Wildlife Society Bulletin 40:806–815.

Montana Fish Wildlife and Parks. 2002. Montana wolf conservation and management planning document. Helena, Montana.

Muhly, T. B., and M. Musiani. 2009. Livestock depredation by wolves and the ranching economy in the Northwestern U.S. Ecological Economics 68:2439–2450.

Murray, D. L., D. W. Smith, E. E. Bangs, C. Mack, J. K. Oakleaf, J. Fontaine, D. Boyd, M. Jiminez, C. Niemeyer, T. J. Meier, D. Stahler, J. Holyan, and V. J. Asher. 2010. Death from anthropogenic causes is partially compensatory in recovering wolf populations. Biological Conservation 143:2514–2524.

O’Donnell, K. M., A. F. Messerman, W. J. Barichivich, R. D. Semlitsch, T. A. Gorman, H. G. Mitchell, N. Allan, D. Fenolio, A. Green, F. A. Johnson, A. Keever, M. Mandica, J. Martin, J. Mott, T. Peacock, J. Reinman, S. S. Romañach, G. Titus, C. P. McGowan, and S. C. Walls. 2017. Structured decision making as a conservation tool for recovery planning of two endangered salamanders. Journal for Nature Conservation 37.

Peyton, R. Ben. 2000. Wildlife management: cropping to manage or managing to crop? Wildlife Society Bulletin 28:774–779.

Poudyal, N., N. Baral, and S. T. Asah. 2016. Wolf lethal control and livestock depredations: counter-evidence from respecified models. PLOS ONE 11:e0148743.

Puterman, M. L. 2014. Markov decision processes: discrete stochastic dynamic programming. John Wiley & Sons.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Rich, L. N., R. E. Russell, E. M. Glenn, M. S. Mitchell, J. A. Gude, K. M. Podruzny, C. A. Sime, K. Laudon, D. E. Ausband, and J. D. Nichols. 2013. Estimating occupancy and predicting numbers of gray wolf packs in Montana using hunter surveys. The Journal of Wildlife Management 77:1280–1289.

Ritchie, E. G., B. Elmhagen, A. S. Glen, M. Letnic, G. Ludwig, and R. A. McDonald. 2012. Ecosystem restoration with teeth: what role for predators? Trends in ecology & evolution 27:265–271.

Robinson, O. J., C. P. McGowan, and J. J. Apodaca. 2016. Decision analysis for habitat conservation of an endangered, range-limited salamander. Animal Conservation 19:561–569.

Robinson, O. J., C. P. McGowan, and P. K. Devers. 2017. Disentangling density-dependent dynamics using full annual cycle models and Bayesian model weight updating. Journal of Applied Ecology 54:670–678.

Rogers, L. E. 2018. Wildlife values of conservation professionals: a case study of bear researchers and managers.

Rotella, J., R. Garrott, K. M. Proffitt, B. Jimenez, M. Forzley, and T. Paterson. 2018. Evaluating carnivore harvest as a tool for increasing elk calf survival and recruitment. Montana.

Runge, M. C., J. B. Grand, and M. S. Mitchell. 2013. Structured decision making. Pages 51–73 in P. R. Krausman and J. W. I. I. I. Cain, editors. Wildlife Management and Conservation: Contemporary Principles and Practices. The Johns Hopkins University Press, Baltimore, MD.

Say-Sallaz, E., S. Chamaillé-Jammes, H. Fritz, and M. Valeix. 2019. Non-consumptive effects of predation in large terrestrial mammals: mapping our knowledge and revealing the tip of the iceberg. Biological Conservation. Volume 235. Elsevier Ltd.

Schmidt, J. H., D. S. Johnson, M. S. Lindberg, and L. G. Adams. 2015. Estimating demographic parameters using a combination of known-fate and open N-mixture models. Ecology 96:2583–2589.

Sells, S. N. 2019. Mechanisms driving territorial and social behavior in a cooperative carnivore. Graduate Student Theses, Dissertations, & Professional Papers. University of Montana, Missoula.

Stenglein, J. L., J. Zhu, M. K. Clayton, and T. R. Van Deelen. 2015. Are the numbers adding up? Exploiting discrepancies among complementary population models. Ecology and Evolution 5:368–376.

Straka, T. M., K. K. Miller, and M. H. Jacobs. 2020. Understanding the acceptability of wolf management actions: roles of cognition and emotion. Human Dimensions of Wildlife 25:33–46.

Teel, T. L., and M. J. Manfredo. 2010. Understanding the diversity of public interests in wildlife conservation. Conservation Biology 24:128–139.

Teel, T. L., M. J. Manfredo, F. S. Jensen, A. E. Buijs, A. Fischer, C. Riepe, R. Arlinghaus, and M. H. Jacobs. 2010. Understanding the Cognitive Basis for Human-Wildlife Relationships as a Key to Successful Protected-Area Management. International Journal of Sociology 40:104–123.

Tortato, F. R., T. J. Izzo, R. Hoogesteijn, and C. A. Peres. 2017. The numbers of the beast: Valuation of jaguar (Panthera onca) tourism and cattle depredation in the Brazilian Pantanal. Global Ecology and Conservation 11:106–114.

Treves, A. 2009. Hunting for large carnivore conservation. Journal of Applied Ecology 46:1350–1356.

Treves, A., L. Naughton-Treves, and V. Shelley. 2013. Longitudinal analysis of attitudes toward wolves. Conservation Biology 27:315–323.

Walters, C. J., and R. Hilborn. 1978. Ecological optimization and adaptive management. Annual Review of Ecology and Systematics 157–188.

Wielgus, R. B., and K. A. Peebles. 2014. Effects of wolf mortality on livestock depredations. PLoS ONE 9.

Williams, B. K. 2009. Markov decision processes in natural resources management: observability and uncertainty. Ecological Modelling 220:830–840.

Williams, B. K., J. D. Nichols, and M. J. Conroy. 2002. Analysis and management of animal populations. Academic Press.

Williams, B. K., R. C. Szaro, and C. D. Shapiro. 2009. Adaptive management: the U.S. Department of the Interior technical guide. Adaptive Management Working Group, U.S. Department of the Interior, Washington, DC.

Williams, P. J., and W. L. Kendall. 2017. A guide to multi-objective optimization for ecological problems with an application to cackling goose management. Ecological Modelling. Volume 343. Elsevier B.V.

Woodroffe, R., H. M. K. O'Neill, and D. Rabaiotti. 2019. Within- and between-group dynamics in an obligate cooperative breeder. Journal of Animal Ecology 1365–2656.13102.

Wydeven, A. P., T. R. van Deelen, and E. Heske, editors. 2009. Recovery of gray wolves in the Great Lakes region of the United States: an endangered species success story. Springer.

Zimmermann, B., H. Sand, P. Wabakken, O. Liberg, and H. P. Andreassen. 2015. Predator-dependent functional response in wolves: from food limitation to surplus killing. The Journal of animal ecology 84:102–12.

TABLES

Table 5.1: Objectives, measurable attributes, and objective weights (relative importance) for an adaptive management framework for gray wolves in Montana. Objectives were developed in 2010 as part of a structured decision making workshop (Runge et al. 2013), and weights were assigned my MFWP representatives including supervisors, wildlife managers, and wolf specialists as part of this work.

Objective	Measureable Attribute	Weight
Reduce wolf impacts on ungulate populations	Scale: 0 (no impact) – 1 (reducing populations)	0.246
Reduce wolf impacts on livestock	# depredation events/year	0.205
Maintain viable and connected wolf population	# wolves and pups recruited	0.255
Maintain hunter opportunity for wolves	# wolves, season length, bag limit	0.183
Increase acceptance of wolf harvest and opportunity	Percent Montanans satisfied with regulations[a]	0.111

[a] We measured this as the percent of Montanans (grouped as either private landowner, deer/elk hunter, wolf hunter, or general household) satisfied with hunting season length, trapping season length, and bag limit.

FIGURES

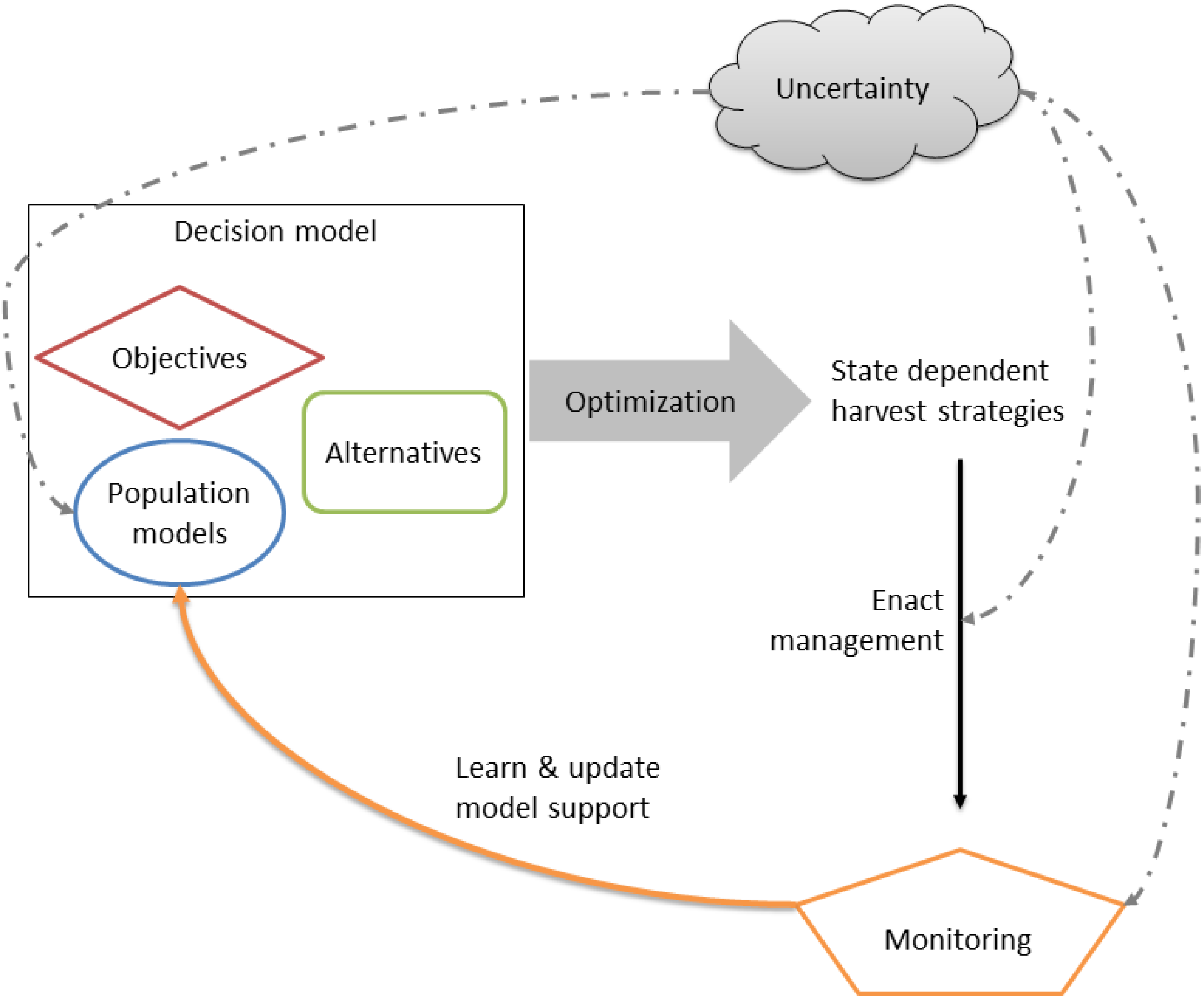

Figure 5.1: Diagram of adaptive management framework showing the five main requisite components: 1) objectives, 2) alternative management actions, 3) models to predict outcomes of actions, 4) optimization methods, and 5) a monitoring program.

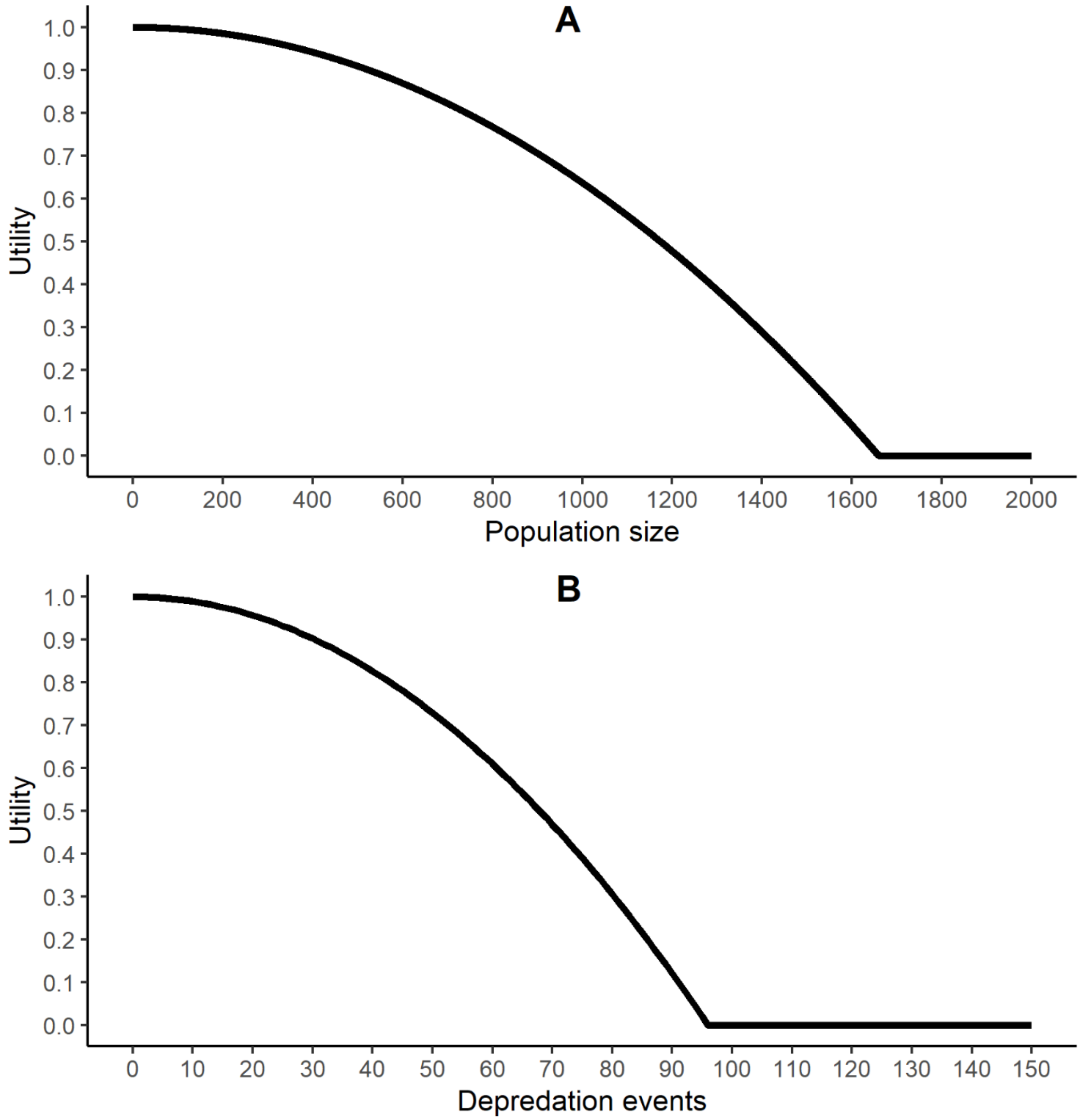

Figure 5.2: Utility functions elicited from MFWP representatives representing the relationship between A) wolf population size and the utility for reducing impacts of wolves on ungulates, and B) the number of depredation events and the utility for reducing impacts of wolves on livestock. Utilities are standardized from 0 (worst) to 1 (best). MFWP representatives included wildlife supervisors, managers, and wolf specialists.

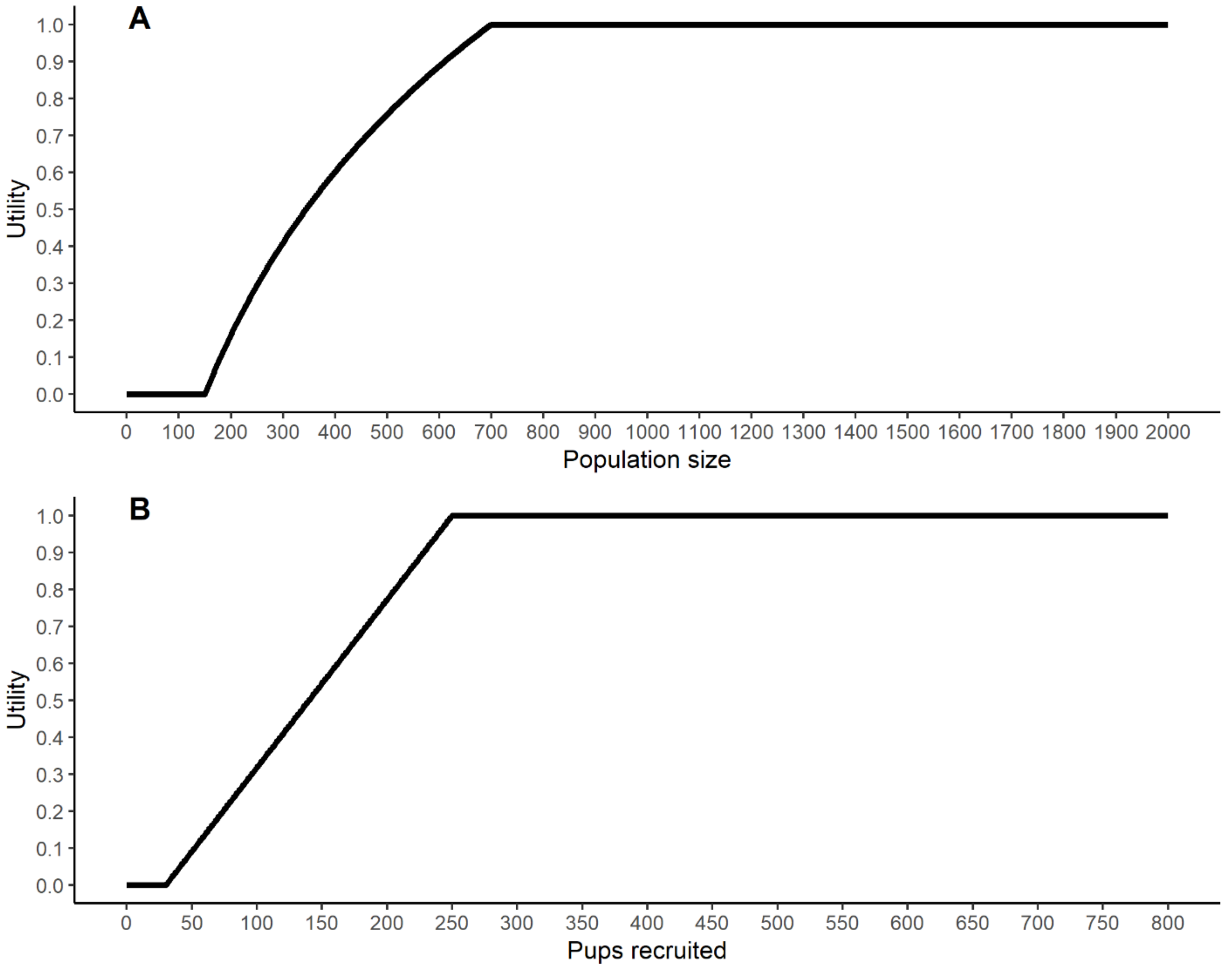

Figure 5.3: Utility functions elicited from MFWP representatives representing the relationship between A) wolf population size and the utility for maintaining a viable wolf population, and B) the number of pups recruited and the utility for maintaining a viable wolf population. Utilities are standardized from 0 (worst) to 1 (best). MFWP representatives included wildlife supervisors, managers, and wolf specialists.

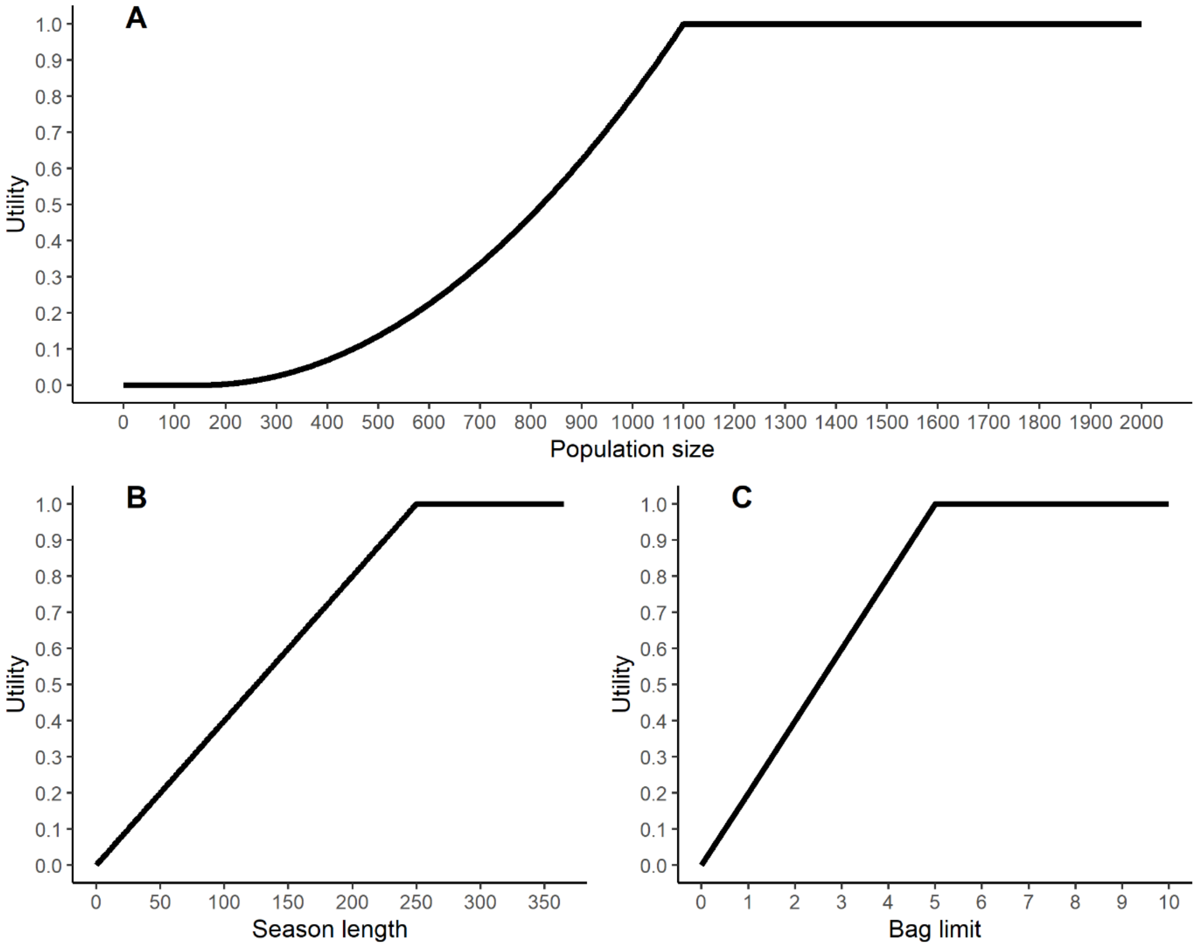

Figure 5.4: Utility functions elicited from MFWP representatives representing the relationship between A) wolf population size, B) season length, and C) bag limit and the utility for maintaining hunting opportunity for wolves. Utilities are standardized from 0 (worst) to 1 (best). MFWP representatives included wildlife supervisors, managers, and wolf specialists.

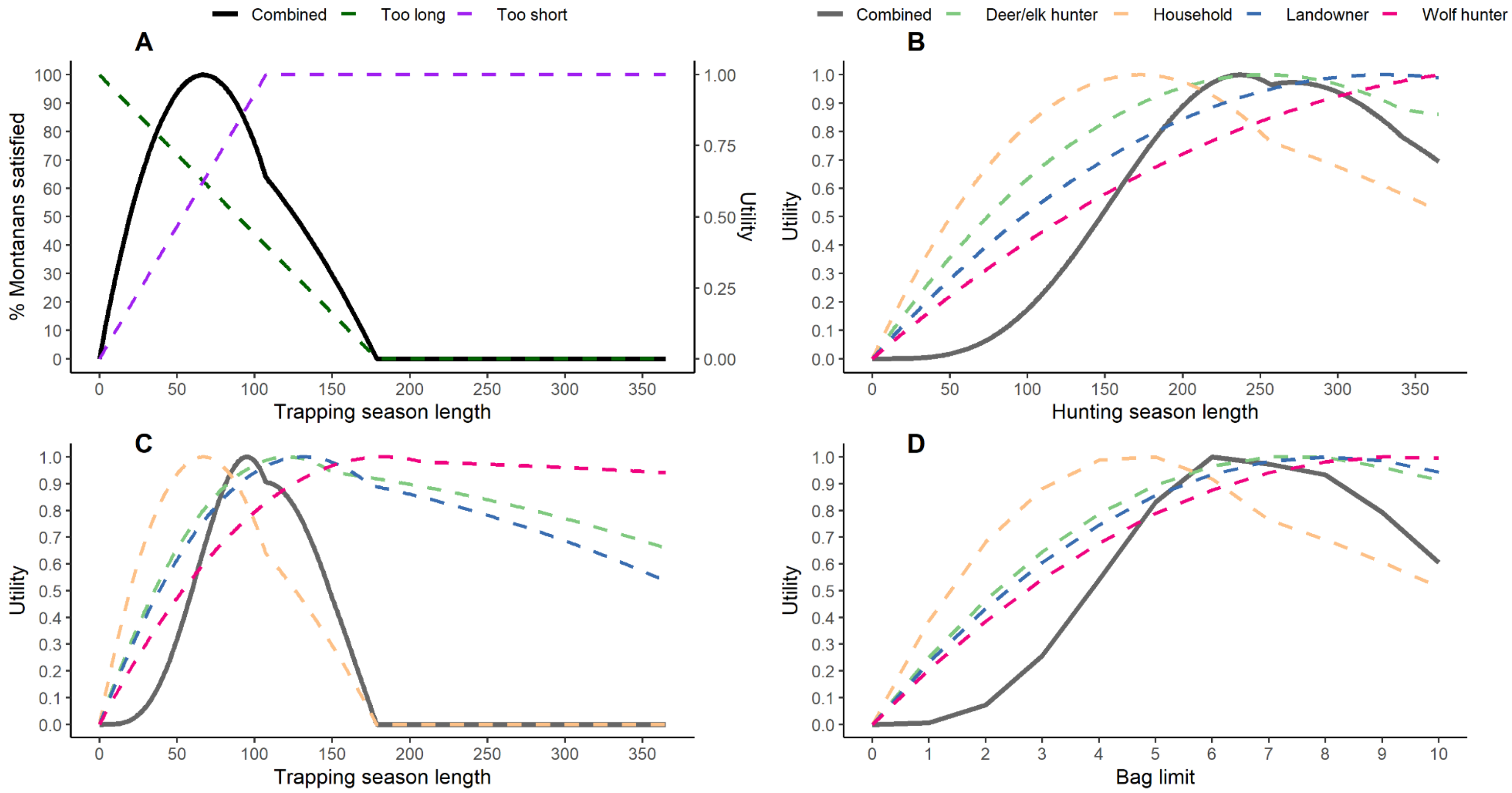

Figure 5.5: Utility functions elicited from MFWP representatives representing the relationship between B) hunting season length, C) trapping season length, and D) bag limit and the utility for increasing acceptance of harvest and hunting opportunity for wolves. Figure A demonstrates how utility functions were created from the percent Montanans that thought the season was too long and would be more satisfied with a shorter season and the percent Montanans that thought the season was too short and would be more satisfied

with a longer season. They were combined using a negative squared-loss error function. Utilities are standardized from 0 (worst) to 1 (best). MFWP representatives included wildlife supervisors, managers, and wolf specialists.

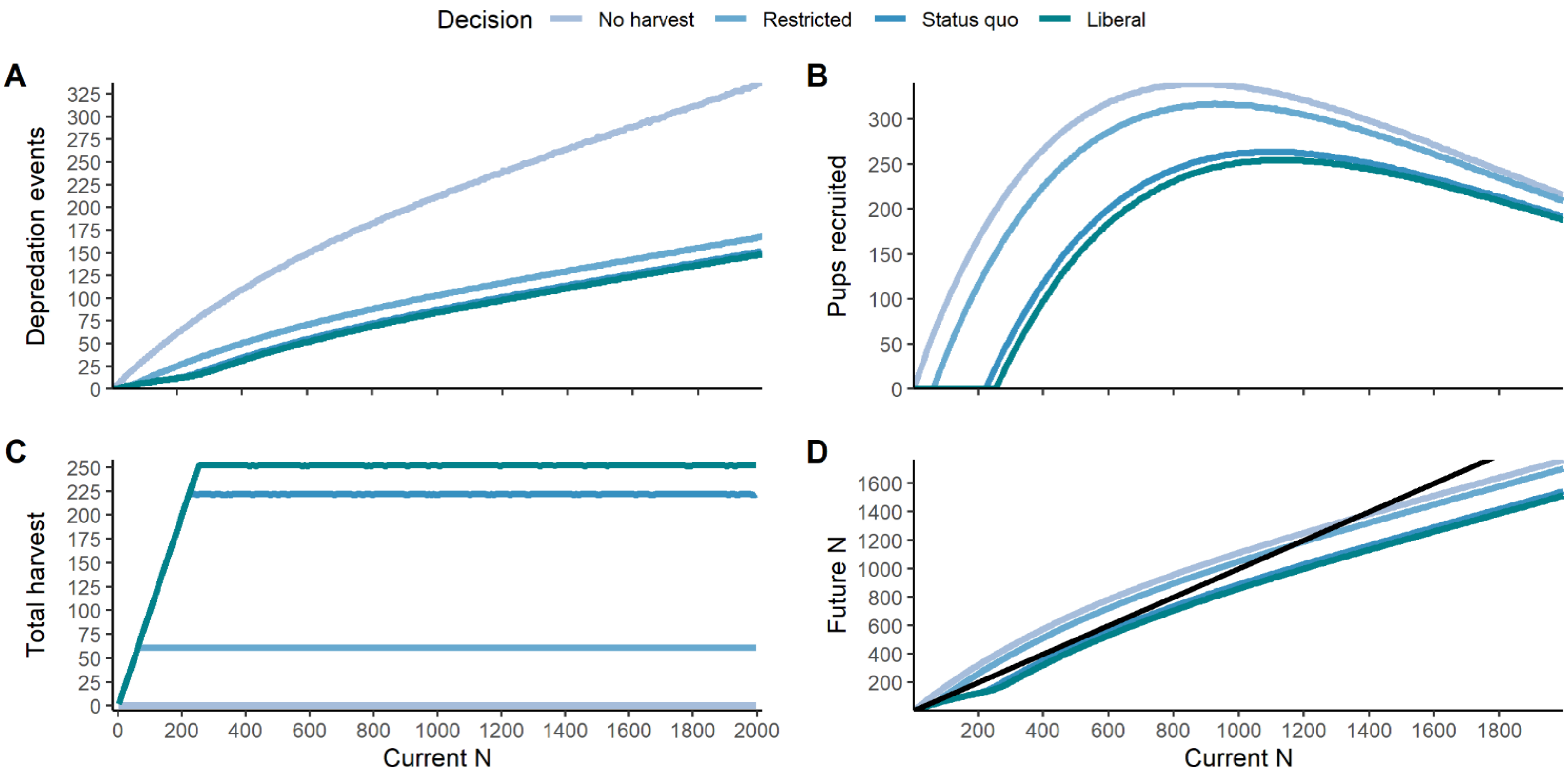

Figure 5.6: Expected future (one year) performance given current abundance from two competing models of wolf population dynamics with equal model weight under four management actions: no harvest, restricted harvest, status quo, and liberal harvest. The figures show the median expected A) number of depredation events, B) number of pups recruited, C) total harvest, and D) future population size as a function of the current state (i.e., abundance) of the population and management action. The solid black line in figure D represents a stationary population.

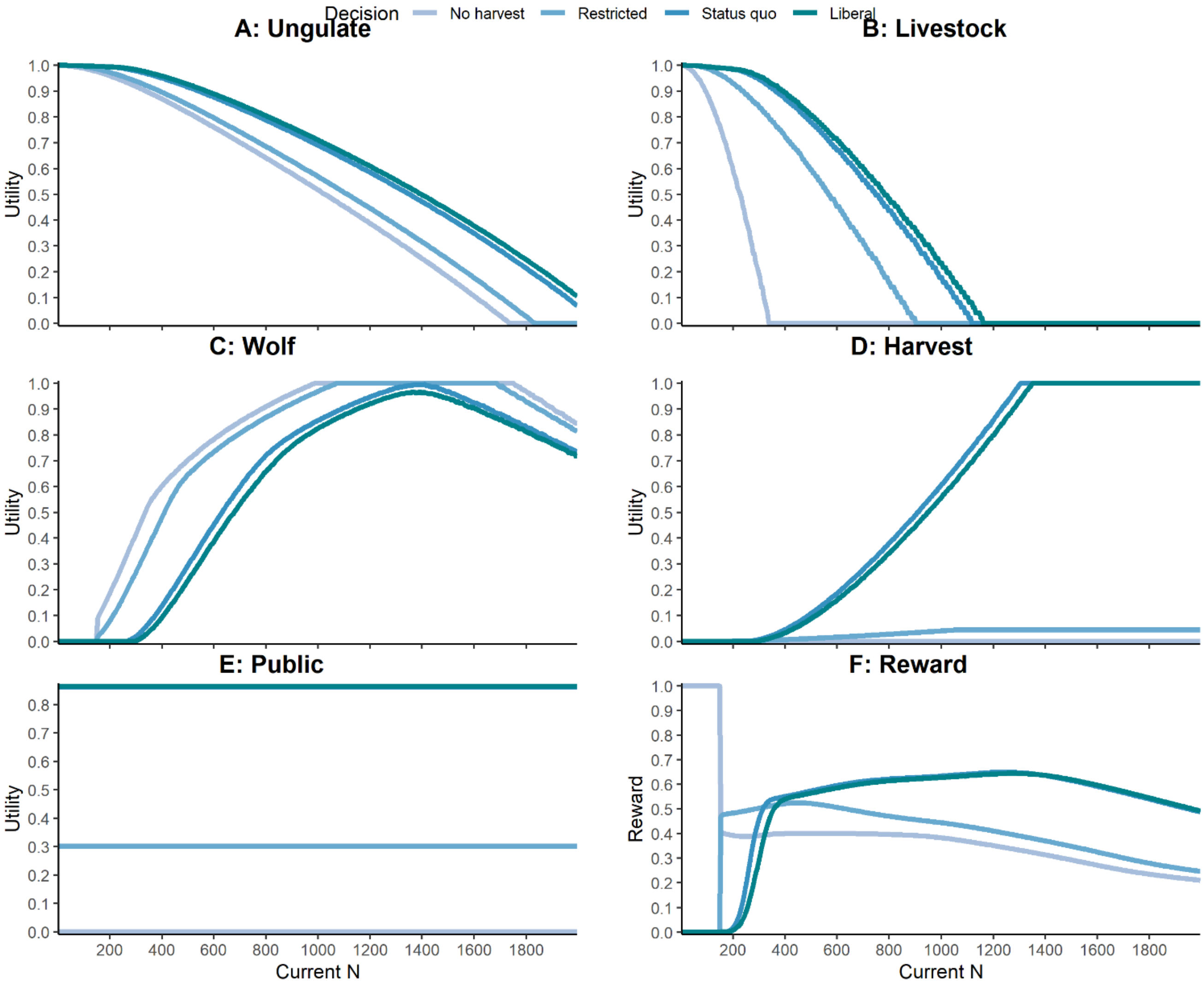

Figure 5.7: Utility values for a 1-year time step for the objectives (A-E) and the mean expected reward value for meeting all objectives (F) for harvest management of wolves in Montana, 2011-2018, as a function of current abundance (Current N). Objectives included: A) reduce impact of wolves on ungulate populations, B) reduce impact of wolves on livestock, C) maintain viable and connected wolf population, D) maintain hunter opportunity for wolves, and E) increase public acceptance of wolf harvest. The management action with the greatest utility or reward does best at meeting that objective given population size.

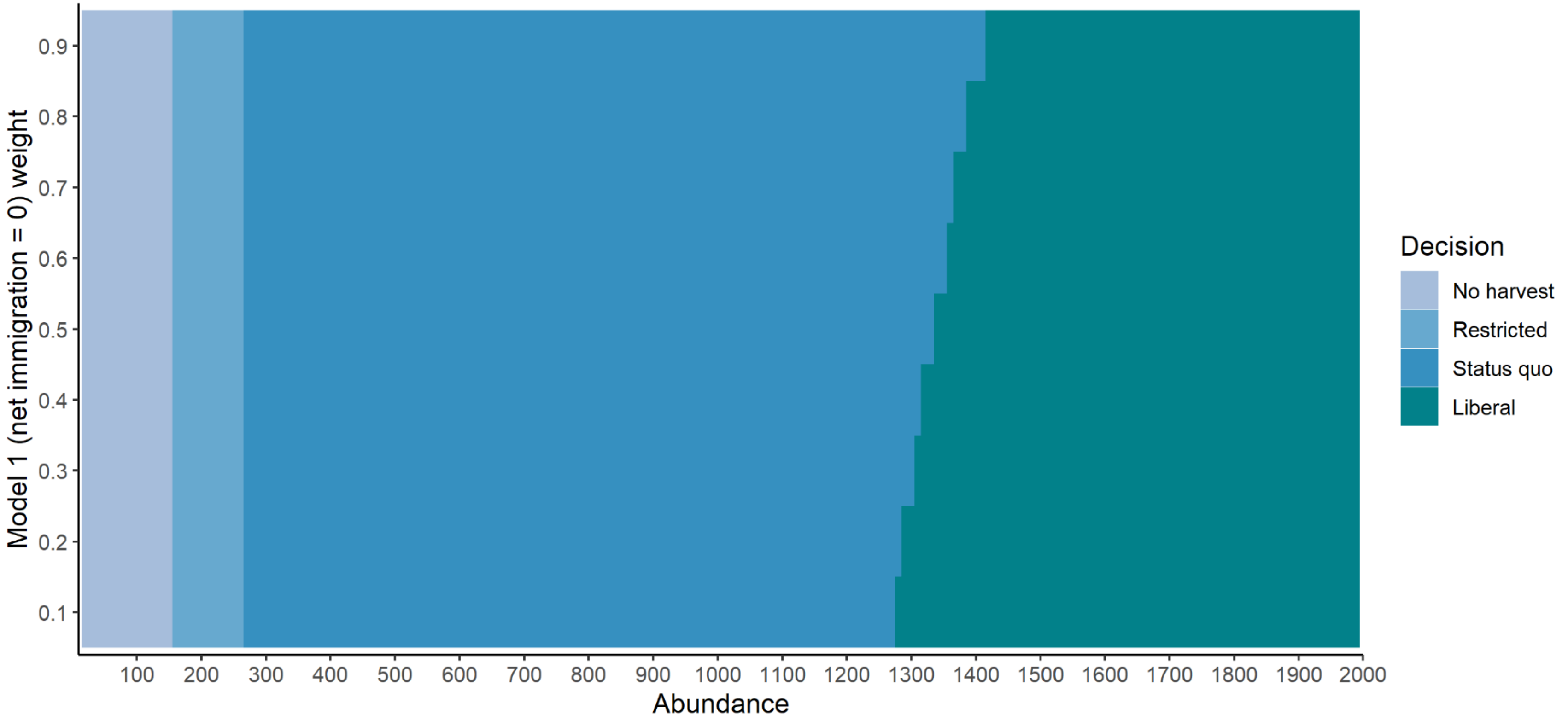

Figure 5.8: Policy plot of optimal harvest management strategies for wolves in Montana as a function of current abundance and support for the model with no net immigration (Model 1 weight). The competing model included positive net immigration into Montana. As Model 1 weight increased, support for the hypothesis of no immigration increased. Therefore, this figure demonstrates how reducing uncertainty influences optimal decisions. The decisions considered included no harvest, restricted harvest, the status quo harvest for wolves in Montana, and liberal harvest.

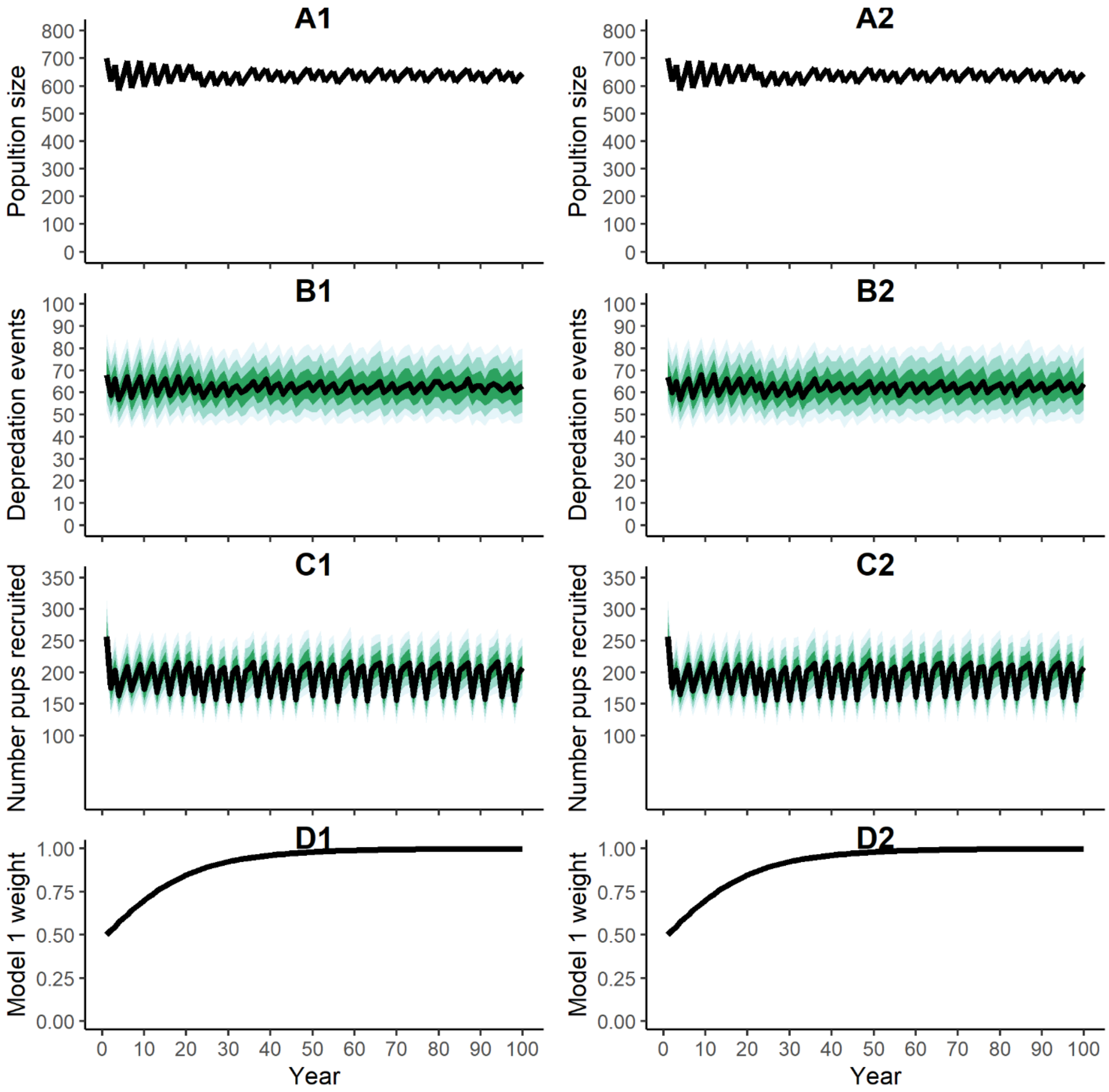

Figure 5.9: Expected performance from simulations of passive adaptive harvest management of wolves. The expected performance metrics were derived from the weighted average of two models of wolf population dynamics (model one: no net immigration, model two: positive net immigration). Performance included expected A) population size, B) number of annual depredation events, C) number of pups recruited, and D) change in model 1 (no net immigration) weight. To update model weights, we assumed that model 1 was the true model (A1, B1, C1, D1)

or that model 2 was the true model (A2, B2, C2, D2). Shaded area represents 50, 80, and 95% quantiles.

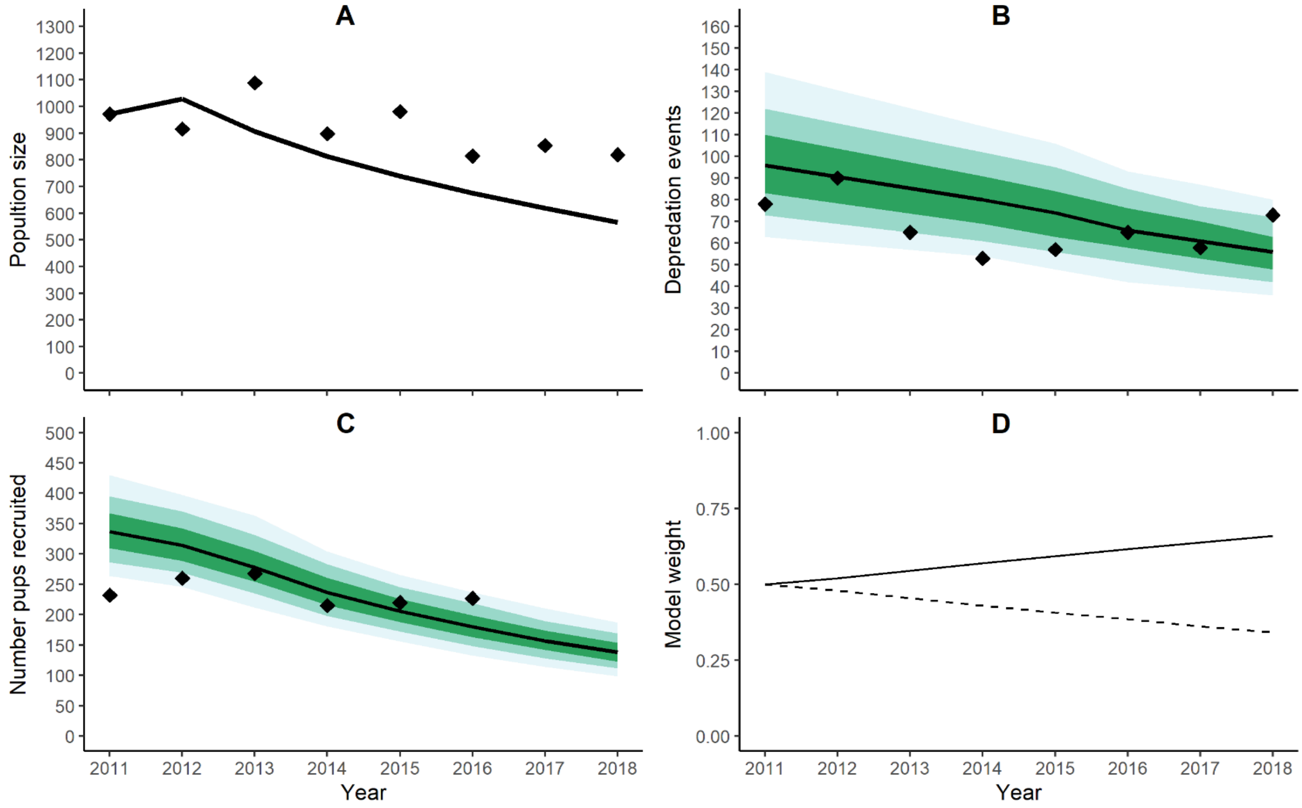

Figure 5.10: Expected annual performance from simulations of passive adaptive management for wolves in Montana from 2011 – 2018 based on harvest decisions implemented by Montana Fish, Wildlife and Parks. The expected performance metrics were derived from the weighted average of two models of wolf population dynamics (model 1: no net immigration, model 2: positive net immigration). Figures include A) predicted population size (line) compared to estimates of abundance (points), B) median number of annual depredation events (line) compared to number of verified depredation events (points), C) median number of pups recruited (line) compared to estimates of recruitment (points), and D) change in model weights with no immigration (solid) and positive immigration (dashed). Shaded area represents 50, 80, and 95% quantiles.

SUPPLEMENTARY MATERIALS

CHAPTER 1

Supplementary Material 1.A: JAGS code to fit the hierarchical demography and per capita IPMs for the Constant scenario

JAGS code to fit the per capita IPM for constant dispersal and recruitment rates for simulated populations of gray wolves (*Canis lupus*).

```
#### PRIORS ####______________________________________________________

  # Population
  N[1] ~ dpois(6 * 100)
  tauy.pop <- pow(sigma.pop, -2)
  sigma.pop ~ dunif(0, 75)
  var.pop <- pow(sigma.pop, 2)

  # Survival
  b0.surv ~ dnorm(0,0.001)
  for(k in 1:(nyears-1)){
    eps.surv[k] ~ dnorm(0, tau.surv)
  }
  sigma.surv ~ dunif(0, 50)
  tau.surv <- pow(sigma.surv, -2)
  var.surv <- pow(sigma.surv, 2)

  # Dispersal
  b0.disp ~ dunif(-10,10)

  # Recruitment
  b0.gam ~ dunif(-10,10)


  #### LIKELIHOODS ####________________________________________________

  # Population__________________________
  for(k in 2:nyears){
    N.surv[k] ~ dbin(annual.s[k-1] * (1 - em.group[k-1]), N[k-1])
    N.rec[k] ~ dpois(N[k-1] * pgamma[k-1])
```

```
  N[k] <- N.surv[k] + N.rec[k]
}

for(k in 1:nyears){
  y.pop[k] ~ dnorm(N[k], tauy.pop)T(0,)
}

# Survival____________________________
for(k in 1:(nyears-1)){
  for(i in 1:nobs){
    event[i,k] ~ dbern(mu.surv[i,k])
    cloglog(mu.surv[i,k]) <- b0.surv + eps.surv[k]
  }
}

for(k in 1:(nyears-1)){
  cloglog(mu.pred[k]) <- b0.surv + eps.surv[k]
  hazard[k] <- -log(1-mu.pred[k])
}

for(k in 1:(nyears-1)){
  H[k] <- hazard[k]
  annual.s[k] <- exp(-H[k])
}

# Dispersal___________________________________
for(k in 1:(nyears-1)){
  logit(em.group[k]) <- b0.disp

  for(i in 1:ndisp){
    y.disp[i,k] ~ dbern(em.group[k])
  }
}

# Recruitment________________________________
for(k in 1:(nyears - 1)){
  logit(pgamma[k]) <- b0.gam
}#i
```

JAGS code to fit the hierarchical demography IPM for constant dispersal and recruitment rates for simulated populations of gray wolves (*Canis lupus*).

```
#### PRIORS ####________________________________________________________

  # Population
  N[1] ~ dpois(Z[1] * 6)
  tauy.pop <- pow(sigma.pop, -2)
  sigma.pop ~ dunif(0, 75)
  var.pop <- pow(sigma.pop, 2)

  # Number of packs
  Z[1] ~ dpois(100)
  tauy.z <- pow(sigma.z, -2)
  sigma.z ~ dunif(0, 20)
  var.z <- pow(sigma.z, 2)

  # Group formation
  p.form ~ dunif(0, 1)
  b0.form ~ dnorm(0,0.001)
  for(k in 1:(nyears-1)){
    eps.form[k] ~ dnorm(0, tau.form)
  }
  sigma.form ~ dunif(0, 50)
  tau.form <- pow(sigma.form, -2)
  var.form <- pow(sigma.form, 2)

  # Group persistence
  b0.persist ~ dnorm(0,0.001)
  for(k in 1:(nyears-1)){
    eps.persist[k] ~ dnorm(0, tau.persist)
  }
  sigma.persist ~ dunif(0, 50)
  tau.persist <- pow(sigma.persist, -2)
  var.persist <- pow(sigma.persist, 2)

  # Group size
  p.G ~ dunif(0, 1)
  lambda ~ dgamma(0.005, 0.005)
```

```
# Survival
b0.surv ~ dnorm(0,0.001)
for(k in 1:(nyears-1)){
  eps.surv[k] ~ dnorm(0, tau.surv)
}
sigma.surv ~ dunif(0, 50)
tau.surv <- pow(sigma.surv, -2)
var.surv <- pow(sigma.surv, 2)

# Dispersal
b0.disp ~ dunif(-10,10)

# Recruitment
b0.gam ~ dnorm(0,0.001)


#### LIKELIHOODS ####______________________________________________________

# Population_________________________
for(k in 2:nyears){
  N[k] <- sum(G[,k]) + (Z[k] - ngroups) * mean.G[k]
}

for(k in 1:nyears){
  y.pop[k] ~ dnorm(N[k], tauy.pop)T(0,)
}

# Number of packs_____________________
for(k in 2:nyears){
  Z.pers[k] ~ dbin(psi[k-1], Z[k-1])
  Z[k] <- Z.pers[k] + F[k]
}

for(k in 1:nyears){
  y.z[k] ~ dnorm(Z[k], tauy.z)T(0,)
}

# Group formation_____________________
for(k in 1:(nyears - 1)){
  muF[k] <- exp(b0.form + eps.form[k])
  F[k] ~ dpois(muF[k])
}

for(k in 1:(nyears - 1)){
  y.form[k] ~ dbin(p.form, F[k])
```

```
}

# Group persistence____________________
for(k in 1:(nyears - 1)){
  logit(psi[k]) <- b0.persist + eps.persist[k]
}
for(k in 1:(nyears - 1)){
  y.persist[k] ~ dbin((1-psi[k]), ngroups)
}

# Group size____________________________
for(i in 1:ngroups) {
  G[i, 1] ~ dpois(lambda)T(2,)
  for(k in 2:nyears){
    mu.g[i,k] ~ dbin(annual.s[k-1] * (1 - em.group[i,k-1]), G[i,k-1])
    G[i,k] <- mu.g[i,k] + gamma[i,k-1]
  }
}

for(i in 1:ngroups){
  for(k in 1:nyears){
    y.group[i,k] ~ dbin(p.G, G[i,k])
  }
}

# Survival___________________________
for(k in 1:(nyears-1)){
  for(i in 1:nobs){
    event[i,k] ~ dbern(mu.surv[i,k])
    cloglog(mu.surv[i,k]) <- b0.surv + eps.surv[k]
  }
}

for(k in 1:(nyears-1)){
  cloglog(mu.pred[k]) <- b0.surv + eps.surv[k]
  hazard[k] <- -log(1-mu.pred[k])
}

for(k in 1:(nyears-1)){
  H[k] <- hazard[k]
  annual.s[k] <- exp(-H[k])
}

# Dispersal__________________________________
for(k in 1:(nyears-1)){
  for(i in 1:ndisp){
```

```
    logit(disp[i,k]) <- b0.disp
  }
}

for(k in 1:(nyears - 1)){
  for(i in 1:ngroups){
    logit(em.group[i,k]) <- b0.disp
  }
}

for(k in 1:(nyears-1)){
  for(i in 1:ndisp){
    y.disp[i,k] ~ dbern(disp[i,k])
  }
}

# Recruitment________________________________
for(i in 1:ngroups){
  for(k in 1:(nyears - 1)){
    mu.gamma[i,k] <- exp(b0.gam)
    gamma[i,k] ~ dpois(mu.gamma[i,k])
  }
}


#### Derived parameters ####__________________________________________________

for(k in 1:(nyears-1)){
  mean.gamma[k] <- mean(gamma[,k])
  mean.delta[k] <- mean(em.group[,k])
}

for(k in 1:nyears){
  mean.G[k] <- mean(G[,k])
}
```

CHAPTER 2

Supplementary Material 2.A: Biological and monitoring timeline for gray wolves in Montana

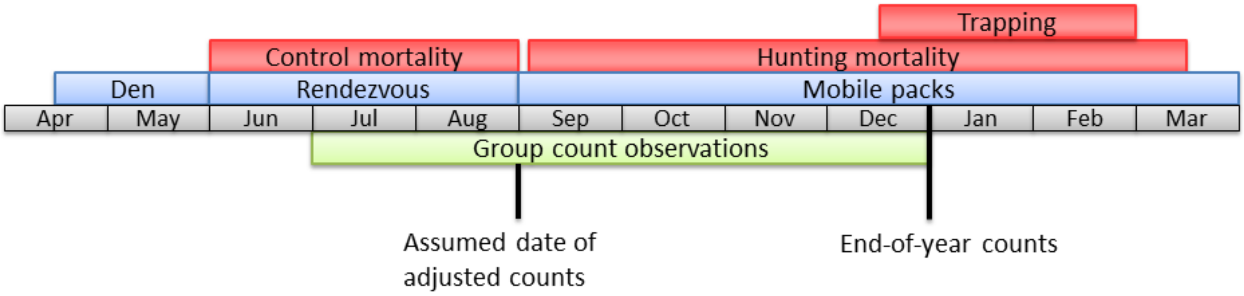

Figure 1: Biological and monitoring timeline for gray wolves in Montana from 2007-2016. Red boxes represent sources of mortality, blue boxes represent biological periods when the pack is denning, using rendezvous sites, or mobile, and the green box represents observations for group counts. Biologists would increase monitoring efforts each December to provide end-of-year counts. The number of wolves harvested and removed for control removals was also recorded for the end of each calendar year. We added the number of wolves harvested from each pack to the end-of-year counts for our adjusted group count data.

Supplementary Material 2.B: JAGS code to an IPM for gray wolves

```
### PRIORS ###_____________________________________________________________

  ## Population
  N[1] ~ dnorm(550, 0.0004)I(0,)
  tauy.pop <- pow(sigma.pop, -2)
  sigma.pop ~ dunif(0, 75)
  var.pop <- pow(sigma.pop, 2)

  ## Number of packs
  Z[1] ~ dnorm(80, 0.01)I(0,)
  tauy.z <- pow(sigma.z, -2)
  sigma.z ~ dunif(0, 10)
  var.z <- pow(sigma.z, 2)
  sd.z.proc ~ dunif(0, 10)
  var.z.proc <- pow(sd.z.proc, 2)
  tau.z.proc <- pow(sd.z.proc, -2)

  ## Pack growth rate
  for(k in 1:(nyears - 1)){
    group.gr[k] ~ dgamma(p.gr[k]^2 / .0158632, p.gr[k] / .0158632)I(0.1,)
  }

  ## Group size
  p.G ~ dunif(0, 1)
  lambda ~ dgamma(0.005, 0.005)

  ## Survival
  sigma.surv ~ dunif(0, 50)
  tau.surv <- pow(sigma.surv, -2)
  var.surv <- pow(sigma.surv, 2)
  for(k in 1:(nyears + 1)){
    eps.surv[k] ~ dnorm(0, tau.surv)
  }
  for(p in 1:nperiods){
    b.period.surv[p] ~ dnorm(0, 0.001)
  }


  ## Dispersal
  for(k in 1:(nyears - 1)){
    em.group[k] ~ dbeta(alpha, beta)
  }
```

```
## Recruitment
b0.gam ~ dnorm(0, 0.001)
sigma.gam ~ dunif(0, 50)
tau.gam <- pow(sigma.gam, -2)
var.gam <- pow(sigma.gam, 2)
for(k in 1:(nyears-1)){
  eps.gam[k] ~ dnorm(0, tau.gam)
}

b0.gam.17 ~ dnorm(0, 0.001)
sigma.gam.17 ~ dunif(0, 50)
tau.gam.17 <- pow(sigma.gam.17, -2)
var.gam.17 <- pow(sigma.gam.17, 2)
for(k in 1:(nyears-2)){
  eps.gam.17[k] ~ dnorm(0, tau.gam.17)
}



### LIKELIHOOD ###_______________________________________________________

## Population
for(k in 2:nyears){
  N[k] <- sum(G[,k]) + (Z[k] - P[k]) * G.mean[k]
}

for(k in 1:nyears){
  y.pop[k] ~ dnorm(N[k], tauy.pop)
}

## Number of packs
for(k in 2:nyears){
  mu.Z[k] <- Z[k-1] * group.gr[k-1]
  Z[k] ~ dnorm(mu.Z[k], tau.z.proc)
}

for(k in 1:nyears){
  y.Z[k] ~ dnorm(Z[k], tauy.z)
}

## Group size
for(i in 1:ngroups){
  G[i, first[i]] ~ dpois(lambda)T(2,)
  for(k in (first[i] + 1)){
    g.mu[i,k] <- G[i,k-1] * annual.s[k-1] * (1 - em.group[k-1]) + gamma[i,k-1] - C[i, k-1]
    G[i,k] ~ dpois(g.mu[i,k])T(2,)
```

```
    }

    for(k in (first[i] + 2):last[i]){
      g.mu[i,k] <- G[i,k-2] * annual.s[k-2] * (1 - em.group[k-2]) * annual.s[k-1] * (1 -
em.group[k-1]) + gamma[i,k-1] + gamma.17[i,k-2] - C[i, k-1] - C[i, k-2]
      G[i,k] ~ dpois(g.mu[i,k])T(2,)
    }
  }

  # Observation proccess
  for(i in 1:ngroups){
    for(k in first[i]:last[i]){
      y.group[i,k] ~ dbin(p.G, G[i,k])
    }
  }

  ## Survival
  for(i in 1:nobs){
    event[i] ~ dbern(mu.surv[i])
    cloglog(mu.surv[i]) <- b.period.surv[Period[i]] + eps.surv[Year[i]]
  }

  # Predicted values
  for(k in 1:(nyears + 1)){
    for(p in 1:nperiods){
      cloglog(mu.pred[p,k]) <- b.period.surv[p] + eps.surv[k]
      hazard[p,k] <- -log(1 - mu.pred[p,k])
    }
  }
  for(k in 1:(nyears + 1)){
    base.H[1,k] <- hazard[1,k] * width.interval[1]
    for(p in 2:nperiods){
      base.H[p,k] <- base.H[p-1,k] + hazard[p,k] * width.interval[p]
    }
  }
  for(k in 1:(nyears + 1)){
    for(p in 1:nperiods){
      base.s[p,k] <- exp(-base.H[p,k])
      noncuml.s[p,k] <- exp(-(hazard[p,k] * width.interval[p]))
    }
    annual.s[k] <- base.s[length(width.interval),k]
  }

  ## Recruitment
  for(i in 1:ngroups){
    for(k in first[i]:(last[i] - 1)){
```

```
    mu.gamma[i, k] <- exp(b0.gam + eps.gam[k])
    gamma[i, k] ~ dpois(mu.gamma[i,k])
  }
}

for(i in n17groups) {
  for(k in first[i]:(last[i] - 2)) {
    mu.gamma.17[i, k] <- exp(b0.gam.17 + eps.gam.17[k])
    gamma.17[i, k] ~ dpois(mu.gamma.17[i,k])
  }
}


### DERIVED PARAMETERS ###_______________________________________________
for(k in 2:nyears){
  pop.growth[k] <- N[k] / N[k-1]
  logla[k] <- log(pop.growth[k])
  N.rec[k] <- Z[k-1] * gamma.mean[k-1]
}

for(k in 2:(nyears-1)){
  N.rec.17[k] <- Z[k-1] * gamma.mean.17[k-1]
}

# Geometric mean lambda
mlam <- exp((1 / (nyears - 1)) * sum(logla[2:nyears]))

# Mean group size and recruitment
for(k in 1:nyears){
  G.mean[k] <- sum(G[,k])/ P[k]
}

for(k in 1:(nyears-1)){
  gamma.mean[k] <- sum(gamma[,k]) / P[k]
}

for(k in 1:(nyears-2)){
  gamma.mean.17[k] <- sum(gamma.17[,k]) / P[k]
}

# Survival and recruitment during years with and without harvest
s.no <- mean(annual.s[c(1:2,4)])
s.harv <- mean(annual.s[c(3,5:11)])
rec.no <- mean(gamma.mean[c(1:2,4)])
rec.harv <- mean(gamma.mean[c(3,5:9)])
rec.no.17 <- mean(gamma.mean.17[c(1:2,4)])
```

```
rec.harv.17 <- mean(gamma.mean.17[c(3,5:8)])

# Survival by period
for(p in 1:nperiods){
  s.p[p] <- mean(noncuml.s[p,])
  s.p.no[p] <- mean(noncuml.s[p,c(1:2,4)])
  s.p.harv[p] <- mean(noncuml.s[p,c(3,5:11)])
}
```

CHAPTER 3

Supplementary Material 3.A: Initial model selection and model fit for top models

Table 1: Initial model selection for the prey and population and pack characteristic (intrinsic) hypotheses for models fit to litter size (l) for wolves in Idaho using leave-one-out cross-validation information criteria (LOO) and the difference in the expected log predictive density (ΔELPD). Models in bold were used for the final model selection step. Independent variables included pack size (PS), abundance (PA), winter severity (WS), deer index (DR), and elk index (E). We also included a random effect of pack (α_p).

Model	Hypothesis	K	LOO (SE)	ΔLOO	ΔELPD (SE)
$\boldsymbol{l \sim b_0 + PS + \alpha_p}$	**Intrinsic**	**3**	**229.3 (7.62)**	**0**	**0 (0)**
$l \sim b_0 + PA + \alpha_p$	Intrinsic	3	230.4 (7.73)	1.1	0.51 (0.712)
$l \sim b_0 + PS + PA + \alpha_p$	Intrinsic	4	231.2 (7.74)	1.9	0.94 (0.232)
$\boldsymbol{l \sim b_0 + DR + \alpha_p}$	**Prey**	**3**	**229.9 (7.67)**	**0**	**0 (0)**
$l \sim b_0 + E + \alpha_p$	Prey	3	230.2 (7.75)	0.3	0.11 (0.381)
$l \sim b_0 + WS + \alpha_p$	Prey	3	230.4 (7.65)	0.5	0.22 (0.544)
$l \sim b_0 + WS + DR + \alpha_p$	Prey	4	232.0 (7.77)	2.1	1.03 (0.415)
$l \sim b_0 + WS + E + \alpha_p$	Prey	4	232.1 (7.88)	2.2	1.05 (0.658)

Table 2: Initial model selection for the prey, population and pack characteristic (intrinsic), and harvest hypotheses for models fit to pup survival (ϕ) for wolves in Idaho using leave-one-out cross-validation information criteria (LOO) and the difference in the expected log predictive density (ΔELPD). Models in bold were used for the final model selection step. Independent variables included harvest (H), pack size (PS), abundance (PA), winter severity (WS), deer index (DR), elk index (E), a random effect of pack (α_p), and a random effect of year (ε_t).

Model	Hypothesis	K	LOO (SE)	Δ LOO	Δ ELPD (SE)
$\boldsymbol{\phi \sim b_0 + H + \alpha_p + \varepsilon_t}$	**Harvest**	**4**	**177.6 (12.97)**	**0**	**0 (0)**
$\phi \sim b_0 + \alpha_p + \varepsilon_t$	Harvest	3	179.5 (14.15)	1.9	0.94 (1.044)
$\boldsymbol{\phi \sim b_0 + PA + \alpha_p + \varepsilon_t}$	**Intrinsic**	**4**	**178.4 (14.35)**	**0**	**0 (0)**
$\phi \sim b_0 + PS + \alpha_p + \varepsilon_t$	Intrinsic	4	179.7 (13.32)	1.3	0.64 (1.439)
$\phi \sim b_0 + PA + PS + \alpha_p + \varepsilon_t$	Intrinsic	5	181.3 (13.88)	2.9	1.50 (1.257)
$\phi \sim b_0 + E + \alpha_p + \varepsilon_t$	Prey	4	177.4 (13.79)	0	0 (0)*****
$\phi \sim b_0 + WS + E + \alpha_p + \varepsilon_t$	Prey	5	177.7 (13.49)	0.3	0.18 (0.724)*
$\boldsymbol{\phi \sim b_0 + DR + \alpha_p + \varepsilon_t}$	**Prey**	**4**	**177.8 (14.04)**	**0.4**	**0.24 (2.156)**
$\phi \sim b_0 + WS + \alpha_p + \varepsilon_t$	Prey	4	178.4 (13.33)	0.7	0.51 (0.946)
$\phi \sim b_0 + WS + DR + \alpha_p + \varepsilon_t$	Prey	5	179.5 (13.95)	1.8	1.08 (1.284)

*Although this model had the smallest ΔELPD there was no effect of elk because the 50% CRI contained 0, therefore it was not supported and we selected the next best model that did not include elk for the next step in model selection.

Table 3: Initial model selection for the prey availability and population and pack characteristic (intrinsic) for models fit to multiple breeding females (m) for wolves in Idaho using leave-one-out cross-validation information criteria (LOO) and the difference in the expected log predictive density (ΔELPD). Models in bold were used for the final model selection step. Independent variables included pack size (PS), abundance (PA), winter severity (WS), deer index (DR), and elk index (E).

Model	Hypothesis	K	LOO (SE)	Δ LOO	Δ ELPD (SE)
$\boldsymbol{m \sim b_0 + PS}$	**Intrinsic**	**2**	**42.4 (9.89)**	**0**	**0 (0)**
$m \sim b_0 + PA + PS$	Intrinsic	3	42.8 (9.99)	0.4	0.21 (0.075)
$m \sim b_0 + PA$	Intrinsic	2	43.9 (10.19)	1.5	0.72 (1.736)
$\boldsymbol{m \sim b_0 + WS + DR}$	**Prey**	**3**	**37.3 (9.70)**	**0**	**0 (0)**
$m \sim b_0 + DR$	Prey	2	40.2 (9.25)	2.9	1.45 (1.081)
$m \sim b_0 + WS$	Prey	2	40.9 (10.31)	3.6	1.80 (1.271)
$m \sim b_0 + WS + E$	Prey	3	41.1 (10.41)	3.8	1.87 (1.196)
$m \sim b_0 + E$	Prey	2	44.6 (10.39)	7.3	3.63 (1.938)

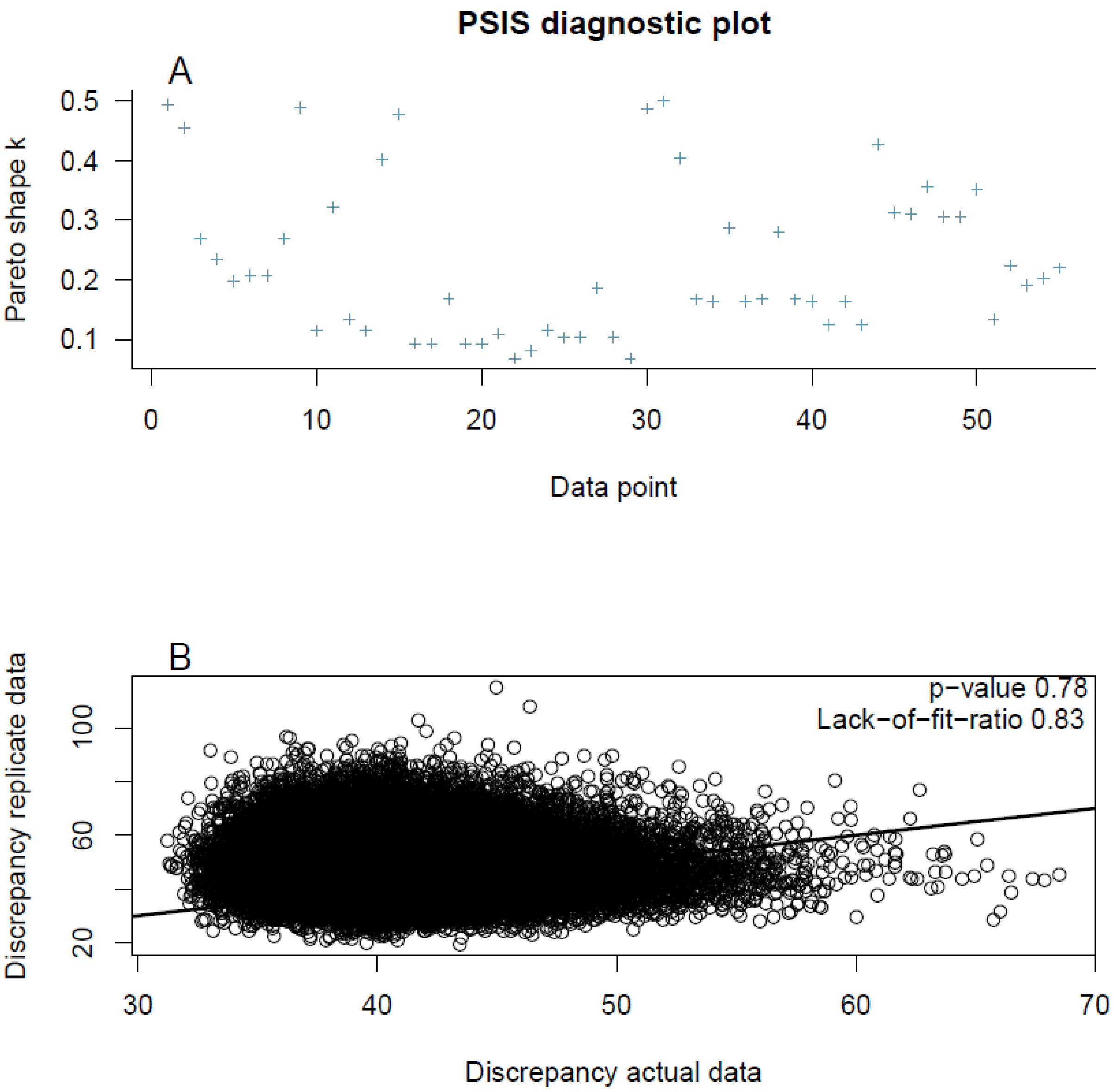

Figure 1: Model adequacy and fit for the top model ($l \sim b_0 + \alpha_p$) fit to litter size (l) of wolves in Idaho with a random effect of pack (α_p); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) Posterior predictive check with χ^2-discrepancy statistic. Bayesian p-value close to 0.5 and lack-of-fit ratio close to 1 represent better model fit.

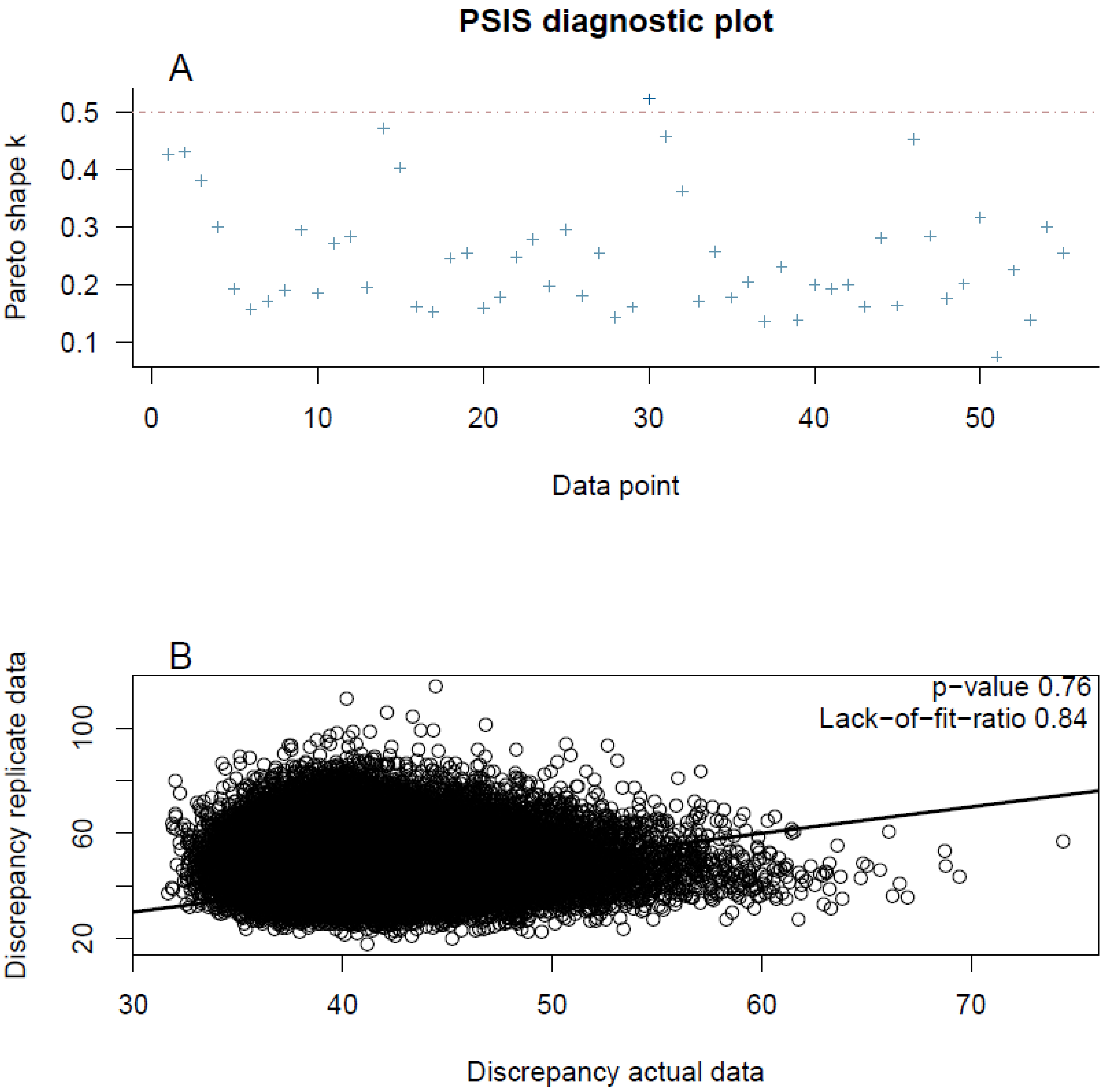

Figure 2: Model adequacy and fit for the pack size model ($l \sim b_0 + PS + \alpha_p$) fit to litter size ($l$) of wolves in Idaho with independent variables for pack size (PS) and a random effect of pack (α_p); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) Posterior predictive check with χ^2-discrepancy statistic. Bayesian p-value close to 0.5 and lack-of-fit ratio close to 1 represent better model fit.

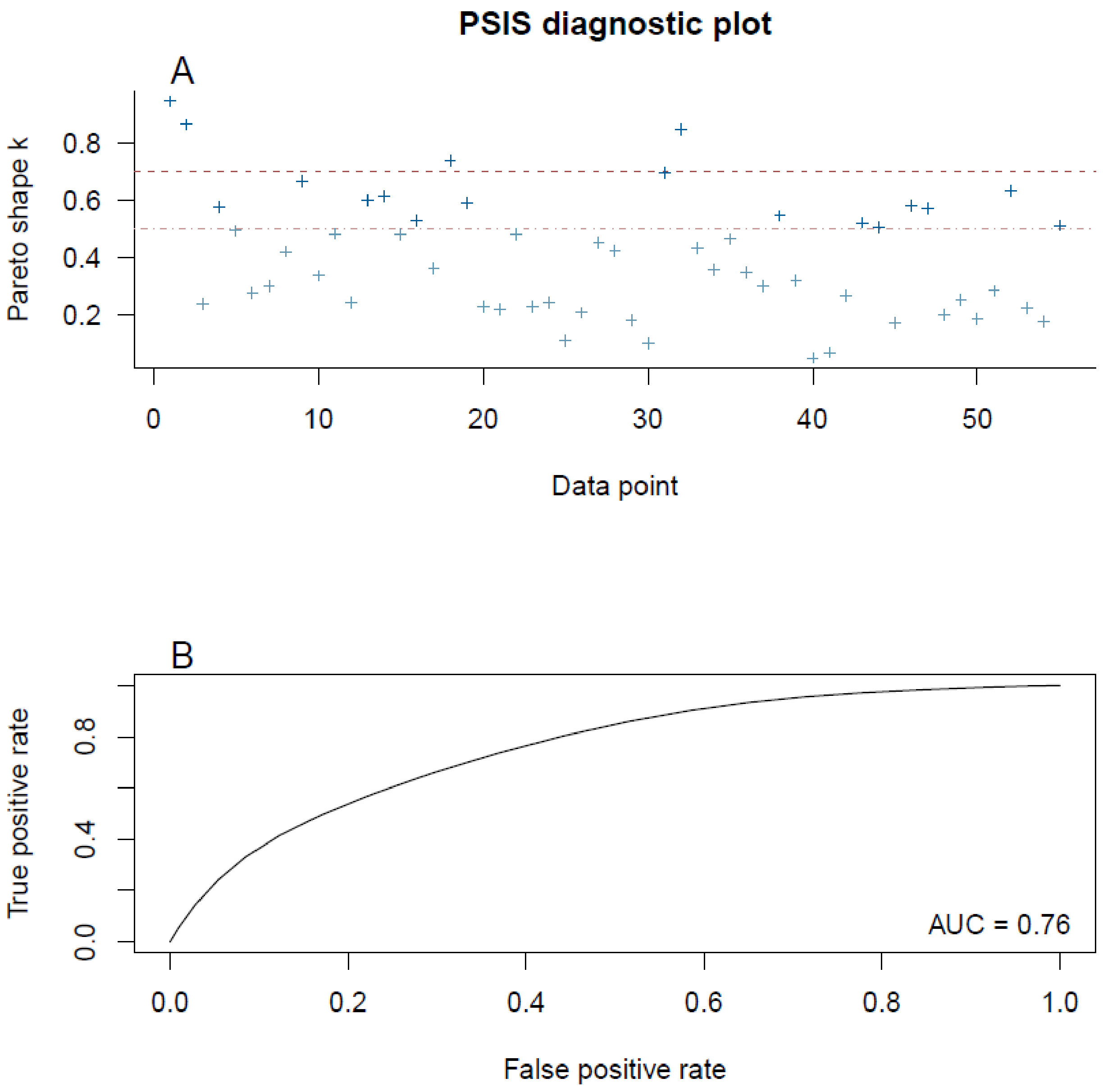

Figure 3: Model adequacy and fit for the prey availability, abundance, and harvest model ($\phi \sim b_0 + DR + PA + H + \alpha_p + \varepsilon_t$) fit to pup survival ($\phi$) of wolves in Idaho with independent variables for deer index (DR), abundance (PA), harvest (H), and a random effect for pack (α_p) and year (ε_t); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) ROC curve and AUC value.

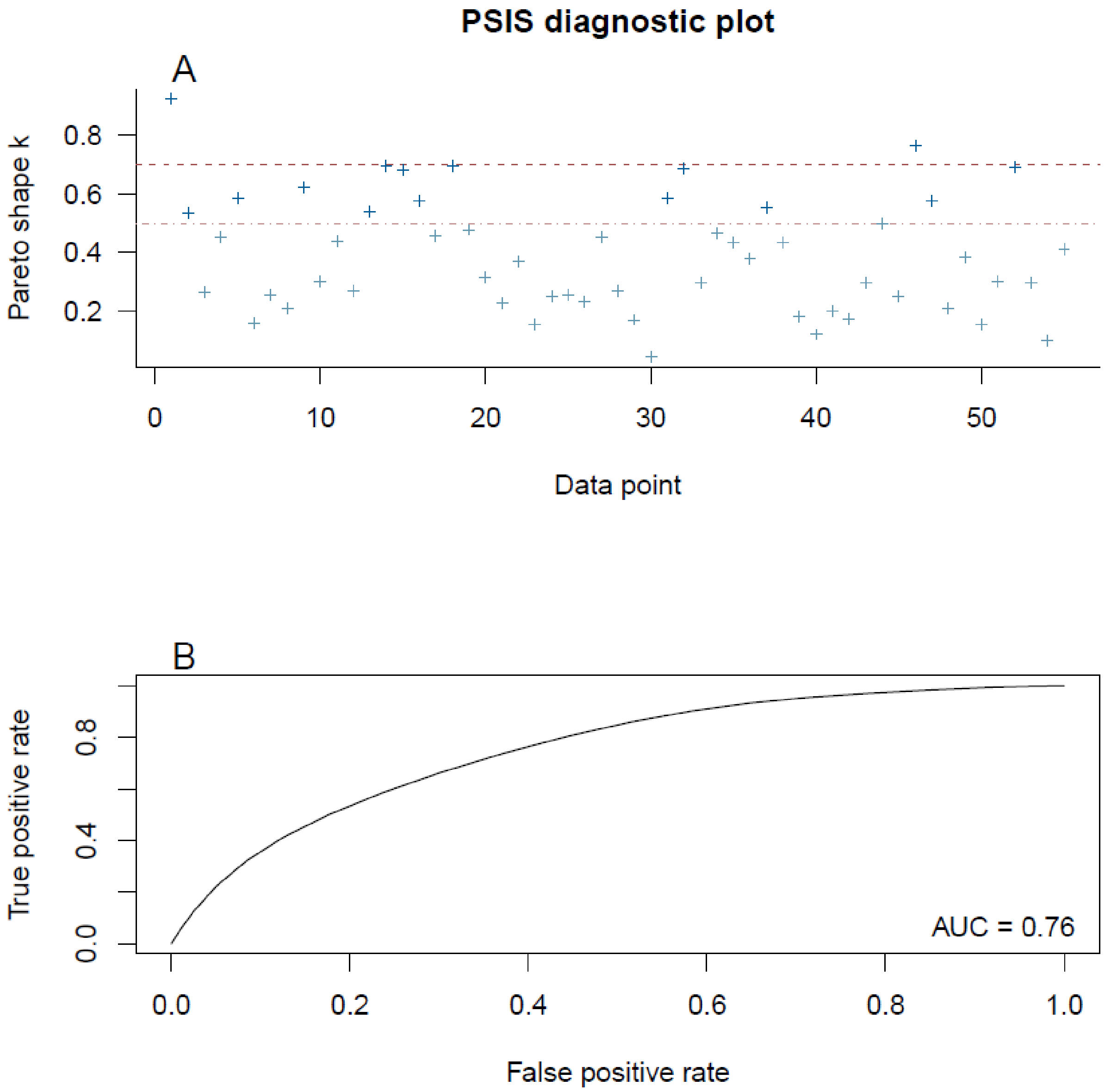

Figure 4: Model adequacy and fit for the harvest model ($\phi \sim b_0 + H + \alpha_p + \varepsilon_t$) fit to pup survival ($\phi$) of wolves in Idaho with an independent variable for harvest (H) and a random effect for pack (α_p) and year (ε_t); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) ROC curve and AUC value.

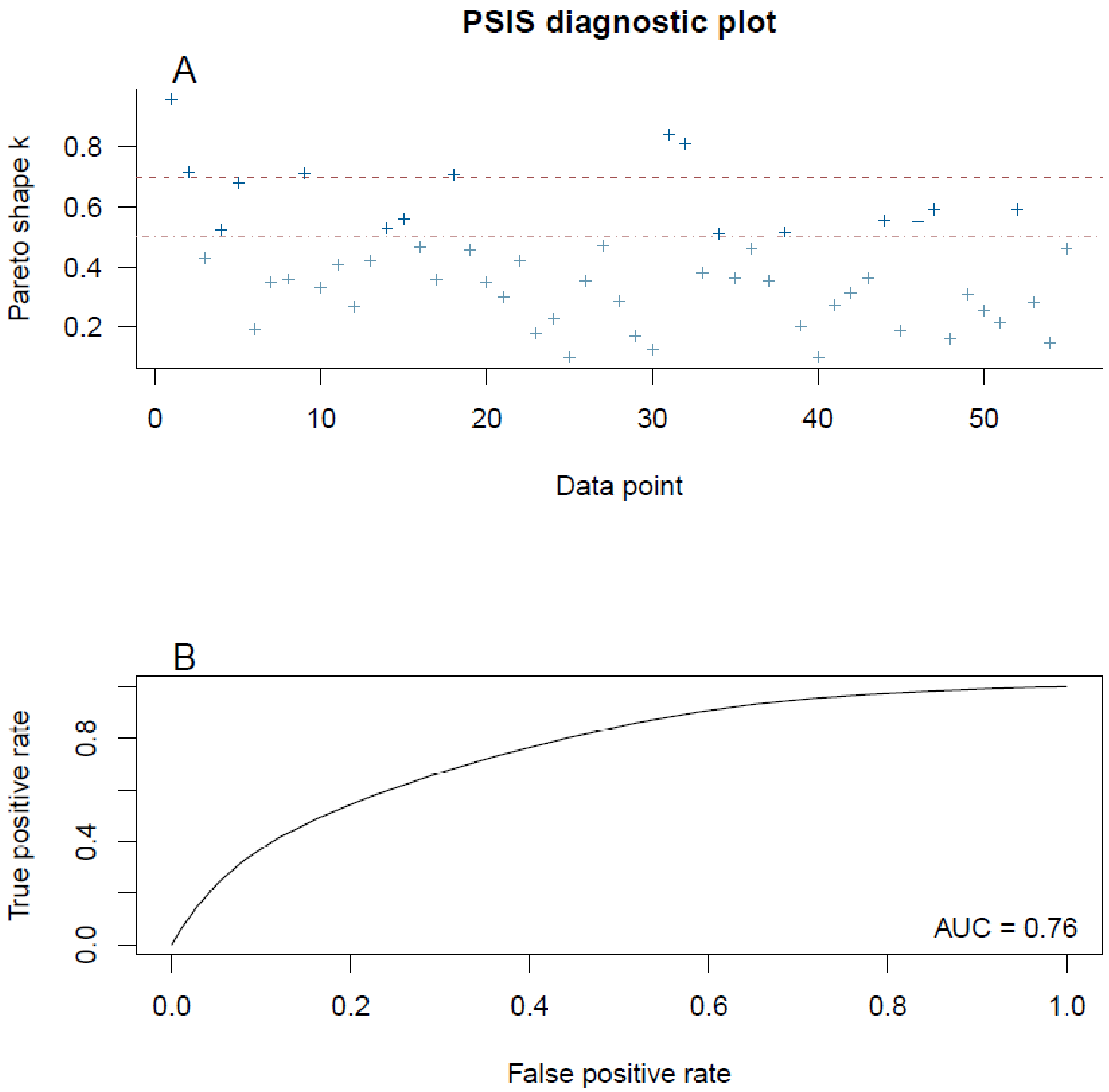

Figure 5: Model adequacy and fit for the prey availability and harvest model ($\phi \sim b_0 + DR + H + \alpha_p + \varepsilon_t$) fit to pup survival ($\phi$) of wolves in Idaho with independent variables for deer index (DR), harvest (H), and a random effect for pack (α_p) and year (ε_t); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) ROC curve and AUC value.

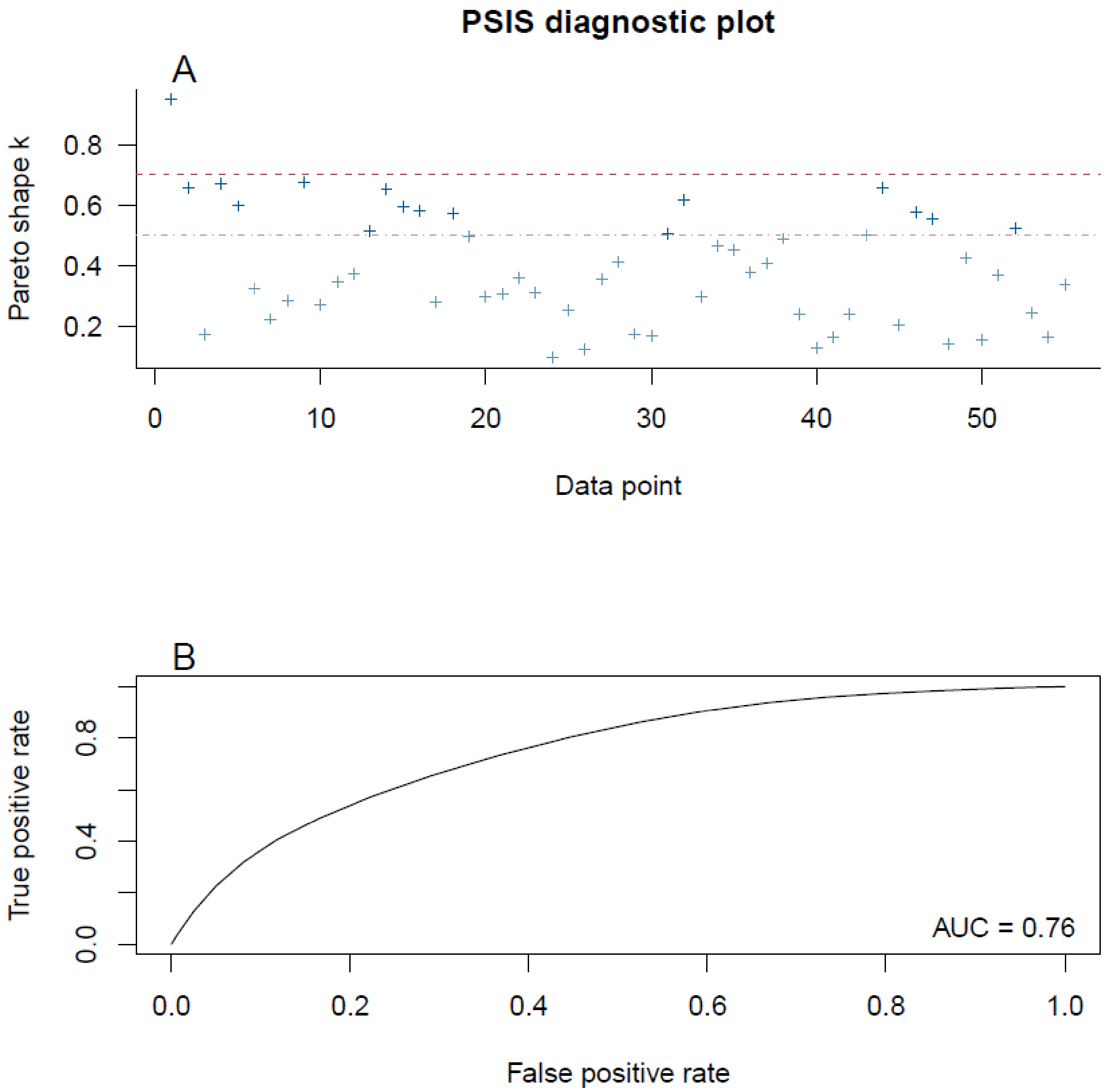

Figure 6: Model adequacy and fit for the prey availability model ($\phi \sim b_0 + DR + \alpha_p + \varepsilon_t$) fit to pup survival ($\phi$) of wolves in Idaho with an independent variable for deer index (DR) and a random effect for pack (α_p) and year (ε_t); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) ROC curve and AUC value.

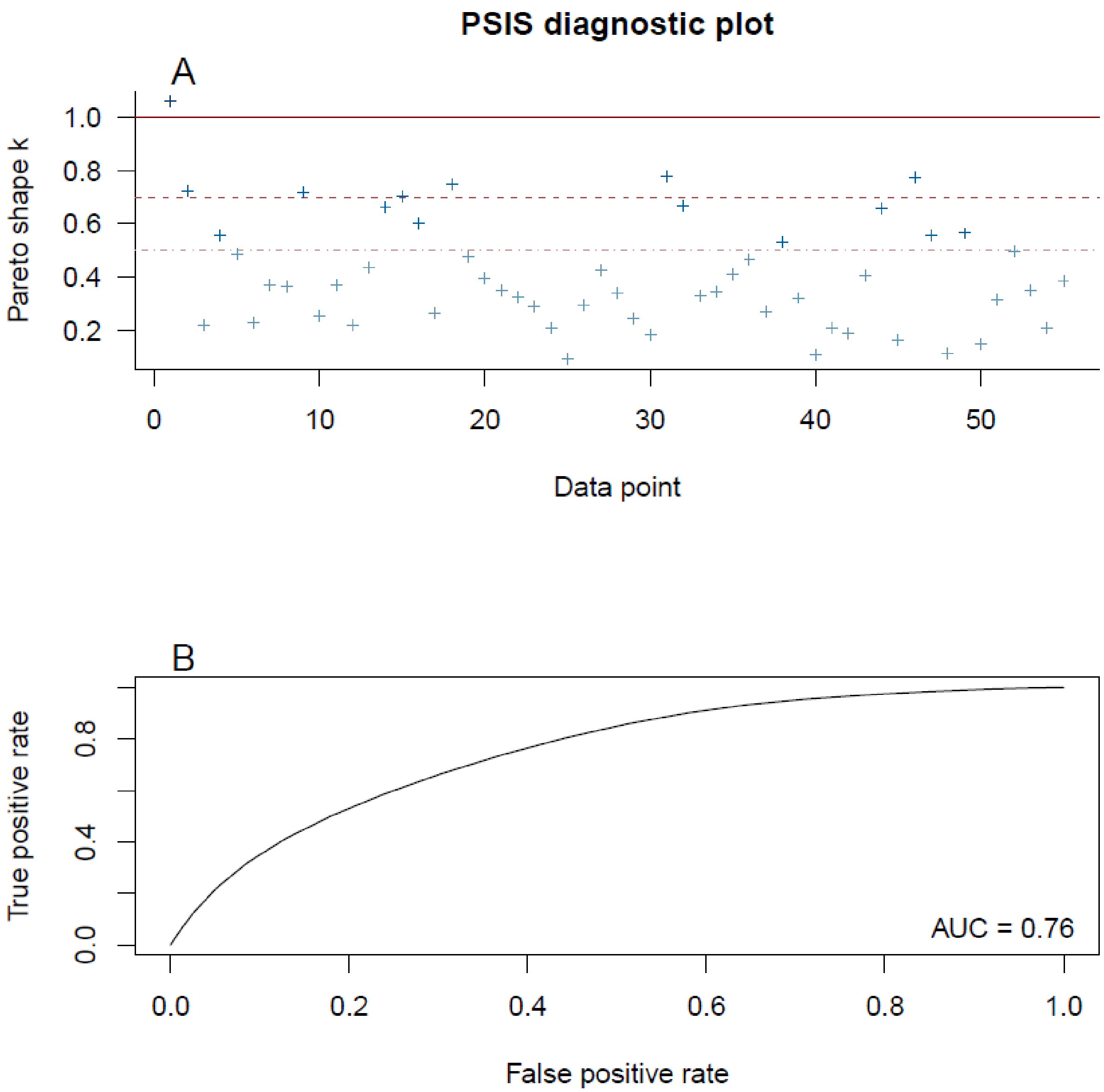

Figure 7: Model adequacy and fit for the abundance and harvest model ($\phi \sim b_0 + PA + H + \alpha_p + \varepsilon_t$) fit to pup survival ($\phi$) of wolves in Idaho with independent variables for harvest (H), abundance (PA), and a random effect for pack (α_p) and year (ε_t); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) ROC curve and AUC value.

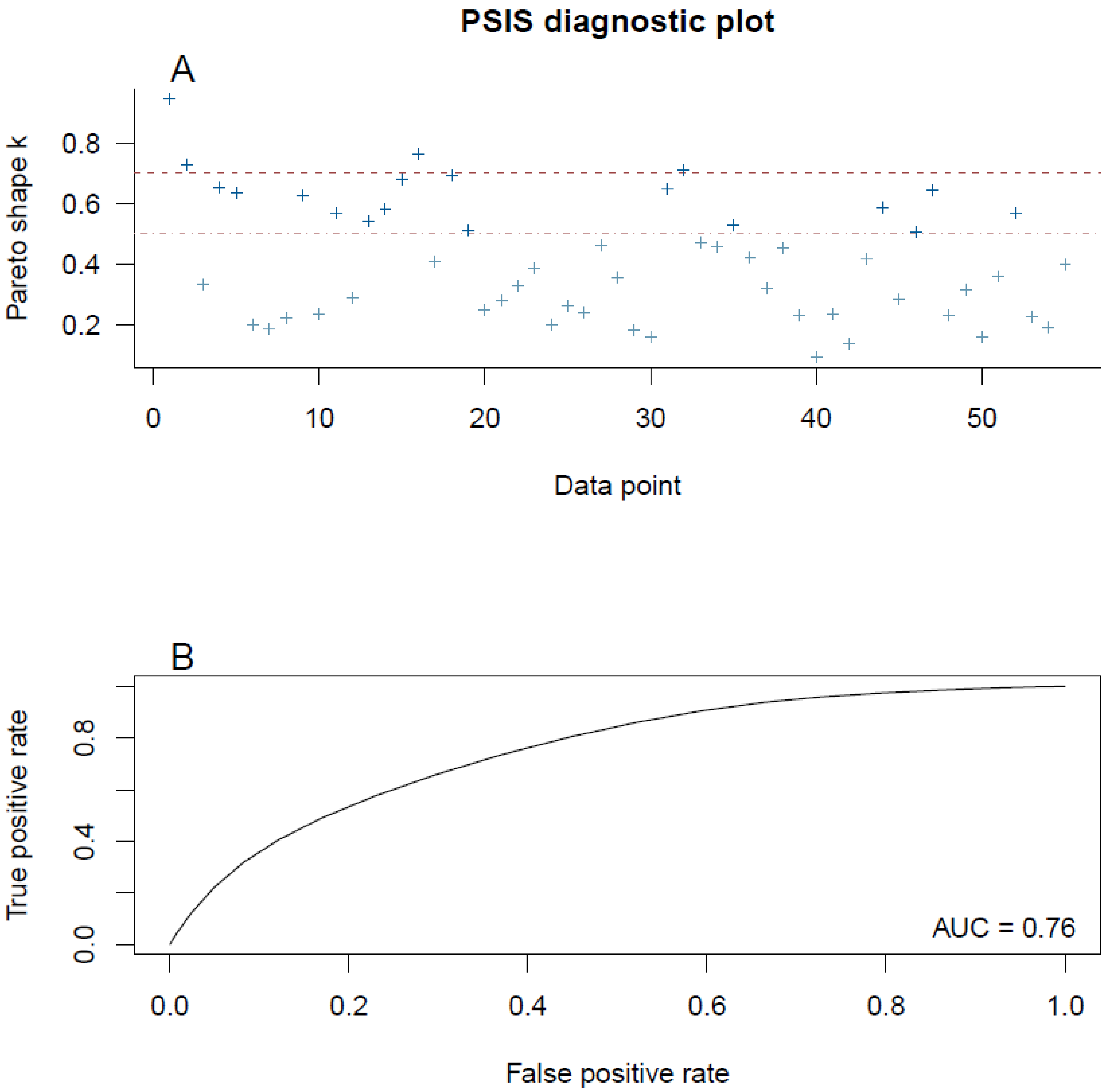

Figure 8: Model adequacy and fit for the prey availability and abundance model ($\phi \sim b_0 + DR + PA + \alpha_p + \varepsilon_t$) fit to pup survival ($\phi$) of wolves in Idaho with independent variables for the deer index (DR), abundance (PA), and a random effect for pack (α_p) and year (ε_t); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) ROC curve and AUC value.

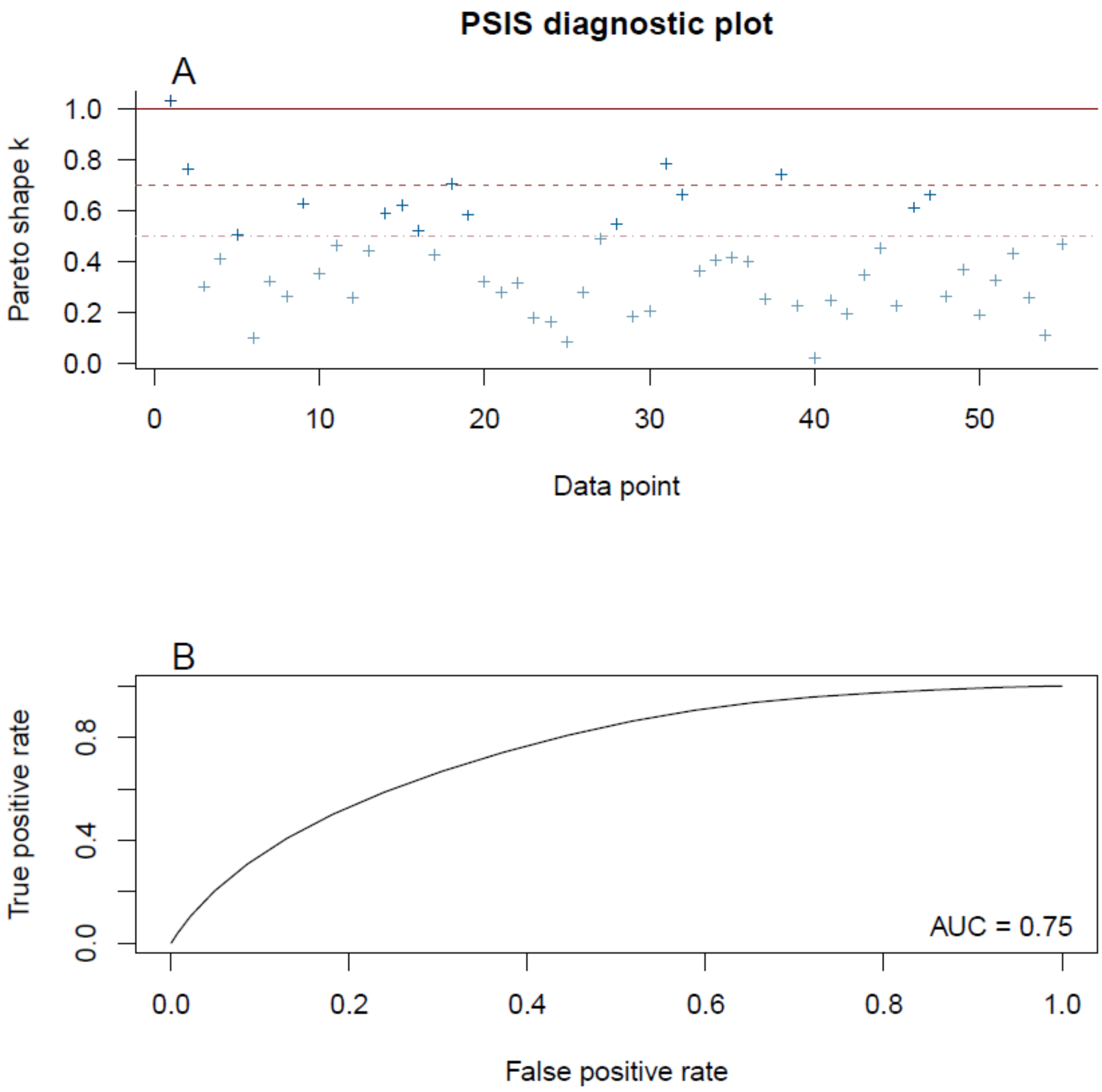

Figure 9: Model adequacy and fit for the abundance model ($\phi \sim b_0 + PA + \alpha_p + \varepsilon_t$) fit to pup survival ($\phi$) of wolves in Idaho with an independent variable for abundance (PA) and a random effect for pack (α_p) and year (ε_t); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) ROC curve and AUC value.

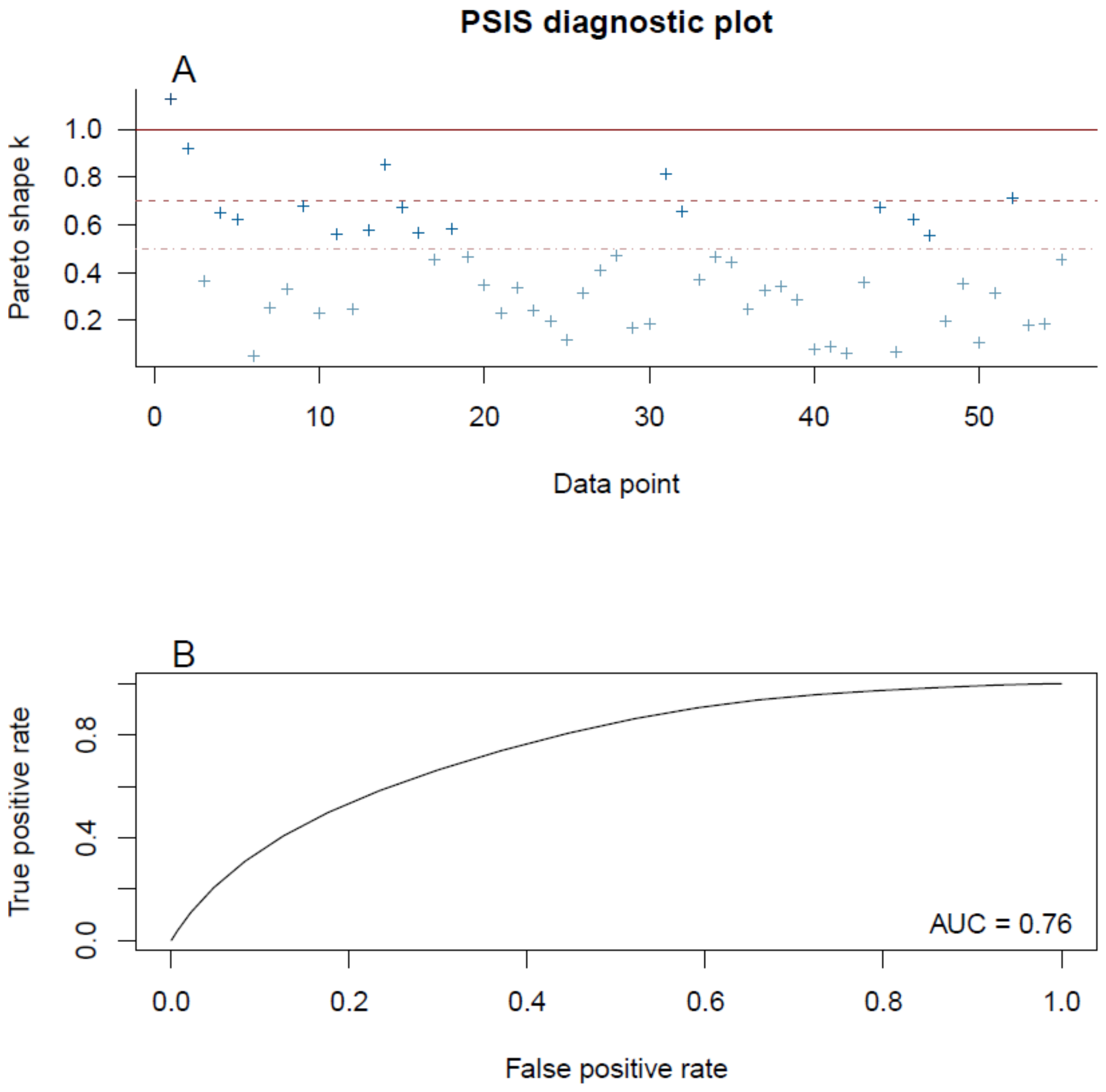

Figure 10: Model adequacy and fit for the null model ($\phi \sim b_0 + \alpha_p + \varepsilon_t$) fit to pup survival ($\phi$) of wolves in Idaho with a random effect for pack (α_p) and year (ε_t); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) ROC curve and AUC value.

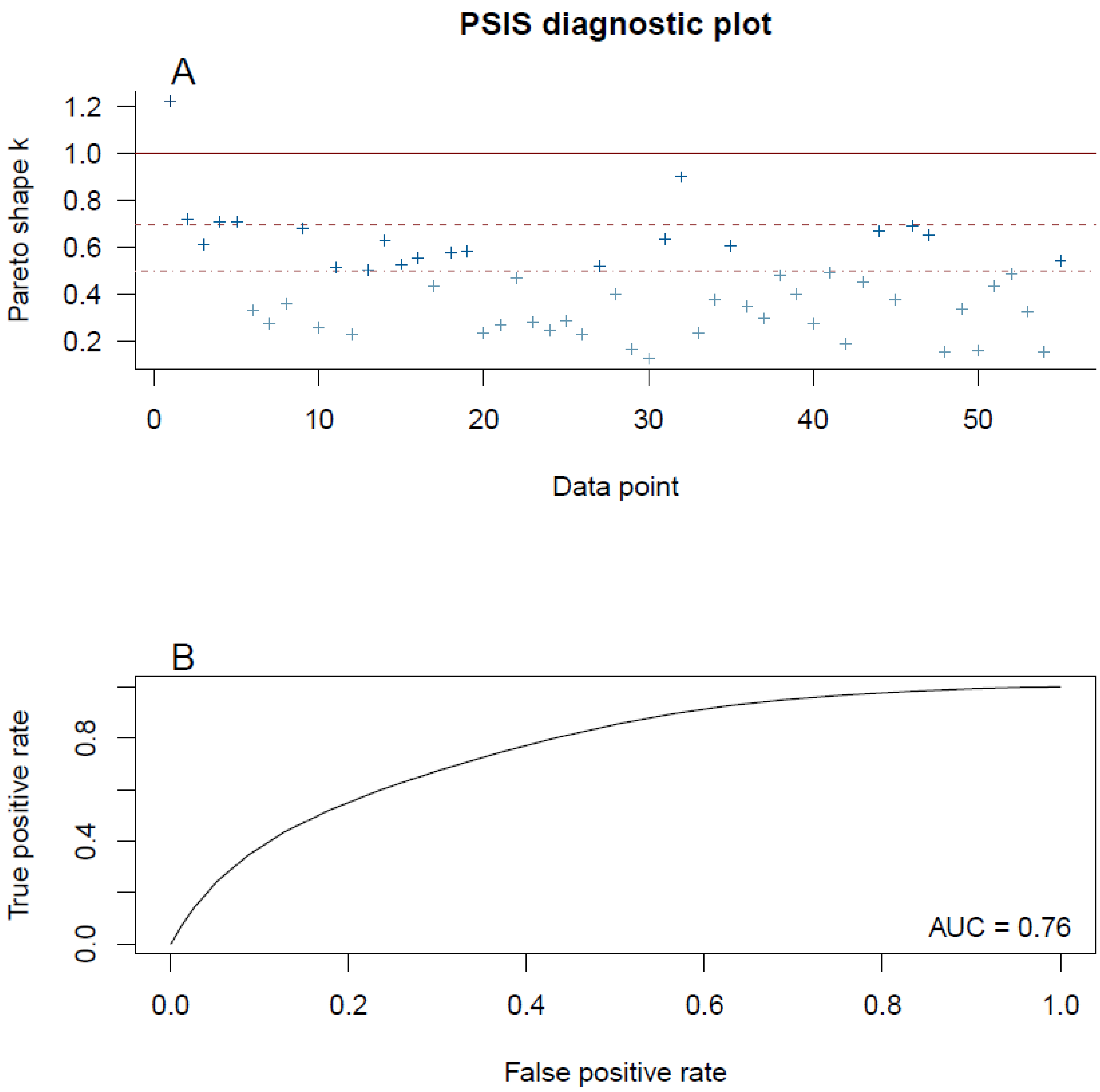

Figure 11: Model adequacy and fit for the harvest interaction model ($\phi \sim b_0 + PS + H + H * PS + \alpha_p + \varepsilon_t$) fit to pup survival ($\phi$) of wolves in Idaho with independent variables for harvest (H), pack size (PS), and a random effect for pack (α_p) and year (ε_t); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) ROC curve and AUC value.

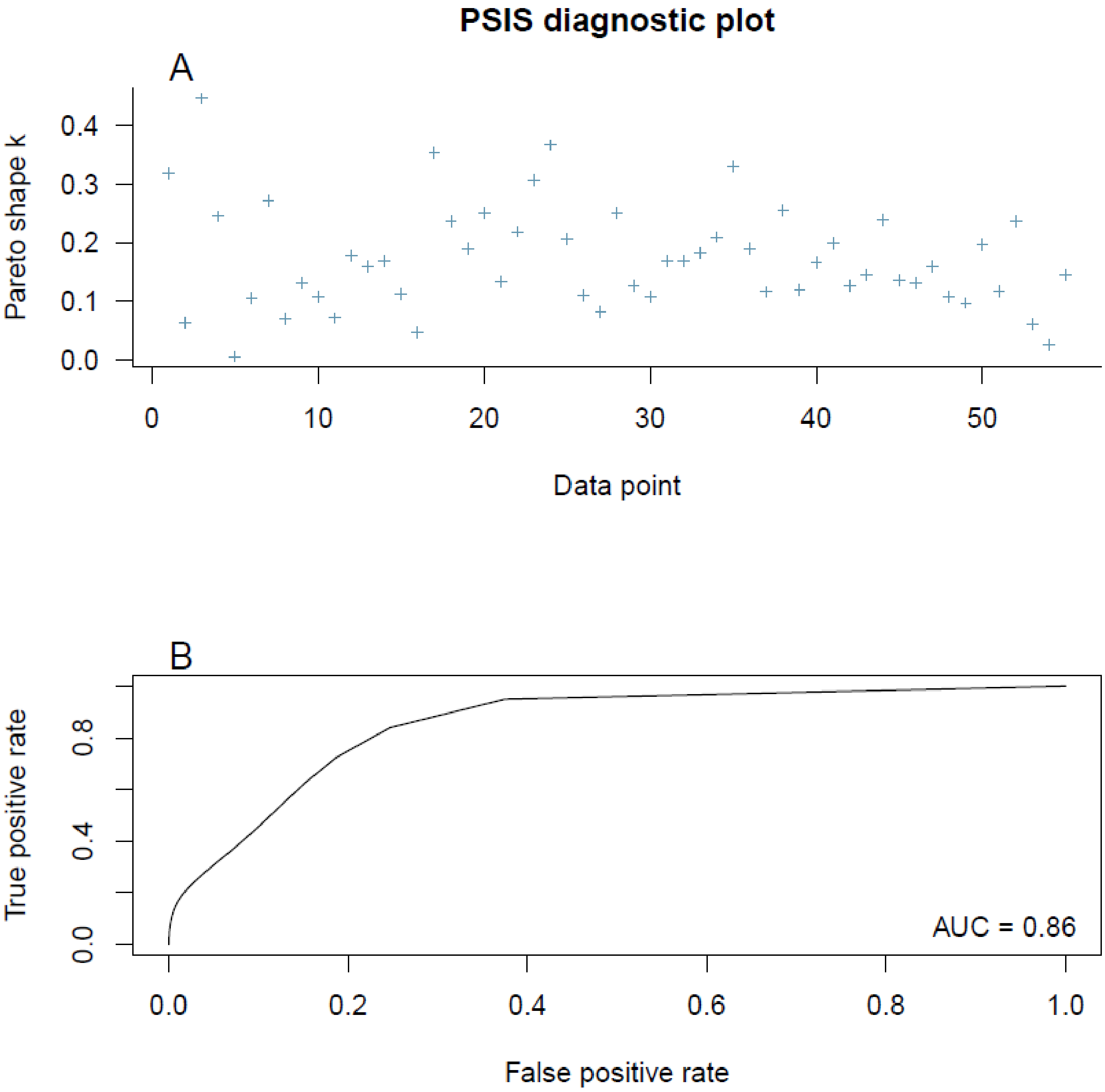

Figure 12: Model adequacy and fit for the prey availability and population and pack characteristics model ($m \sim b_0 + WS + DR + PS$) fit to multiple breeding females (m) of wolves in Idaho with independent variables for winter severity (WS), deer index (DR), and pack size (PS); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) ROC curve and AUC value.

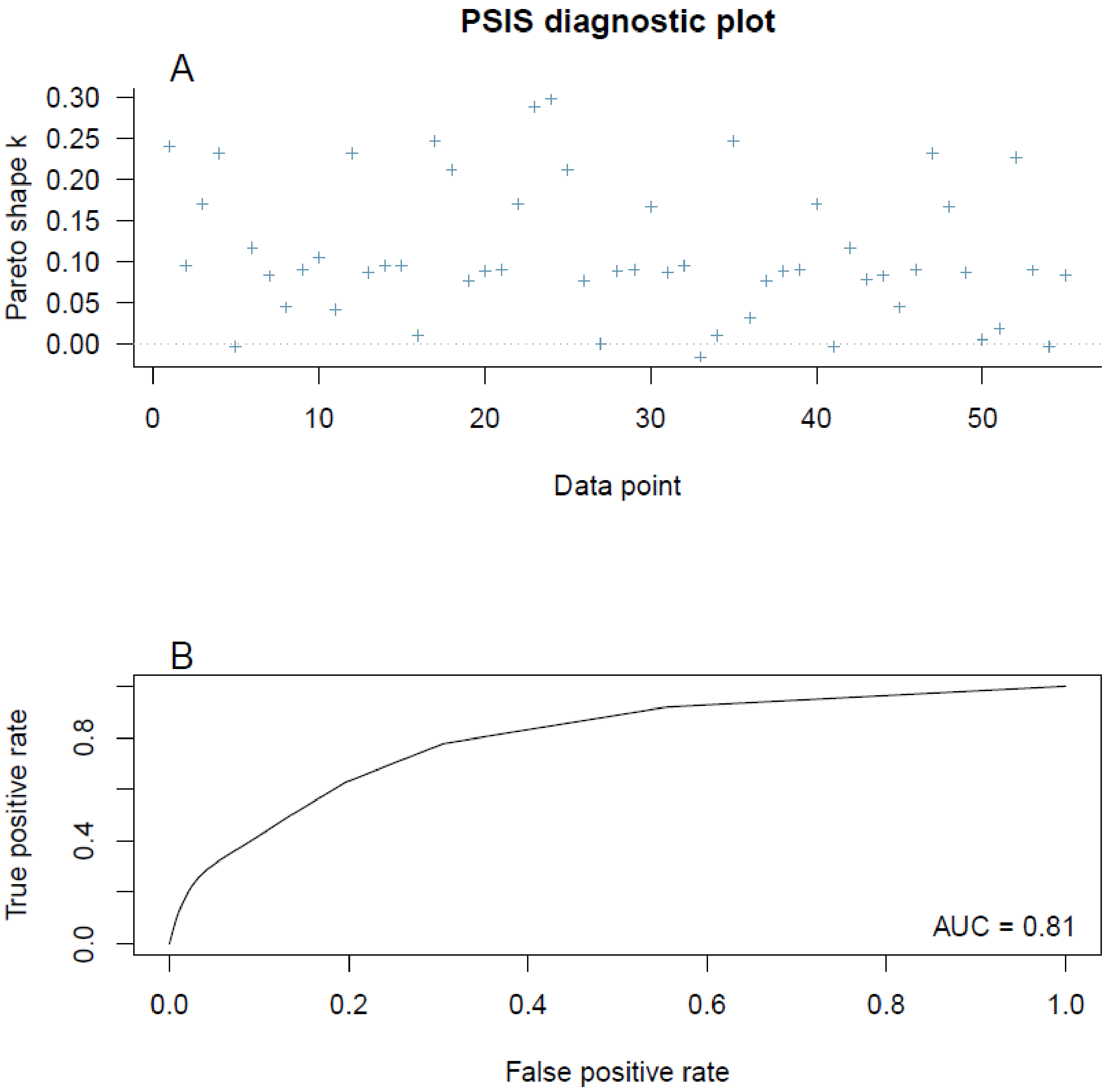

Figure 13: Model adequacy and fit for the prey availability model ($m \sim b_0 + WS + DR$) fit to multiple breeding females (m) of wolves in Idaho with independent variables for winter severity (WS) and the deer index (DR); A) Pareto k diagnostic plot from Pareto smoothed importance-sampling (PSIS), B) ROC curve and AUC value.

Supplementary Material 3B: Model code for null model

```
model {

   ### Priors ###
   b0.l ~ dnorm(0, 0.001)
   b0.surv ~ dnorm(0, 0.001)
   b0.mb ~ dnorm(0, 0.001)
   tau.pack <- 1 / (sd * sd)
   sd ~ dunif(0,10)
   for(i in 1:npacks) {
     eps.pack[i] ~ dnorm(0, tau.pack)
   }
   tau.year <- 1 / (sd.year * sd.year)
   sd.year ~ dunif(0,10)
   for(t in 1:nyears) {
     eps.year[t] ~ dnorm(0, tau.year)
   }
   tau.pack.l <- 1 / (sd.l * sd.l)
   sd.l ~ dunif(0,10)
   for(i in 1:npacks) {
     eps.pack.l[i] ~ dnorm(0, tau.pack.l)
   }

   ### Likelihood ###

   for(i in 1:nobs) {
     # Litter size
     litter.size[i] <- exp(b0.l + eps.pack.l[packs[i]])
     y.pups[i] ~ dpois(litter.size[i])T(0,)

     # Pup survival
     logit(surv[i]) <- b0.surv + eps.pack[packs[i]] + eps.year[year[i]]
     y.surv[i] ~ dbin(surv[i], potn.rec[i])

     # Multiple breeders
     logit(p.mb[i]) <- b0.mb
     y.mb[i] ~ dbern(p.mb[i])

     # Fit statistics for observed data
     eval.litter[i] <- litter.size[i]
     E.litter[i] <- pow((y.pups[i] - eval.litter[i]), 2) /(eval.litter[i] + 0.5)

     # Fit statistics for replicate data
     new.y.pups[i] ~ dpois(litter.size[i])
```

```
  new.E.litter[i] <- pow((new.y.pups[i] - eval.litter[i]), 2) /(eval.litter[i] + 0.5)
}


### Derived Parameters ###

# Recruitment
for(i in 1:nobs) {
  E.rec[i,1] <- 1
  E.rec[i,2] ~ dpois(litter.size[i])
  E.rec[i,3] ~ dbern(p.mb[i])
  E.rec[i,4] ~ dbin(surv[i], (E.rec[i,1] * E.rec[i,2] + E.rec[i,3] * E.rec[i,1] * E.rec[i,2]))
  est.rec[i] <- litter.size[i] * surv[i] + p.mb[i] * litter.size[i] * surv[i]
}

# Log likelihood for probability breeding, litter size, and survival
for(i in 1:nobs) {
  loglik.l[i] <- logdensity.pois(y.pups[i], litter.size[i])
  loglik.surv[i] <- logdensity.bin(y.surv[i], surv[i], potn.rec[i])
  loglik.mb[i] <- logdensity.bin(y.mb[i], p.mb[i], 1)
}

# Fit statistics
fit.litter <- sum(E.litter[])
new.fit.litter <- sum(new.E.litter[])

# ROC and AUC calculations
for(t in 1:length(thr)) {
  sens.mb[t] <- sum((p.mb > thr[t]) && (y.mb == 1)) / sum(y.mb)
  spec.mb[t] <- sum((p.mb < thr[t]) && (y.mb == 0)) / n0
  fpr.mb[t] <- 1 - spec.mb[t]
  fnr.mb[t] <- 1 - sens.mb[t]
  sens.surv[t] <- sum(ifelse(surv[] > thr[t], y.surv[], 0)) / sum(y.surv)
  spec.surv[t] <- sum(ifelse(surv[] < thr[t], potn.rec[] - y.surv[], 0)) / sum(potn.rec - y.surv)
  fpr.surv[t] <- 1 - spec.surv[t]
  fnr.surv[t] <- 1 - sens.surv[t]
}

# Calculate AUC
auc.mb <- sum((sens.mb[2:length(sens.mb)] + sens.mb[1:(length(sens.mb) - 1)]) /
2 * - (fpr.mb[2:length(fpr.mb)] - fpr.mb[1:(length(fpr.mb) - 1)]))
auc.surv <- sum((sens.surv[2:length(sens.surv)] + sens.surv[1:(length(sens.surv) - 1)]) /
2 * - (fpr.surv[2:length(fpr.surv)] - fpr.surv[1:(length(fpr.surv) - 1)]))
}
```

CHAPTER 4

Supplementary Material 4.A: Code for fitting the geometric and logistic growth models

The geometric growth model code:

```
model {
   # Geometric growth model. Model was log transformed and y.N (data)
   # were supplied on the log scale.

   ## Priors
   logR ~ dunif(-4, 2)

   # Observation and process error
   var.obs <- pow(sd.obs, 2)
   tau.obs <- pow(sd.obs, -2)
   sd.obs ~ dunif(0, log(100))
   var.process <- pow(sd.process, 2)
   tau.process <- pow(sd.process, -2)
   sd.process ~ dunif(0, log(100))

   # Initial state
   N[1] ~ dnorm(init.N, 0.001)

   # Transform log parameters to fit in model
   R <- exp(logR)


   ## Likelihood
   # Ecological process
   for(t in 2:nyears) {
     mu[t] <- N[1] + log((1 + R)^ (t - 1))
     N[t] ~ dnorm(mu[t], tau.process)
   }

   # Observation
   for(t in 1:nyears) {
     y.N[t] ~ dnorm(N[t], tau.obs)
     N.nat[t] <- exp(N[t])
   }
}
```

Logistic growth model:

```
model {
   # Theta logistic model. Model was log-transformed and y.N (data) are
   # supplied on the log scale. y.r is supplied on the log scale as log(Nt+1 / Nt)

   ## Priors
   logR ~ dunif(-4, 2)
   K ~ dunif(1, 30000)

   # Observation and process error
   var.obs <- pow(sd.obs, 2)
   tau.obs <- pow(sd.obs, -2)
   sd.obs ~ dunif(0, log(100))
   var.process <- pow(sd.process, 2)
   tau.process <- pow(sd.process, -2)
   sd.process ~ dunif(0, log(100))
   var.r.obs <- pow(sd.r.obs, 2)
   tau.r.obs <- pow(sd.r.obs, -2)
   sd.r.obs ~ dunif(0, 1)

   # Initial state
   N[1] ~ dnorm(init.N, 0.001)

   # Transform parameters to fit in model
   R <- exp(logR)


   ## Likelihood
   for(t in 2:nyears) {
     mu[t] <- N[t-1] + R * (1 - exp(N[t-1]) / K)
     N[t] ~ dnorm(mu[t], tau.process)
   }

   for(t in 1:nyears) {
     y.N[t] ~ dnorm(N[t], tau.obs)
     N.nat[t] <- exp(N[t])
   }

   for(t in 1:(nyears - 1)){
     rm[t] <- R + (-R / K) * exp(y.N[t])
     y.r[t] ~ dnorm(rm[t], tau.r.obs)
 }}
```

CHAPTER 5

Supplementary Material 5.A: Partial controllability in harvest

Our objectives were to 1) evaluate effects of harvest regulations, social, and environmental/ecological factors on harvest of wolves, 2) determine patterns in variation of harvest, and 3) develop models to predict harvest under alternative sets of management regulations for use in an adaptive harvest management framework. We developed models for both hunting and trapping separately because we hypothesized factors would have different effects on those types of harvest. Further, because there was little variation in season length we evaluated patterns in the proportion of harvest by week.

For hunting we hypothesized that: 1) season length and method type (bow or rifle) would have a greater effect on the number of wolves harvested than bag limit because season length and method influence the number of hunters and hunter success and few hunters get more than one wolf per season; 2) number of days spent hunting by deer and elk hunters would be positively related to the number of wolves harvested because there are more hunters; 3) snow depth would have a parabolic (increasing and then decreasing beyond a threshold) relationship with the number of wolves harvested because snow moves ungulate populations down to lower elevations or increases movements and wolves may follow or because snow increases ability of hunters to track animals which would increase success however too much snow may deter some hunters from going out; 4) wolf density would be positively correlated to the number of wolves harvested because of increased encounter rates with wolves; 5) type of season (i.e., archery, general, trapping, and post-trapping) would affect the proportion of wolves that were harvested each week because more hunters may be out during the general hunting season and hunters may be less successful during archery season; 6) the calendar week of harvest may affect the proportion of wolves harvested in each week because of holidays and changes in snow conditions over the course of the year affecting hunter numbers and success; and 7) the week of the hunting season because the number of hunters may change as the season progresses.

For trapping we hypothesized that: 1) bag limit would have a greater effect on the number of wolves trapped because trappers are more likely to get more than one wolf; 2) number of wolf tags sold would be positively related the number of wolves trapped because there are more trappers on the landscape; 3) snow depth would have a parabolic (increasing and then decreasing beyond a threshold) relationship with the number of wolves trapped; 4) snow water equivalent, which may indicate winter severity, would be negatively related to the number of wolves trapped due to decreased success in severe conditions; 5) wolf density would be positively correlated to the number of wolves trapped because of increased chance of success; 6) the calendar week of trapping may affect the proportion of wolves trapped in each week because of holidays, changes in snow conditions, and duration of trap line over the course of the year; and 7) the week of the trapping season because the number of trappers may change as the season progresses.

METHODS

Number of wolves harvested and proportion during each week

We used the annual reported harvest from hunting and trapping (fwp.mt.gov) for the state for license years 2011-2018 to determine the number of wolves hunted and trapped each year. We took the reported number of wolves harvested from hunting and trapping each week (beginning on Monday) and divided by the total number of wolves hunted or trapped that license year to determine the proportion of wolves hunted or trapped by week.

Independent predictor variables

We used reported regulations from MFWP (fwp.mt.gov) to determine independent variables related to hunting regulations. We determined season length and bag limit for each year based on the Montana hunting and trapping regulations for wolves. Hunting season lengths included the archery and general seasons. We used the maximum annual bag limit for statewide harvest rate analyses although a bag limit of one was implemented in three of the 18 wolf management units (WUM). To evaluate the effects of hunting method on harvest we used reported weapon of harvest to classify method of harvest as either firearm/crossbow or archery. We determined the number of wolves harvested separately for the two method types for each year and included method as an independent predictor variable.

We used reported hunting statistics from MFWP (fwp.mt.gov) to determine independent variables related social factors (e.g., hunting and trapping effort). We used the reported number of days spent hunting by deer and elk hunters each year as an index of effort, or the potential number of people passively pursuing wolves. We used the reported wolf licenses sold for each year as a metric of the number of people passively or actively pursuing wolves.

To evaluate the effects of environmental/ecological factors we calculated snow depth and snow water equivalent (i.e., water content of snow; SWE) for each year. We used the average daily snow depth and SWE for the following water year (e.g., for 2009 we used the 2010 water year from October 1 2009 – September 30 2010) reported from SNOTEL (https://www.wcc.nrcs.usda.gov/snow/). Additionally, we used the log transformed reported annual estimates of abundance as an index for wolf density (MFWP 2018).

Determining patterns in the number of wolves harvested

We used generalized linear mixed-effects models to test our hypotheses of how harvest regulations and environmental factors affected the number of wolves hunted and trapped. We modeled the linear predictor for year t with fixed and random effects using a log link function as $log(\mu_t) = \beta_0 + \beta_1 X_1 + \cdots \beta_k X_k + \alpha_t$ for independent predictor variables X_i for $i = 1$ to K. We then modeled the number of wolves harvested (y_t) with a negative binomial error structure as

$$y_t \sim NegativeBinomial\left(\frac{r}{r+\mu_t}, r\right)$$

where r is the overdispersion parameter. We tested a random effect of year (α_t) that was modeled using a normal distribution with mean 0 and an estimated variance parameter.

To determine whether a single category of independent variables (i.e., regulations, social, or environmental/ecological) or a combination of categories best explained patterns in wolf hunting and trapping we constructed seven *a priori* candidate models (Table 1). For hunting, we had two models for the regulations category to test our hypothesis that bag limit had little effect on the number of wolves hunted, one model each for the social and environmental/ecological categories, one model that included an independent variable from each category, the null model, and the global model. For trapping, we had one model each for the regulations and social category, two models for the environmental/ecological category because SWE and snow depth were correlated (r > |0.60|; Zuur et al. 2010), one model that included an independent variable from each category, the null model, and the global model.

Determining patterns in the proportion of wolves harvested each week

We used linear mixed-effects models to test our hypotheses about how the proportion of harvest varied weekly. We modeled the expected proportion of harvest during each week using fixed effects and a random effect of year. The fixed effects included calendar week, week of the season (i.e., the first week of the season was 1 regardless of when the season began), and the type of season (i.e., archery, general, trapping, and post-trapping) the week occurred within. For calendar week and season week we also included up to a 3rd order polynomial relationship to test whether the patterns in the proportion harvested each week was non-linear (e.g., proportion of harvest each week increased, peaked, then declined through time). We had eight candidate models for hunting and seven candidate models for trapping (Table 2).

Posterior prediction of total wolves harvested

We were interested in developing models that could be used to predict annual harvest under combinations of harvest regulations, social, and environmental/ecological factors that might occur under adaptive harvest management. We used the posterior predictive distributions (Gelman et al. 2004) of the coefficient estimates from the most supported model for total wolves hunted, total wolves trapped, the proportion of wolves hunted each week, and the proportion of wolves trapped each week to generate predictions of the number of wolves harvested under different scenarios.

We predicted the number of wolves harvested by week under three different, hypothetical scenarios. First, we predicted harvest under the status quo scenario where all regulations were set to the regulations from 2018 (i.e., 29 total weeks, two weeks of archery, 12 weeks of general, 13 weeks of trapping, and two weeks post-trapping). Second, we predicted harvest under a restricted scenario where hunting was limited to the archery season and two weeks of the general season (i.e, four total weeks) and trapping was limited to the first four weeks of the status quo trapping season. Last, we predicted harvest under a liberal scenario where trapping season extended until the end of March and hunting season extended until mid-April (i.e., 35 total weeks, status quo archery and general season, 17 weeks of trapping, and four weeks post-trapping). These scenarios were hypothetical to demonstrate predictions of harvest under extreme regulations, and aside from the status quo were not implemented nor devised by MFWP.

Model implementation and evaluation

We used JAGS v4.2.0 (Plummer 2003) via the R2jags package (Su and Yajima 2015) in R v3.6.1 (R Core Team 2017) to fit models for the number of wolves hunted and trapped and the proportion of wolves hunted in trapped in each week. We ran three markov chains for 100,000 iterations with 50,000 discarded and a thinning rate of 5. We continued to run an additional 50,000 iterations until chains converged. We monitored convergence using visual inspection of the MCMC chains and the Gelman-Rubin diagnostic (Gelman and Rubin 1992). We used non-informative priors for all parameters. We used leave-one-out cross-validation (LOOCV), LOO information criterion (LOO), and the expected log predictive density (ELPD) using Pareto-smoothed importance-sampling in the loo package (Vehtari et al. 2019) to assess model fit and to compare models (Vehtari et al. 2017; Gabry et al. 2019). As an additional measure of model fit we performed posterior predictive checks using Bayesian p-values calculated from the χ^2-discrepancy statistic (Gelman et al. 2004). We report all coefficient values with the mean and 95% credible interval (CRI) unless stated otherwise. When the 95% CRI contained 0 we calculated the probability the coefficient is $>$ or $<$ 0 using the MCMC samples from the posterior distribution.

RESULTS

From the 2011-2018 license years there was 1833 recorded harvests (1197 hunted and 636 trapped). The sex ratio of harvest was approximately 1:1 (49% females, 51% males). Total reported wolves harvested ranged from 128-167 for hunting and 76-129 for trapping.

All models for total number of wolves hunted and the proportion of wolves hunted each week converged with Gelman-Rubin statistics of < 1.01. The most supported model for total wolves hunted included season length and method of hunting (Table 1). The next best model included bag limit, however because the standard error in the difference in ELPD did not overlap

0 we did not consider it competitive (Table 1). Both models fitted the data well (Bayesian p-values ~ 0.61; all Pareto-*k* diagnostic values < 0.5). We found that firearm/crossbow had a positive effect ($\beta = 4.02;\ CRI = 3.56 - 4.57$) and that season length had no discernable effect ($\beta = -0.01;\ 55\%\ CRI = -0.07 - 0.04$) on the number of wolves hunted (Figure 1). The most supported model for the proportion of wolves hunted each week was season type (Table 2). We found that the proportion of wolves hunted each week during the archery season ($\beta = 0.01;\ CRI = 0.001 - 0.020$), the trapping season ($\beta = 0.01;\ CRI = 0.003 - 0.023$), and the post-trapping season ($\beta = 0.01;\ CRI = -0.009 - 0.024$) were similar (Figure 2). Most wolves were hunted during the general season ($\beta = 0.05;\ CRI = 0.037 - 0.059$; Figure 2).

All models for total number of wolves trapped and the proportion of wolves trapped each week converged with Gelman-Rubin statistics of < 1.01. The most supported model for total wolves trapped was the null model, or mean effect model (Table 1). The next best model included bag limit, however the standard error in the difference in ELPD did not overlap 0, therefore we did not consider it competitive (Table 1). The most supported model for the proportion of wolves trapped each week was a quadratic relationship with the week of the season. The next best model included a cubic relationship with the week of the season and the proportion of wolves trapped, however because the standard error in the difference in ELPD did not overlap 0 we did not consider it competitive (Table 2). We found that the proportion of wolves trapped increased and peaked around week six of the season and then declined (Figure 3).

For the status quo scenario, we found that predicted total wolves hunted and trapped was 142 (95% quantile: 98-197) and 83 (95% quantile: 55-118) wolves, respectively (Figures 4 and 5). We found that 0.01 (95% quantile: 0.000-0.045) of the total wolves were harvested per week of the archery season (Figure 6). For the general season, we found that 0.05 (95% quantile:

0.017-0.089) of the total wolves hunted were taken per week for the status quo scenario (Figure 6). We found that the proportion of wolves hunted per week was 0.02 (95% quantile: 0.000-0.056) for both trapping and post-trapping season (Figure 6). The mean proportion of wolves trapped per week for the status quo scenario was 0.08 (SD = 0.02), and peaked during week six at 0.10 (95% quantile: 0.020-0.170) of total wolves trapped (Figure 7).

For the restricted scenario, we found that predicted total wolves hunted and trapped was 19 (95% quantile: 10-31) and 25 (95% quantile: 13-40) wolves, respectively (Figures 4 and 5). We found that 0.10 (95% quantile: 0.000-0.315) of the total wolves were harvested per week of the archery season (Figure 6). For the general season, we found that 0.42 (95% quantile: 0.170-0.684) of the total wolves hunted were taken per week for the restricted scenario (Figure 6). The mean proportion of wolves trapped per week for the restricted scenario was 0.25 (SD = 0.04), and peaked during week four at 0.30 (95% quantile: 0.096-0.540) of total wolves trapped (Figure 8).

For the liberal scenario, we found that predicted total wolves hunted and trapped was 160 (95% quantile: 114-217) and 94 (95% quantile: 63-140) wolves, respectively (Figures 4 and 5). We found that 0.01 (95% quantile: 0.000-0.037) of the total wolves were harvested per week of the archery season (Figure 6). For the general season, we found that 0.05 (95% quantile: 0.017-0.087) of the total wolves hunted were taken per week for the liberal scenario (Figure 6). We found that the proportion of wolves hunted per week was 0.02 (95% quantile: 0.000-0.050) for both trapping and post-trapping season (Figure 6). The mean proportion of wolves trapped per week for the liberal scenario was 0.06 (SD = 0.02), and peaked during week six at 0.09 (95% quantile: 0.021-0.163) of total wolves trapped (Figure 9).

LITERATURE CITED

Gabry, J., D. Simpson, A. Vehtari, M. Betancourt, and A. Gelman. 2019. Visualization in Bayesian workflow. Journal of the Royal Statistical Soceity A 182:389–402.

Gelman, A., J. B. Carlin, H. S. Stern, and D. B. Rubin. 2004. Bayesian data analysis. Second edition. Chapman and Hall/CRC Press.

Gelman, A., and D. B. Rubin. 1992. Inference from iterative simulation using multiple sequences. Statistical Science 7:457–472.

Montana Fish Wildlife and Parks. 2018. Montana gray wolf conservation and management 2017 annual report. Helena, Montana.

Plummer, M. 2003. JAGS: A program for analysis of Bayesian graphical models using Gibbs sampling.

R Core Team. 2017. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.

Su, Y.-S., and M. Yajima. 2015. R2jags: using R to run "JAGS."

Vehtari, A., J. Gabry, Y. Yao, and A. Gelman. 2019. loo: efficient leave-one-out cross-validation and WAIC for Bayesian models.

Vehtari, A., A. Gelman, and J. Gabry. 2017. Practical Bayesian model evaluation using leave-one-out cross-validation and WAIC. Statistics and Computing 27:1413–1432.

Zuur, A. F., E. N. Ieno, and C. S. Elphick. 2010. A protocol for data exploration to avoid common statistical problems. Methods in Ecology and Evolution 1:3–14.

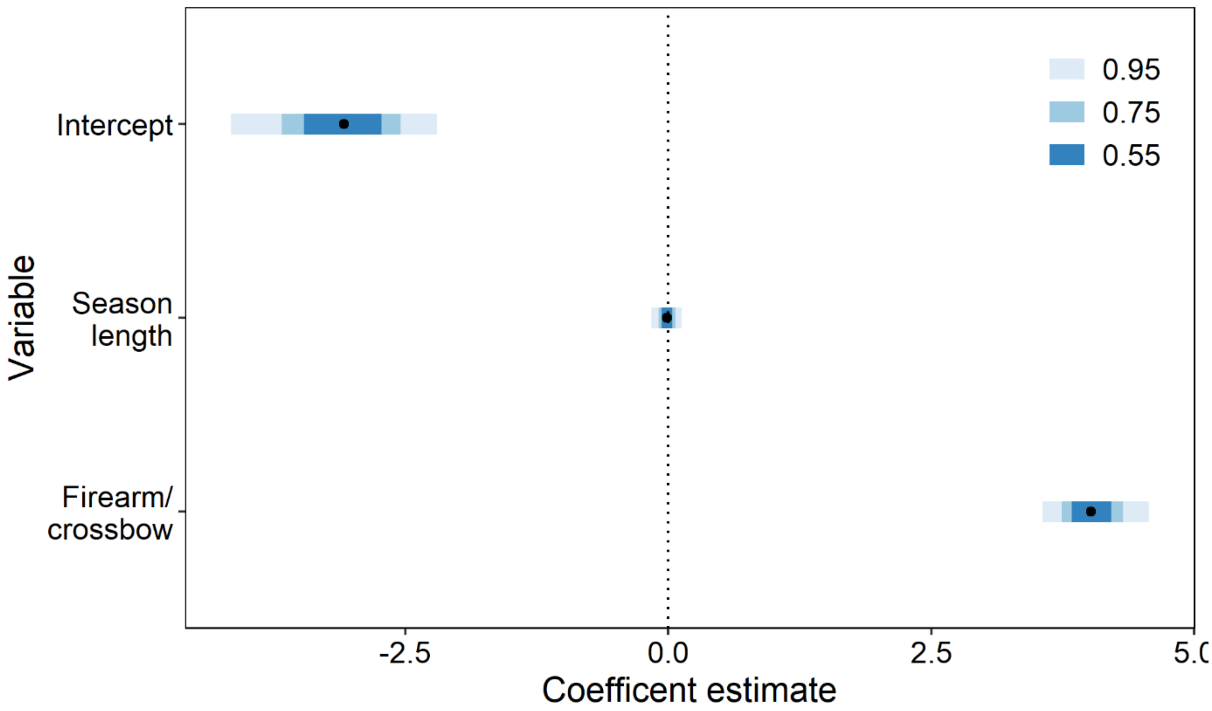

Figure 1: Coefficient estimates for the effects of season length and firearm/crossbow on the total number of wolves hunted in Montana from 2011-2018. The colored bands represent the 95%, 75%, and 55% credible intervals. The intercept for the model included the effect of archery as the method of harvest.

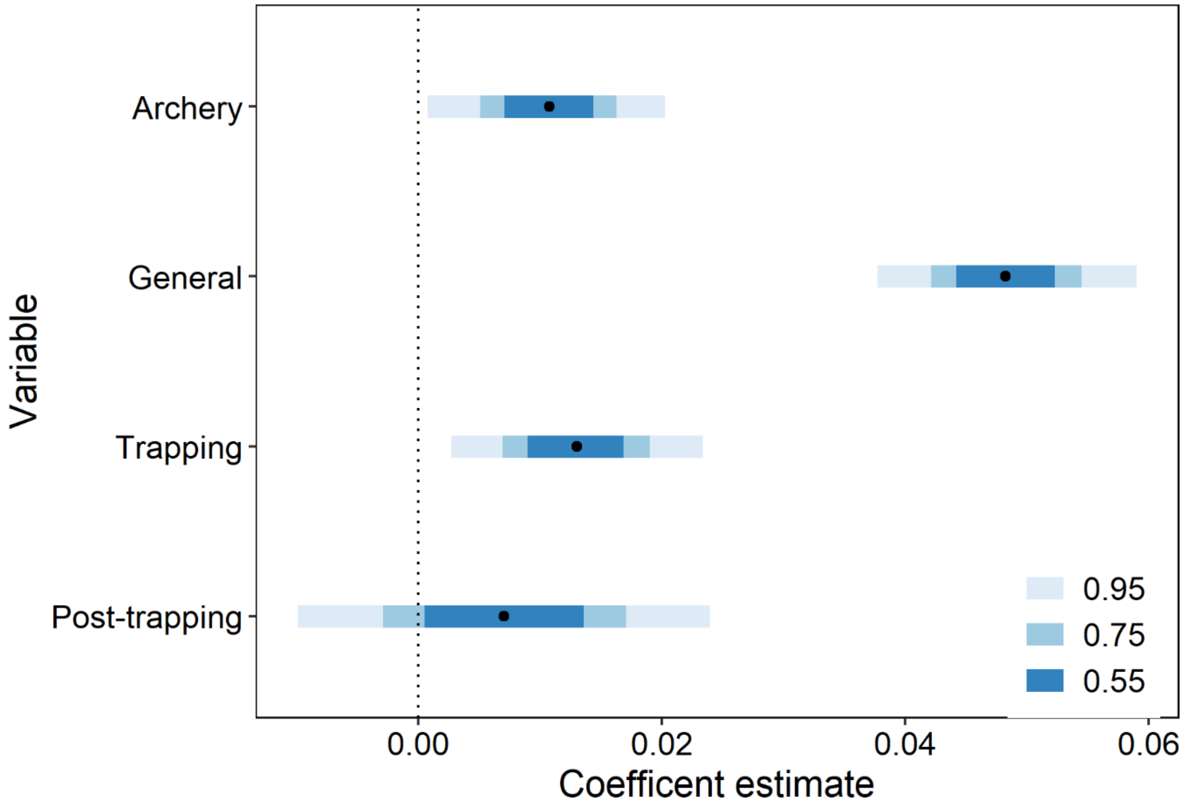

Figure 2: Coefficient estimates for the effects of type of season on the proportion of wolves hunted each week in Montana from 2011-2018. The colored bands represent the 95%, 75%, and 55% credible intervals.

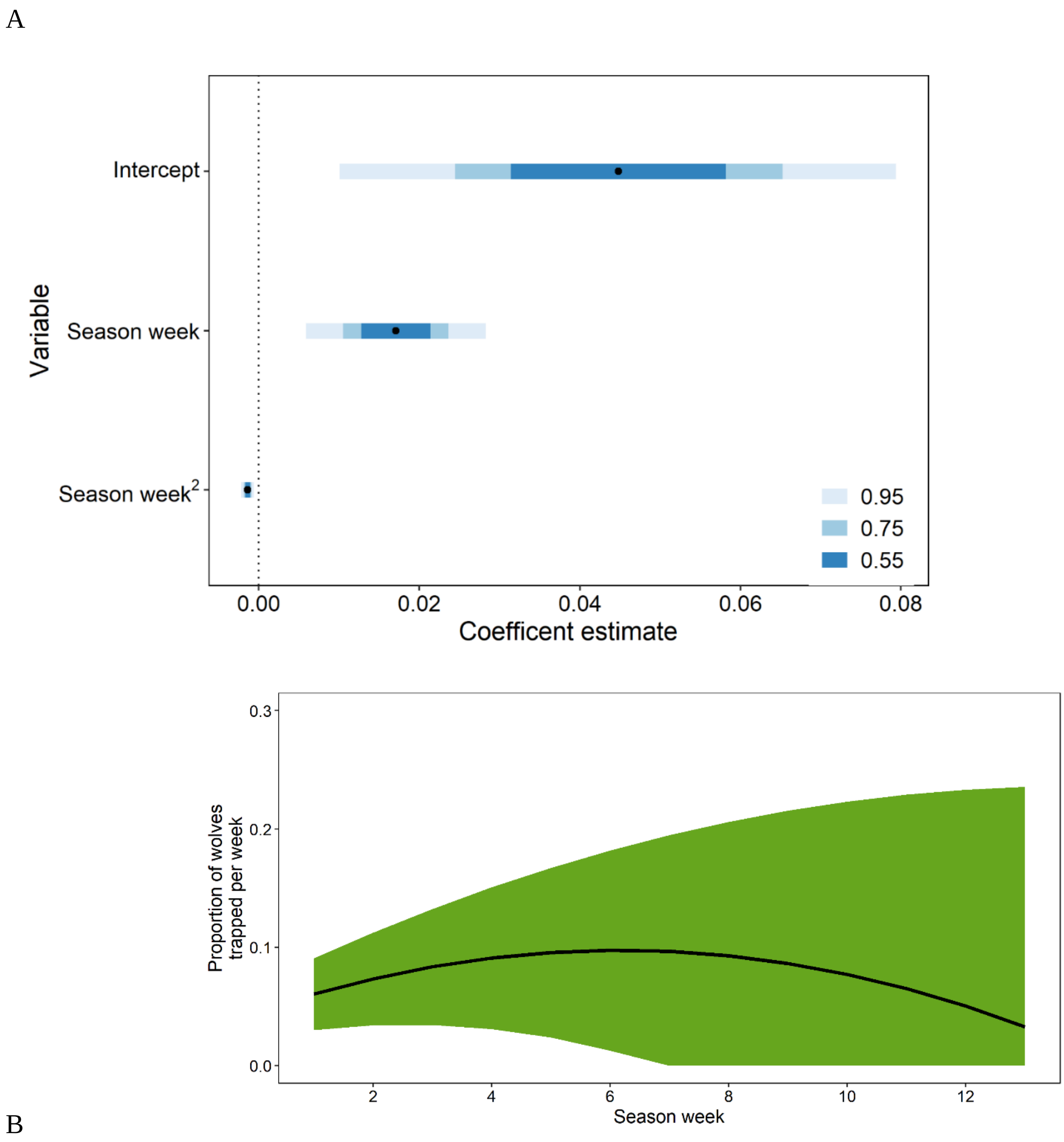

Figure 3: The A: coefficient estimates, and B: the predicted relationship for the effects of the week of the season on the proportion of wolves trapped each week in Montana from 2011-2018. The colored bands represent the 95%, 75%, and 55% credible intervals.

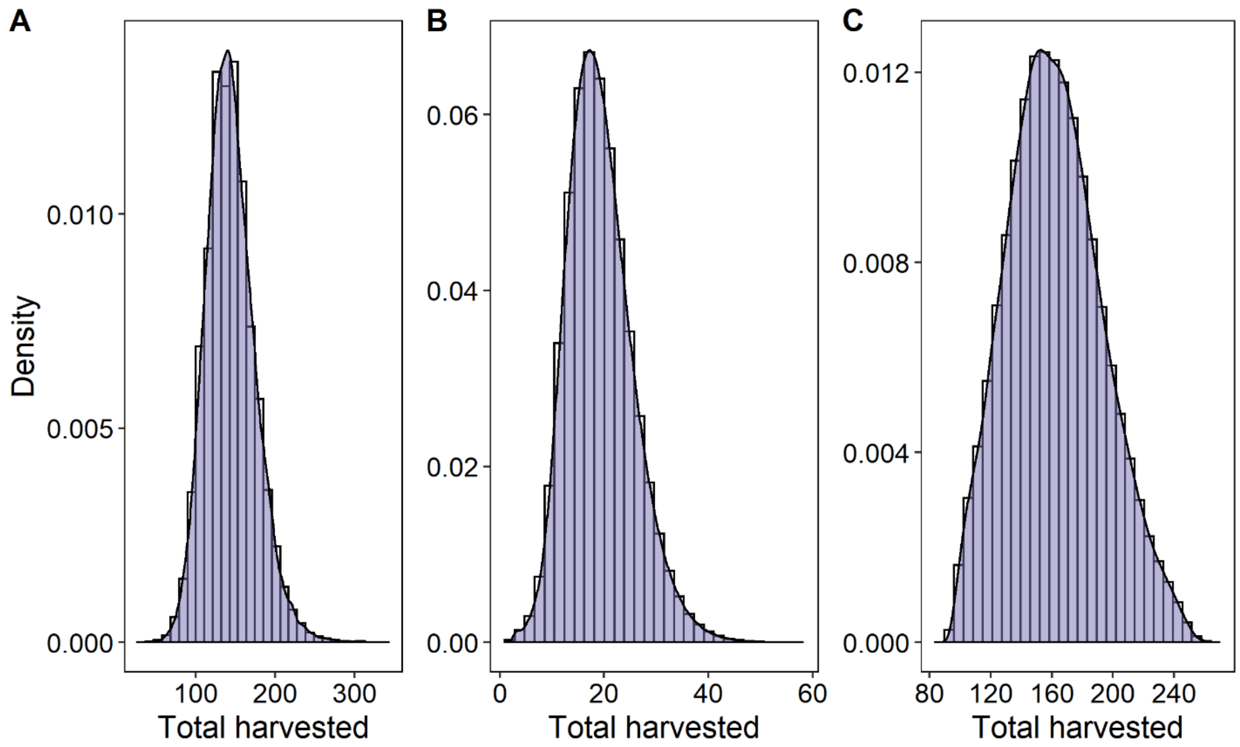

Figure 4: The predicted posterior distribution for the total number of wolves hunted under three different hunting season lengths for wolves in Montana. A) The status quo season was 29 weeks long and consisted of two weeks of archery, 12 weeks of general season, 13 weeks of hunting during trapping season, and two weeks during post-trapping season. B) The restricted season was a hypothetical scenario with four total weeks of hunting and consisted of two weeks of archery and two weeks of general season. C) The liberal hunting season was a hypothetical scenario with 35 total weeks of hunting and consisted of two weeks of archery, 12 weeks of general, 17 weeks of hunting during the trapping season, and four weeks post-trapping season.

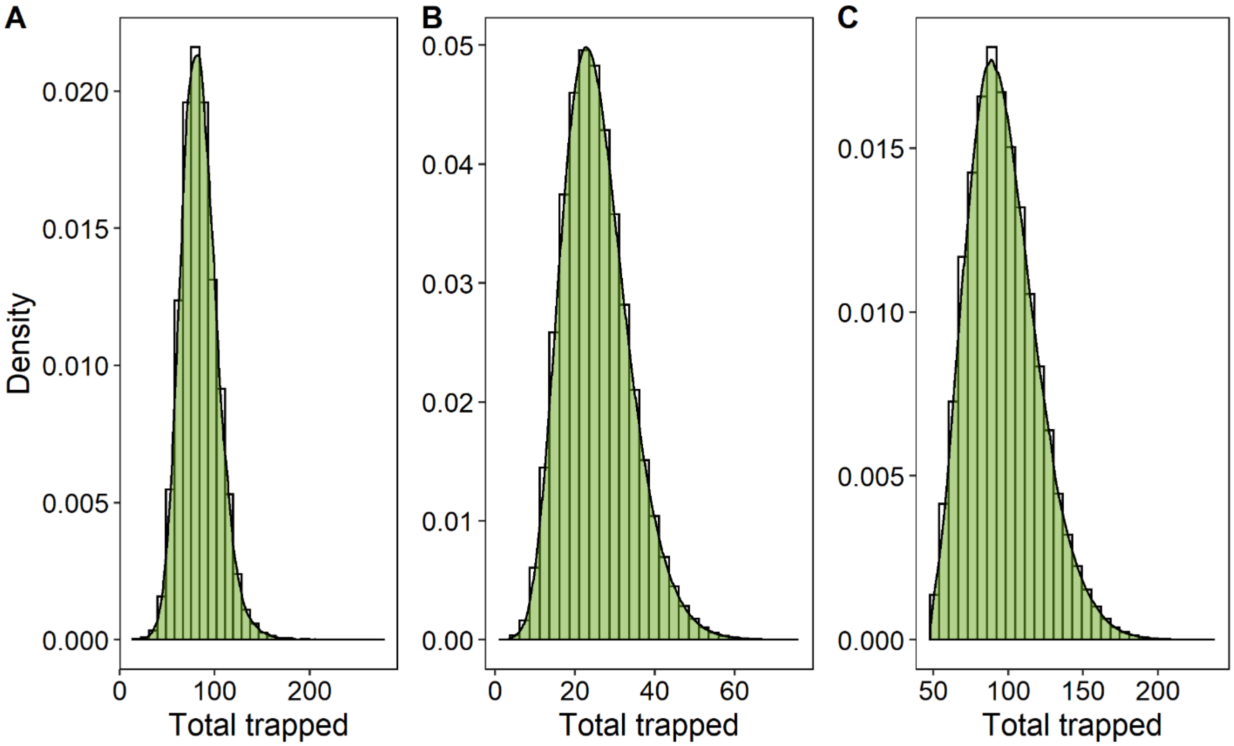

Figure 5: The predicted posterior distribution for the total number of wolves trapped under three different trapping season lengths for wolves in Montana. A) The status quo season was 13 weeks, B) the restricted season was a hypothetical scenario with four weeks of trapping, and C) the liberal trapping season was a hypothetical scenario with 17 weeks of trapping.

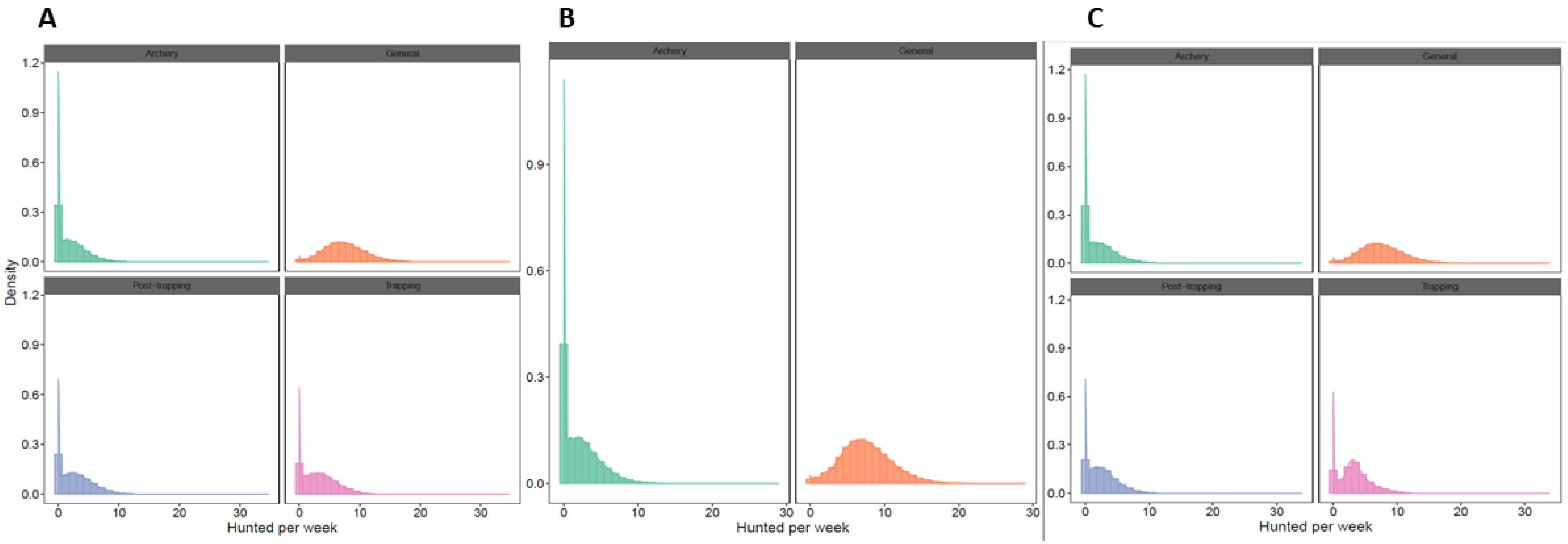

Figure 6: The predicted posterior distribution for the number of wolves hunted per week during the archery season, general season, trapping season, and post-trapping season under three different hunting season lengths for wolves in Montana. A) The status quo season was 29 weeks long and consisted of two weeks of archery, 12 weeks of general season, 13 weeks of hunting during trapping season, and two weeks during post-trapping season, B) the restricted season was a hypothetical scenario with two weeks of archery and two weeks of general, and C) the liberal season was a hypothetical scenario with two weeks of archery, 12 weeks of general, 17 weeks of hunting during the trapping season, and four weeks post-trapping season.

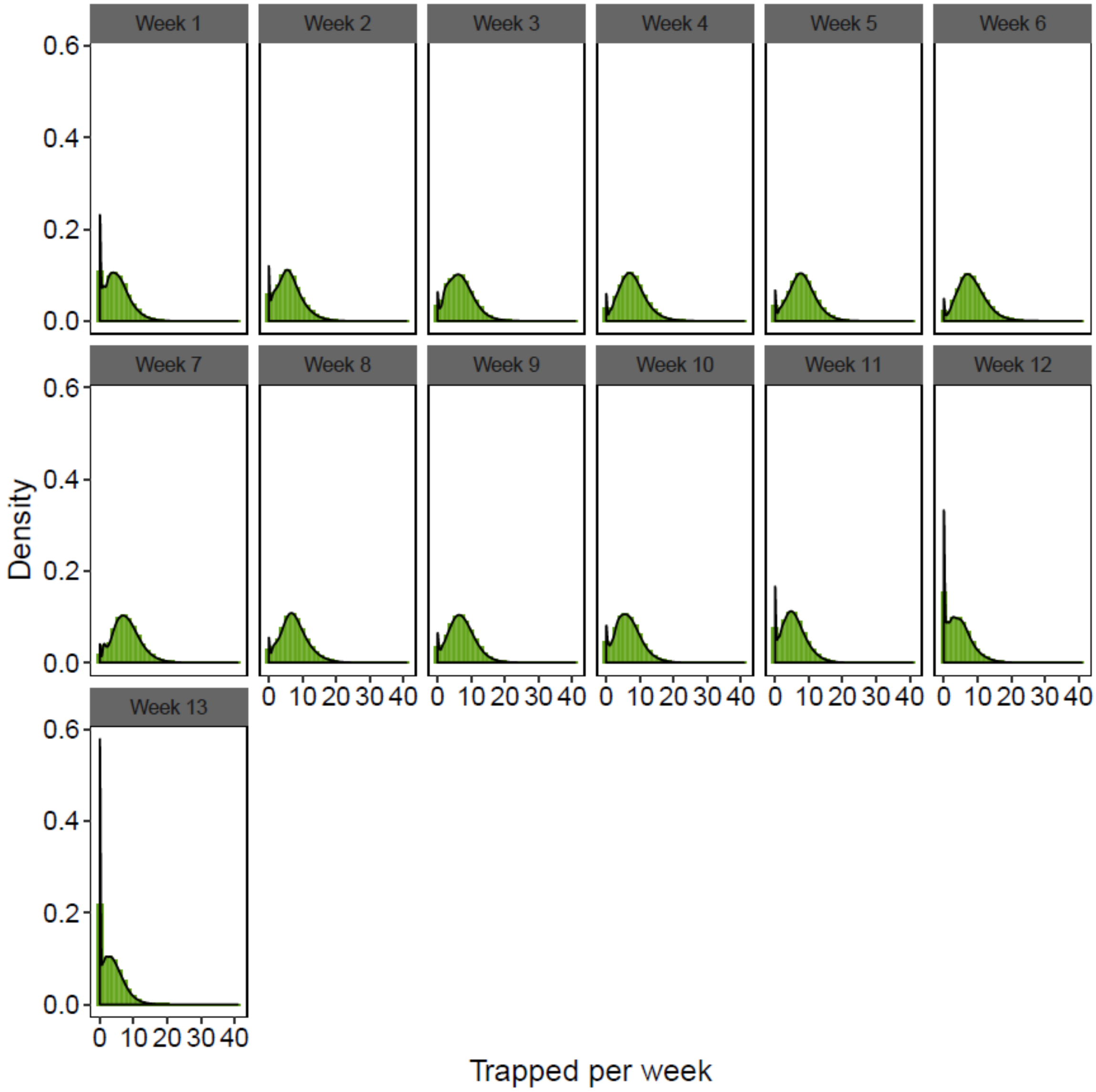

Figure 7: The predicted posterior distribution for the number of wolves trapped per week for the status quo season of 13 weeks.

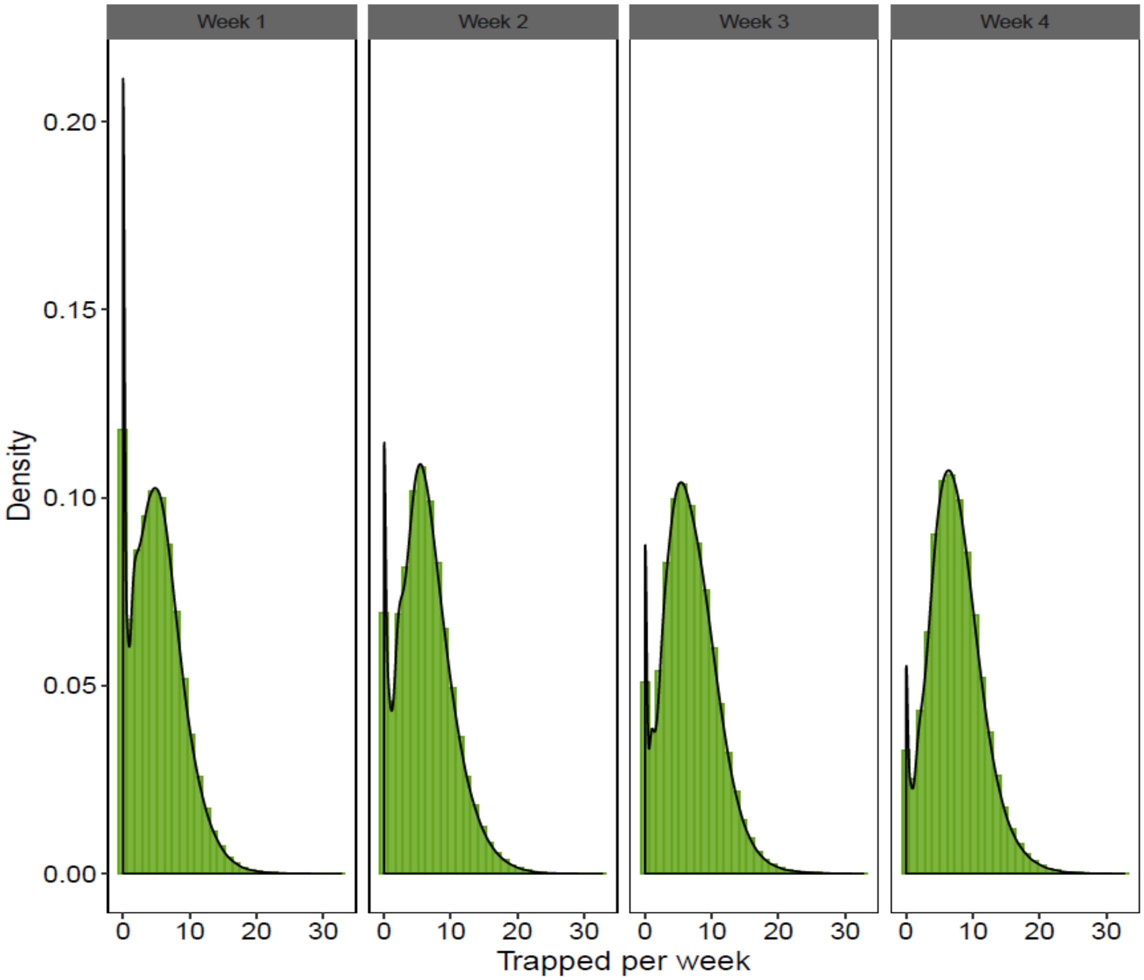

Figure 8: The predicted posterior distribution for the number of wolves trapped per week for the restricted season, which was a hypothetical scenario with four weeks of trapping.

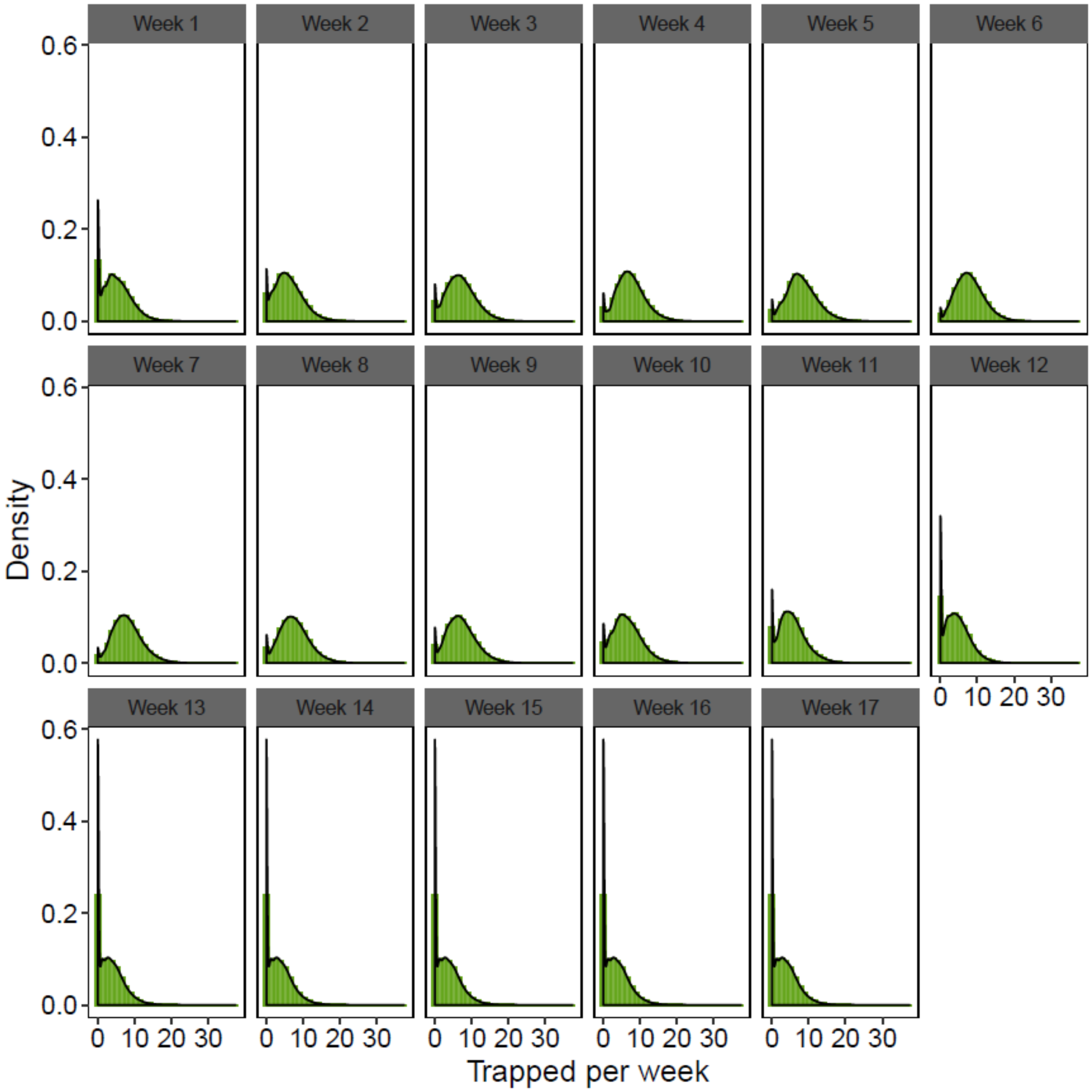

Figure 9: The predicted posterior distribution for the number of wolves trapped per week for the liberal trapping season was a hypothetical scenario with 17 weeks of trapping.

Table 1: Model selection results for generalized linear mixed-effects models for the number of wolves hunted or trapped in Montana from 2011-2018. Independent predictor variables included season length (SL), method type (archery or firearm/crossbow), bag limit (bag), the number of wolf tags sold (tags), total number of days spent hunting by deer and elk hunters (elk), wolf density in wolves/1000 km^2 (dens), daily average snow water equivalent (SWE), and daily average snow depth (SD) for the following water year. Models were compared using the difference in leave-one-out cross-validation information criteria (ΔLOO), mean and standard error of the difference in the expected log predictive density (ΔELPD), and the deviance information criterion (DIC). Models in bold were considered competitive.

Harvest Type	Model	K*	ΔLOO	ΔELPD (SE)	DIC (pD)
Trapping	$\boldsymbol{\beta_0}$	**2**	**0**	**0**	**49 (1.9)**
	$\beta_0 + bag$	3	2.31	1.15 (0.995)	52 (3.4)
	$\beta_0 + tags$	3	2.5	1.25 (0.813)	53 (3.5)
	$\beta_0 + dens + SWE$	4	3.88	1.94 (0.771)	55 (5.2)
	$\beta_0 + dens + SD$	5	6.58	3.29 (0.767)	59 (8.2)
	$\beta_0 + bag + dens + SD$	6	11.07	5.53 (1.247)	63 (11.4)
	$\beta_0 + bag + dens + SD + tags$	7	15.79	7.89 (0.241)	70 (16.3)
Hunting	$\boldsymbol{\beta_0 + SL + method}$	**4**	**0**	**0**	**96 (4.4)**
	$\beta_0 + SL + method + bag$	5	1.61	0.81 (0.562)	98 (6.0)
	$\beta_0 + SL + method + elk + SD$	7	4.15	2.08 (1.196)	136 (11.0)
	$\beta_0 + SL + method + bag + tags + elk + dens + SD$	10	9.75	4.88 (2.141)	143 (16.9)

	β_0	2	47.89	23.95 (2.438)	143 (2.2)
	$\beta_0 + tags + elk$	4	52.51	26.26 (2.944)	181 (4.8)
	$\beta_0 + dens + SD$	5	54.2	27.10 (2.982)	150 (5.6)

* Number of parameters including the overdispersion parameter

Table 2: Model selection results for linear mixed-effects models for the proportion of wolves hunted or trapped each week in Montana from 2011-2018. Independent predictor variables included the calendar week (CW), the week of the season (SW), the type of season the week was in (i.e., archery, general, trapping, post-trapping), and a random effect for year (α_{YR}). Models were compared using the difference in leave-one-out cross-validation information criteria (ΔLOO), mean and standard error of the difference in the expected log predictive density (ΔELPD), and the deviance information criterion (DIC). Models in bold were considered competitive.

Harvest Type	Model	K*	ΔLOO	ΔELPD (SE)	DIC (pD)
Trapping	$\boldsymbol{\beta_0 + SW + SW^2 + \alpha_{YR}}$	**4**	**0**	**0**	**-295.49 (5.370)**
	$\beta_0 + SW + SW^2 + SW^3 + \alpha_{YR}$	5	1.85	0.93 (0.602)	-293.38 (6.668)
	$\beta_0 + CW + CW^2 + \alpha_{YR}$	4	5.53	2.77 (1.115)	-290.31 (5.424)
	$\beta_0 + CW + CW^2 + CW^3 + \alpha_{YR}$	5	8.52	4.26 (1.367)	-288.18 (6.604)
	$\beta_0 + SW + \alpha_{YR}$	3	10.38	5.19 (3.551)	-285.33 (4.127)
	$\beta_0 + \alpha_{YR}$	2	10.89	5.45 (3.121)	-284.43 (3.128)
	$\beta_0 + CW + \alpha_{YR}$	3	13.59	6.79 (3.031)	-282.22 (4.396)
Hunting	$\boldsymbol{\beta_0 + type + \alpha_{YR}}$	**3**	**0**	**0**	**-1042.25 (8.626)**
	$\beta_0 + SW + SW^2 + SW^3 + \alpha_{YR}$	5	35.8	17.89 (6.133)	-1006.90 (6.216)
	$\beta_0 + CW + CW^2 + CW^3 + \alpha_{YR}$	5	71.75	35.87 (7.014)	-970.48 (6.221)
	$\beta_0 + SW + SW^2 + \alpha_{YR}$	4	73.96	36.97 (6.694)	-968.84 (5.151)
	$\beta_0 + CW + \alpha_{YR}$	3	89.91	44.95 (7.193)	-953.22 (4.047)
	$\beta_0 + CW + CW^2 + \alpha_{YR}$	4	90.08	45.03 (7.244)	-952.84 (5.118)
	$\beta_0 + SW + \alpha_{YR}$	3	91.99	45.96 (7.951)	-951.39 (4.131)

	$\beta_0 + \alpha_{YR}$	2	103.5	51.74 (8.259)	-940.10 (3.099)

* Number of parameters

Supplementary Material 5.B: Sensitivity analyses for a decision model for gray wolves

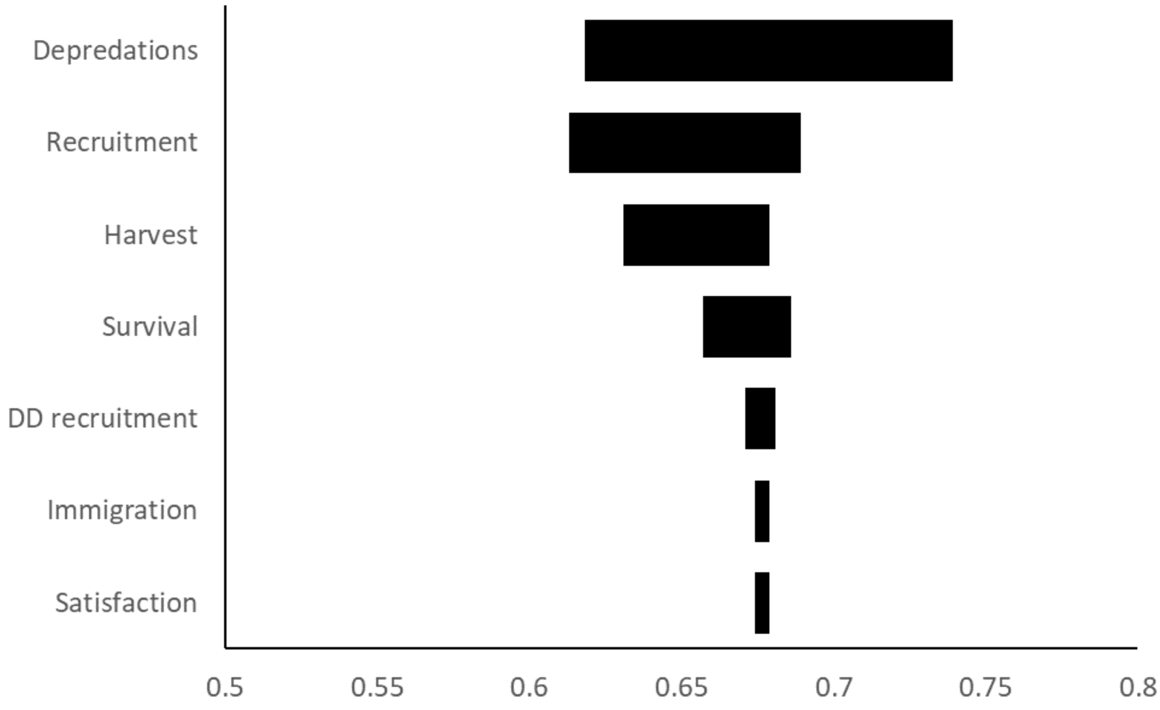

Figure 5.B.1: Results of one-way sensitivity analyses for a model of wolf population dynamics in an adaptive harvest management framework for wolves in Montana in a tornado diagram. We tested sensitivity of the reward value in meeting all objectives to uncertainty in parameter values. The wider the bar, the more sensitive reward value was to uncertainty in the parameter value. Parameters included number of depredation events per wolf, mean recruitment, total harvest, adult survival, the effect of density dependence on recruitment, net immigration rate, and the change in coefficient values for the effect of harvest regulations on public satisfaction.

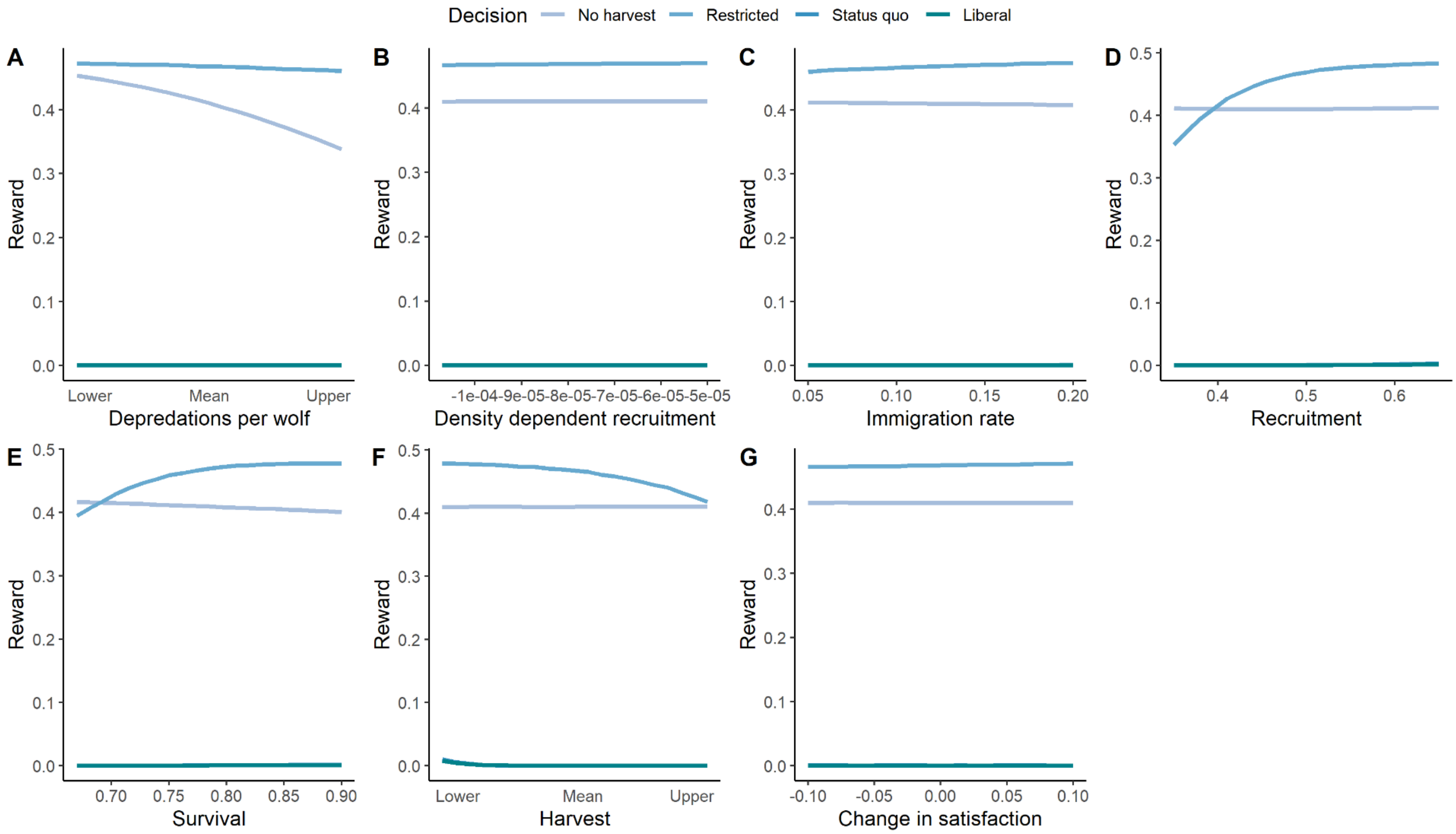

Figure 5.B.2: Indifference curves of the sensitivity of the reward in meeting objectives to uncertainty in parameter values for harvest management of wolves in Montana when the current abundance was 200 wolves. We varied the parameter value from the lower to the upper credible interval and determined the reward for the four management actions. The higher overall reward indicates greater

support. Parameters included depredations per wolf during years with and without harvest (A), the effect of density dependence on recruitment (B), net immigration rate (C), mean recruitment rate (D), adult survival (E), total harvest (F), and the percent change in the coefficients for the relationship between harvest regulations and the percent Montanans satisfied (G).

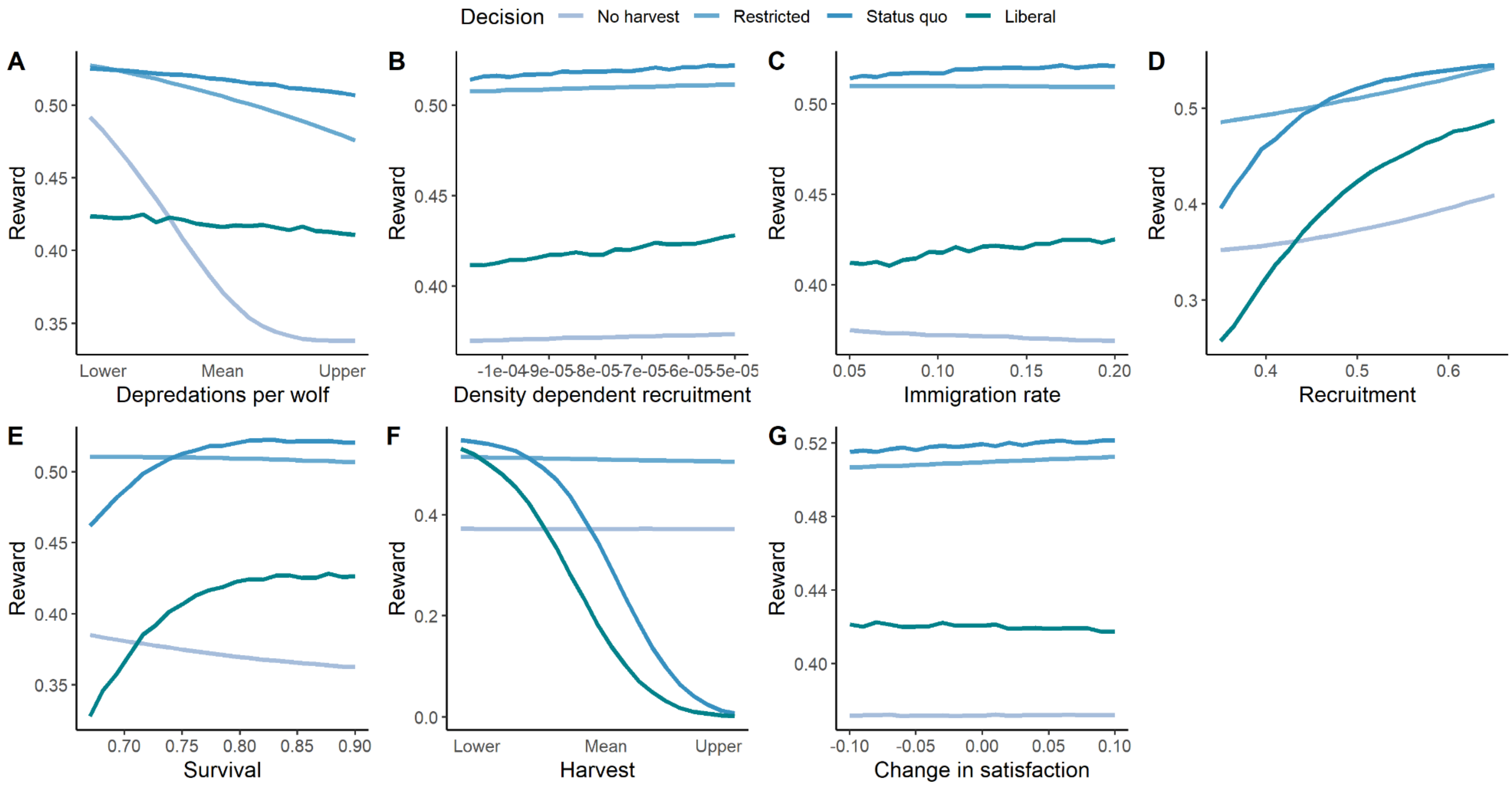

Figure 5.B.3: Indifference curves of the sensitivity of the reward in meeting objectives to uncertainty in parameter values for harvest management of wolves in Montana when the current abundance was 350 wolves. We varied the parameter value from the lower to the upper credible interval and determined the reward for the four management actions. The higher overall reward indicates greater support. Parameters included depredations per wolf during years with and without harvest (A), the effect of density dependence on

recruitment (B), net immigration rate (C), mean recruitment rate (D), adult survival (E), total harvest (F), and the percent change in the coefficients for the relationship between harvest regulations and the percent Montanans satisfied (G).

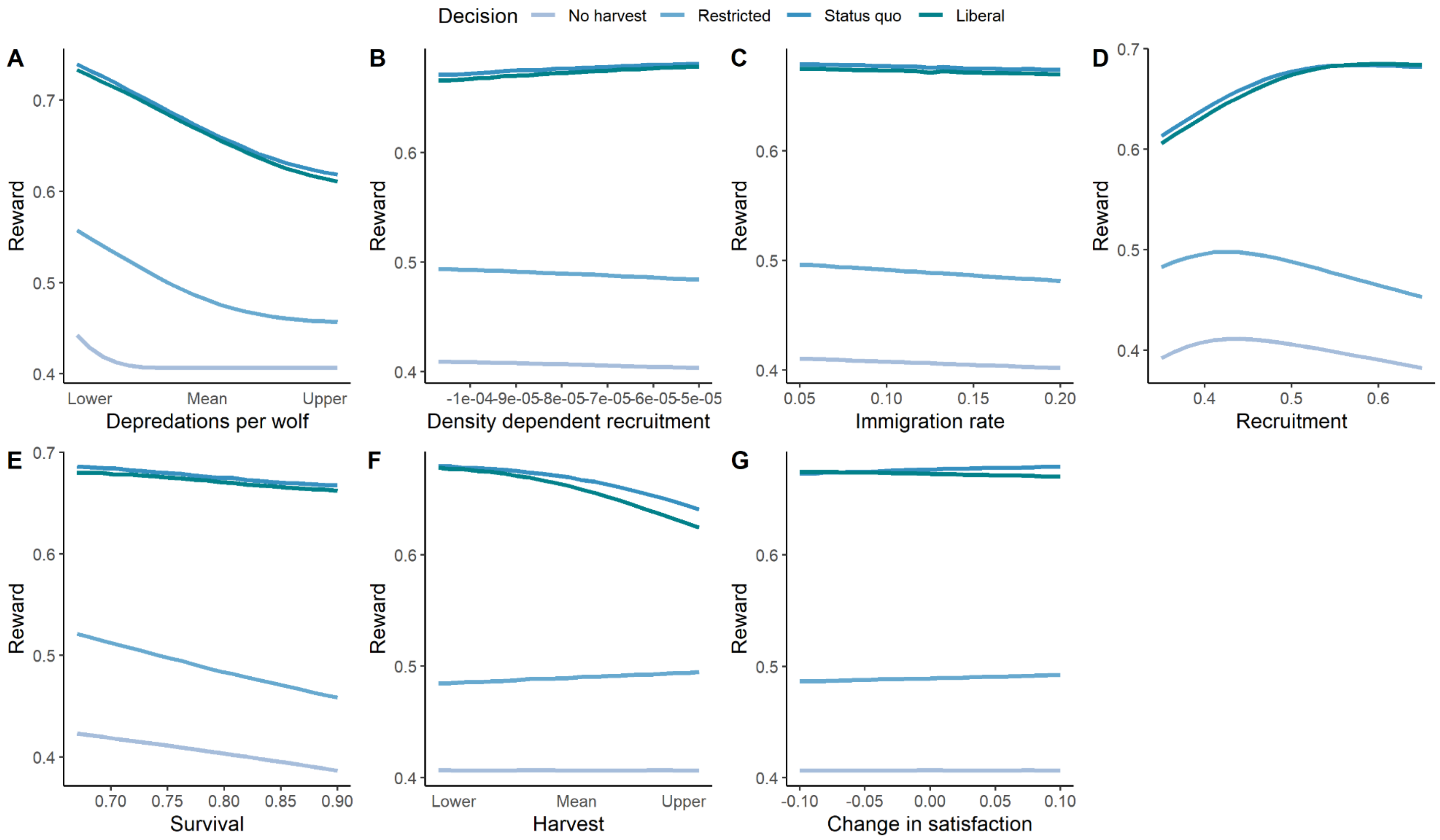

Figure 5.B.4: Indifference curves of the sensitivity of the reward in meeting objectives to uncertainty in parameter values for harvest management of wolves in Montana when the current abundance was 810 wolves. We varied the parameter value from the lower to the

upper credible interval and determined the reward for the four management actions. The higher overall reward indicates greater support. Parameters included depredations per wolf during years with and without harvest (A), the effect of density dependence on recruitment (B), net immigration rate (C), mean recruitment rate (D), adult survival (E), total harvest (F), and the percent change in the coefficients for the relationship between harvest regulations and the percent Montanans satisfied (G).

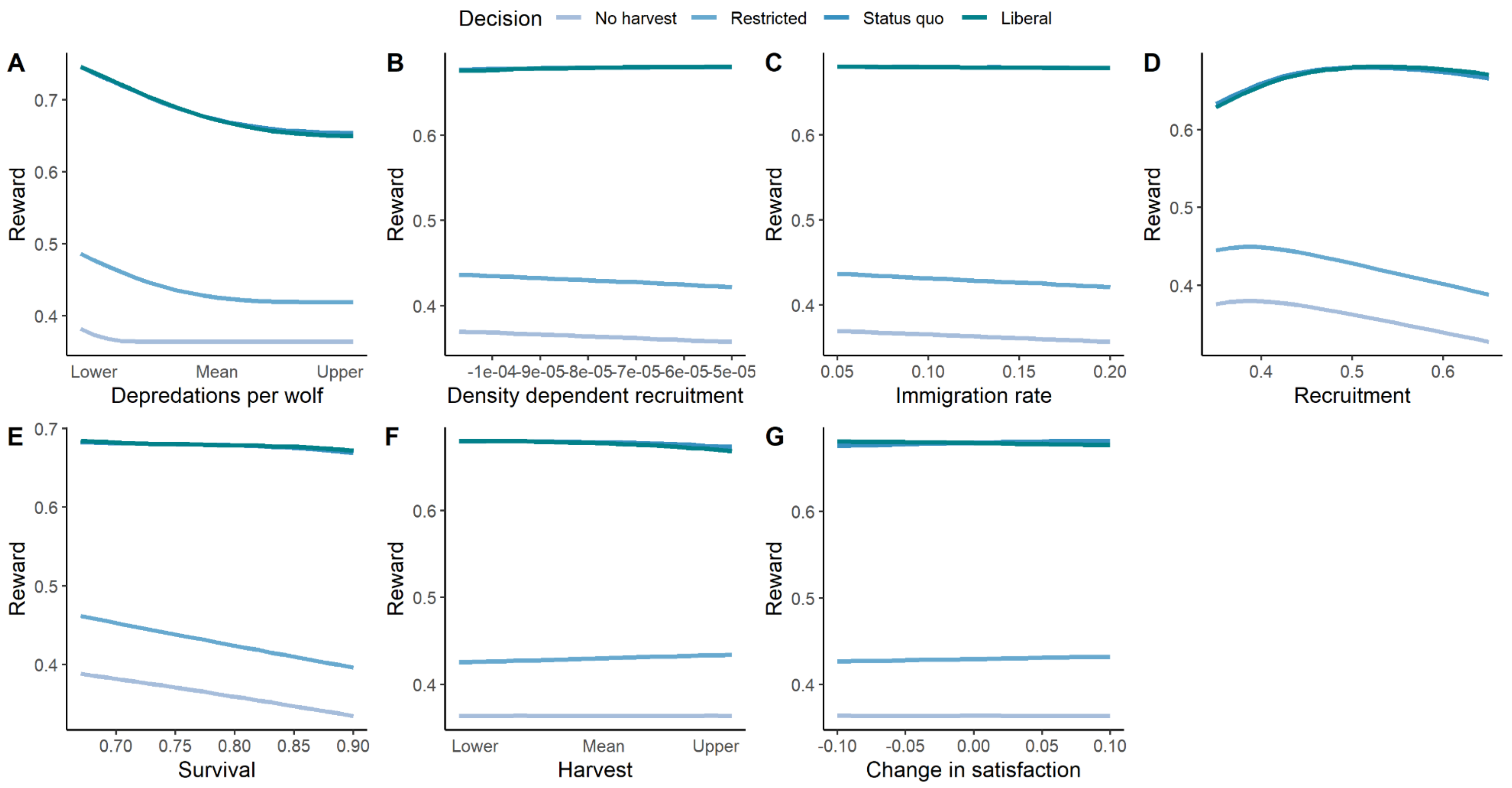

Figure 5.B.5: Indifference curves of the sensitivity of the reward in meeting objectives to uncertainty in parameter values for harvest management of wolves in Montana when the current abundance was 1000 wolves. We varied the parameter value from the lower to the upper credible interval and determined the reward for the four management actions. The higher overall reward indicates greater support. Parameters included depredations per wolf during years with and without harvest (A), the effect of density dependence on

recruitment (B), net immigration rate (C), mean recruitment rate (D), adult survival (E), total harvest (F), and the percent change in the coefficients for the relationship between harvest regulations and the percent Montanans satisfied (G).

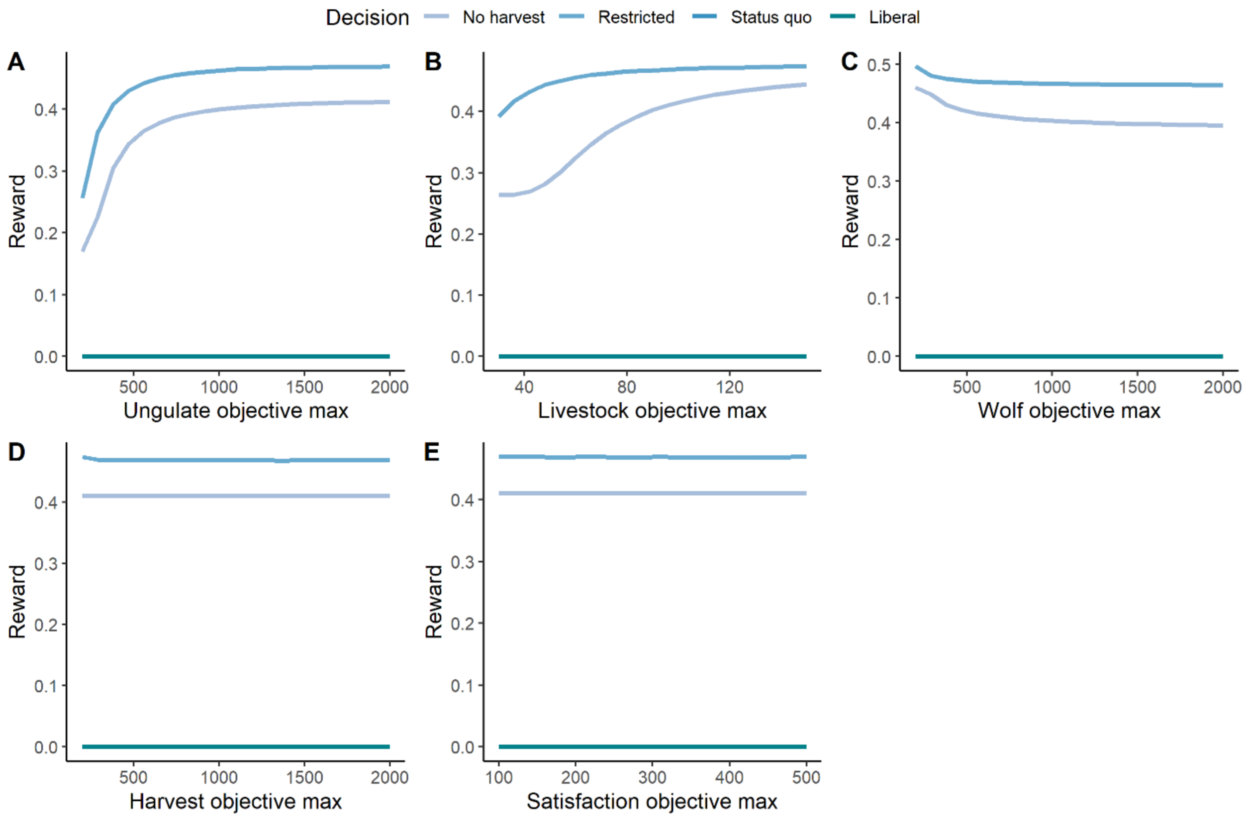

Figure 5.B.6: Indifference curves of the sensitivity of the reward in meeting objectives to uncertainty in the maximum values used to create utility functions for objectives for harvest management of wolves in Montana when the current abundance was 200 wolves. The higher overall reward indicates greater support. Objectives included A) reduce wolf impacts on ungulates, B) reduce wolf impacts on livestock, C) maintain a viable and connected wolf population, D) maintain hunter opportunity for wolves, and E) increase public acceptance of wolf harvest.

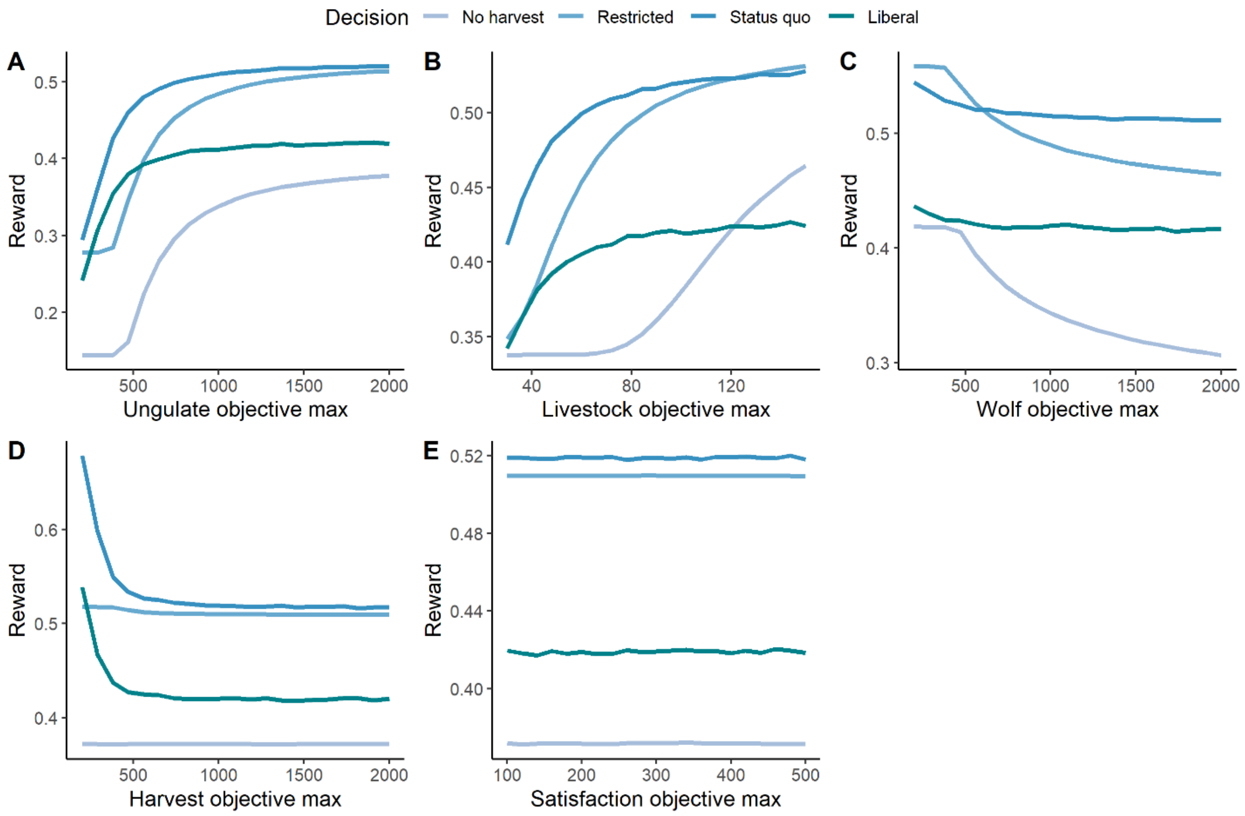

Figure 5.B.7: Indifference curves of the sensitivity of the reward in meeting objectives to uncertainty in the maximum values used to create utility functions for objectives for harvest management of wolves in Montana when the current abundance was 350 wolves. The higher overall reward indicates greater support. Objectives included A) reduce wolf impacts on ungulates, B) reduce wolf impacts on livestock, C) maintain a viable and connected wolf population, D) maintain hunter opportunity for wolves, and E) increase public acceptance of wolf harvest.

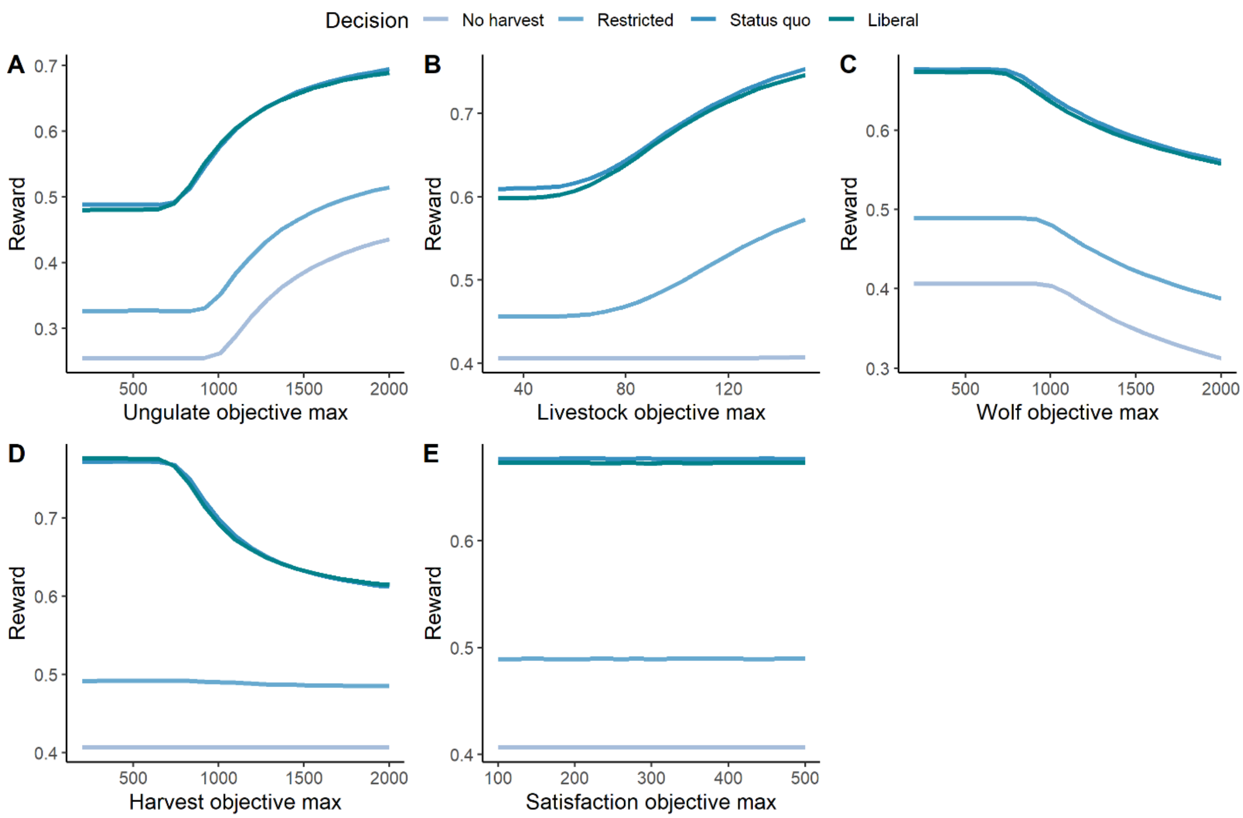

Figure 5.B.8: Indifference curves of the sensitivity of the reward in meeting objectives to uncertainty in the maximum values used to create utility functions for objectives for harvest management of wolves in Montana when the current abundance was 810 wolves. The higher overall reward indicates greater support. Objectives included A) reduce wolf impacts on ungulates, B) reduce wolf impacts on livestock, C) maintain a viable and connected wolf population, D) maintain hunter opportunity for wolves, and E) increase public acceptance of wolf harvest.

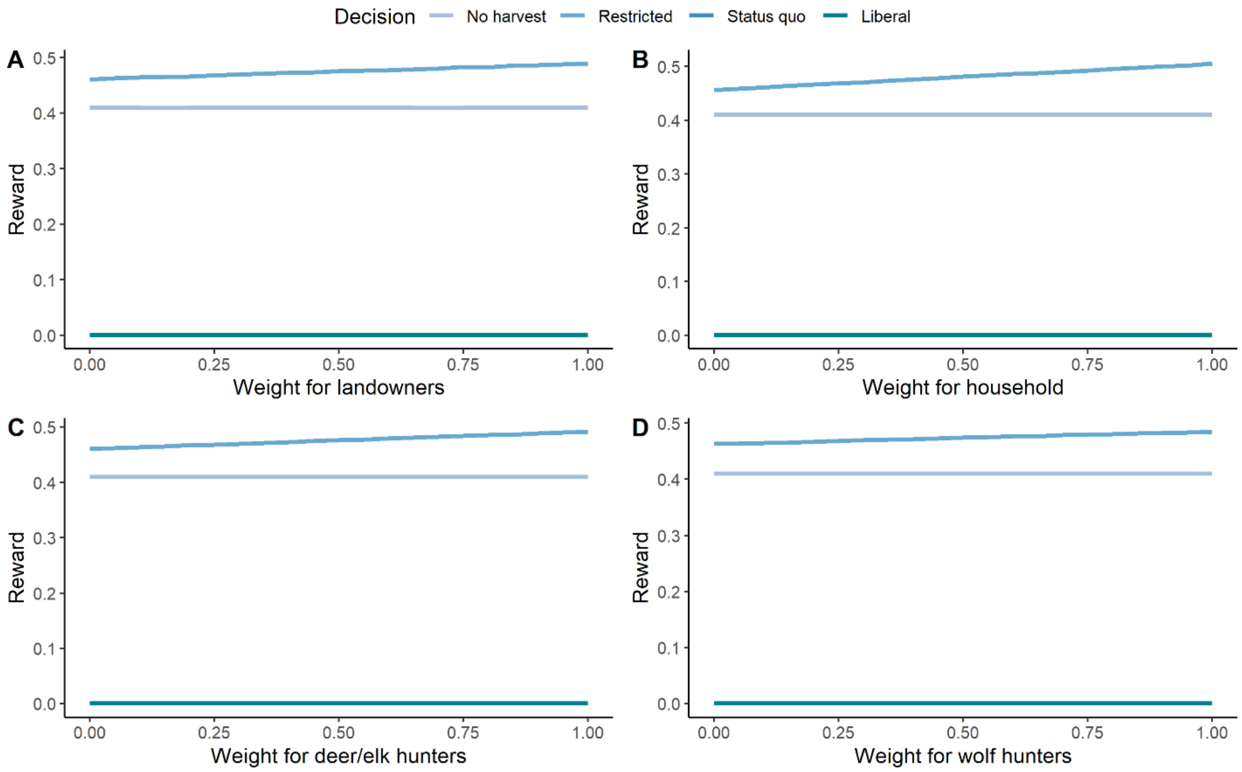

Figure 5.B.9: Indifference curves of the sensitivity of the reward in meeting objectives to weight of different stakeholder groups used to evaluate the objective to increase public acceptance of wolf harvest for harvest management of wolves in Montana when the current abundance was 200 wolves. The percent Montanans satisfied with harvest regulations was determined for private landowners (A), the general household (B), deer and elk license hunters (C), and wolf hunters (D), and then combined by multiplying the weight for the group by utility value. The higher overall reward indicates greater support.

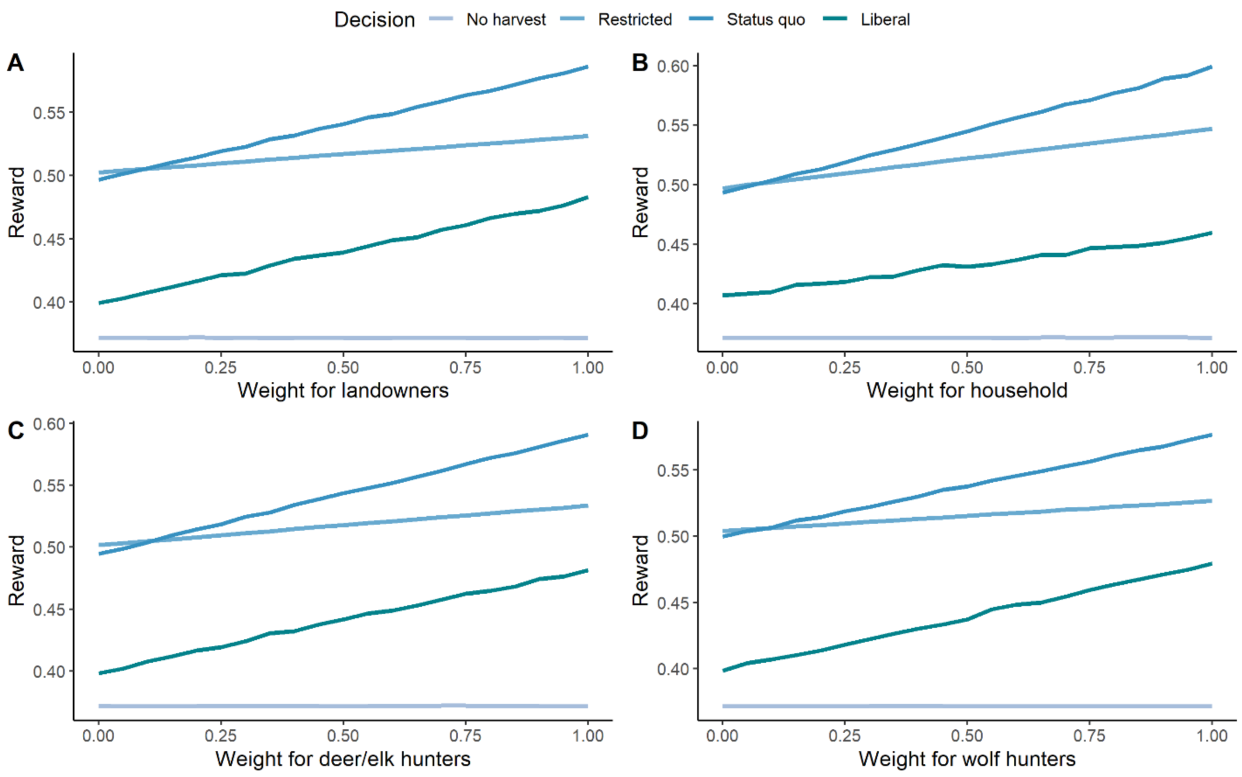

Figure 5.B.10: Indifference curves of the sensitivity of the reward in meeting objectives to weight of different stakeholder groups used to evaluate the objective to increase public acceptance of wolf harvest for harvest management of wolves in Montana when the current abundance was 350 wolves. The percent Montanans satisfied with harvest regulations was determined for private landowners (A), the general household (B), deer and elk license hunters (C), and wolf hunters (D), and then combined by multiplying the weight for the group by utility value. The higher overall reward indicates greater support.

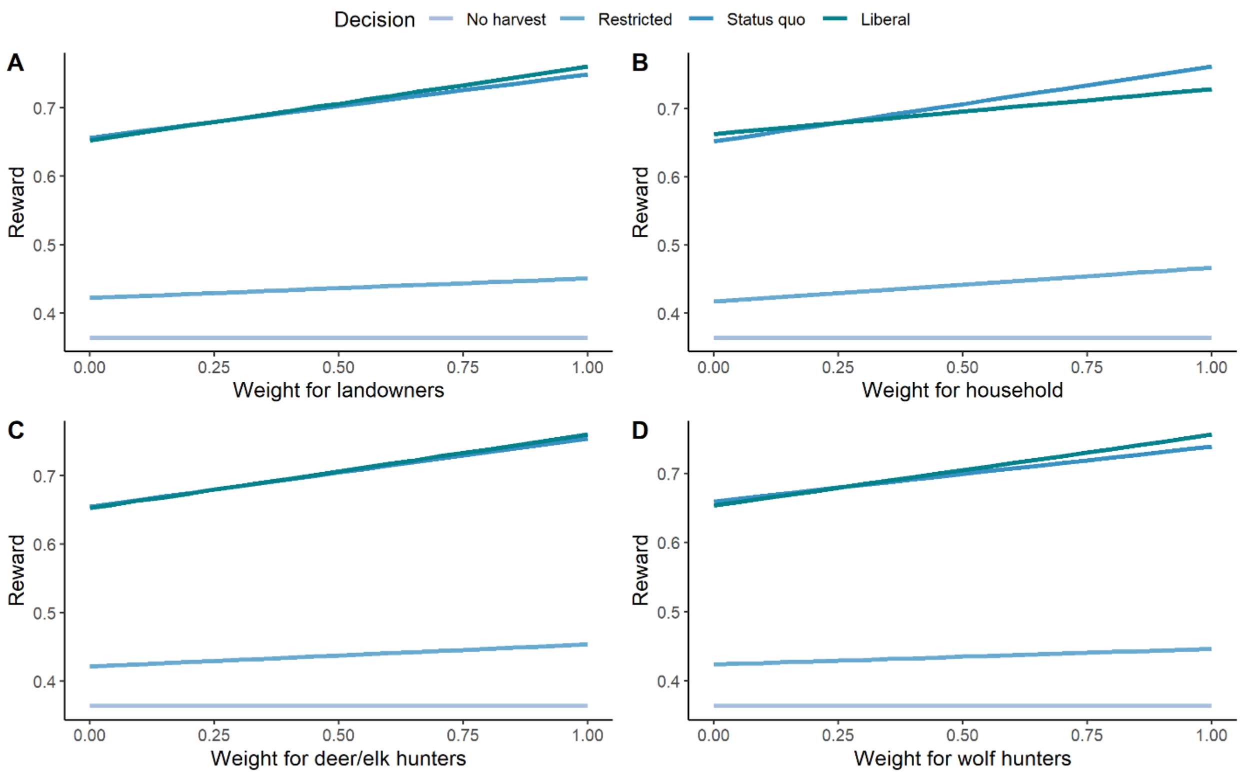

Figure 5.B.11: Indifference curves of the sensitivity of the reward in meeting objectives to weight of different stakeholder groups used to evaluate the objective to increase public acceptance of wolf harvest for harvest management of wolves in Montana when the current abundance was 1000 wolves. The percent Montanans satisfied with harvest regulations was determined for private landowners (A), the general household (B), deer and elk license hunters (C), and wolf hunters (D), and then combined by multiplying the weight for the group by utility value. The higher overall reward indicates greater support.

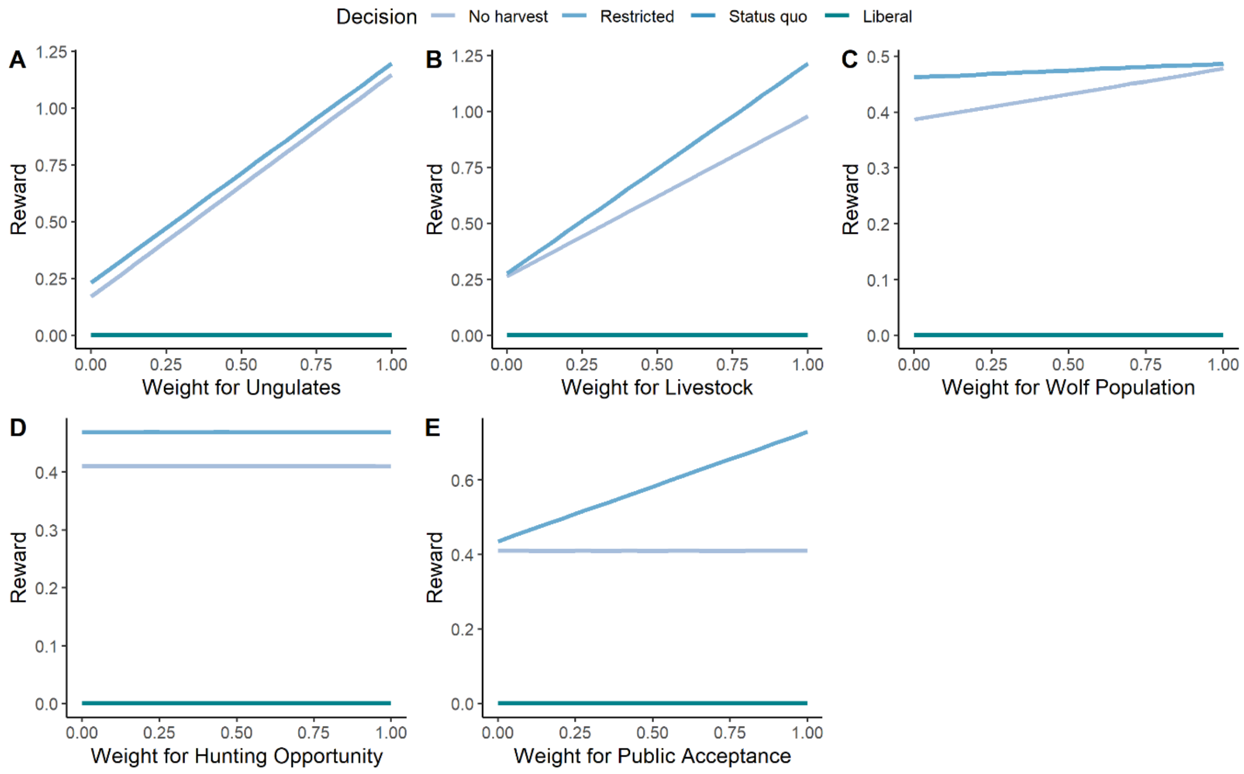

Figure 5.B.12: Indifference curves of the sensitivity of the reward value in meeting objectives to weight on objectives for an adaptive management framework for managing wolf harvest regulations in Montana when the current abundance was 200 wolves. Objectives included A) reduce wolf impacts on ungulates, B) reduce wolf impacts on livestock, C) maintain a viable and connected wolf population, D) maintain hunter opportunity for wolves, and E) increase public acceptance of wolf harvest. We varied the weight for each objective from zero to one while holding the other objective weights at their original value. The management action with the greatest reward value indicates greater support.

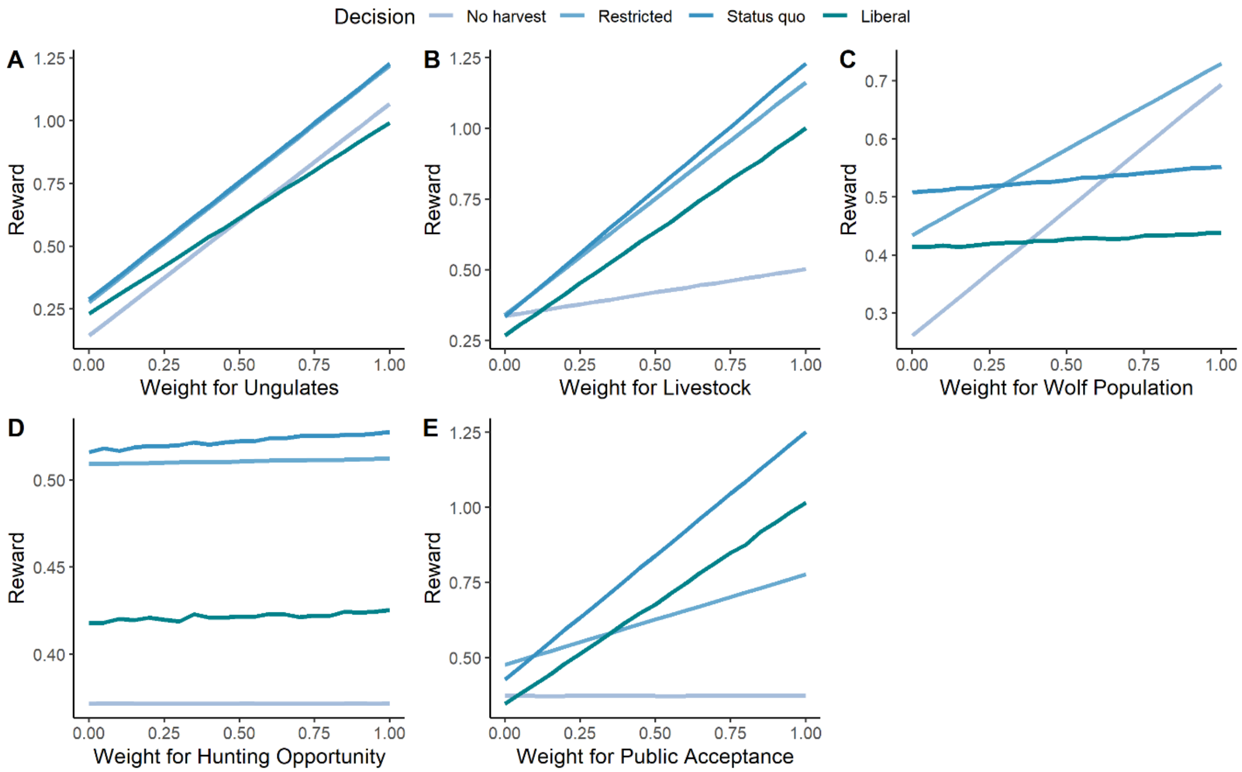

Figure 5.B.13: Indifference curves of the sensitivity of the reward value in meeting objectives to weight on objectives for an adaptive management framework for managing wolf harvest regulations in Montana when the current abundance was 350 wolves. Objectives included A) reduce wolf impacts on ungulates, B) reduce wolf impacts on livestock, C) maintain a viable and connected wolf population, D) maintain hunter opportunity for wolves, and E) increase public acceptance of wolf harvest. We varied the weight for each objective from zero to one while holding the other objective weights at their original value. The management action with the greatest reward value indicates greater support.

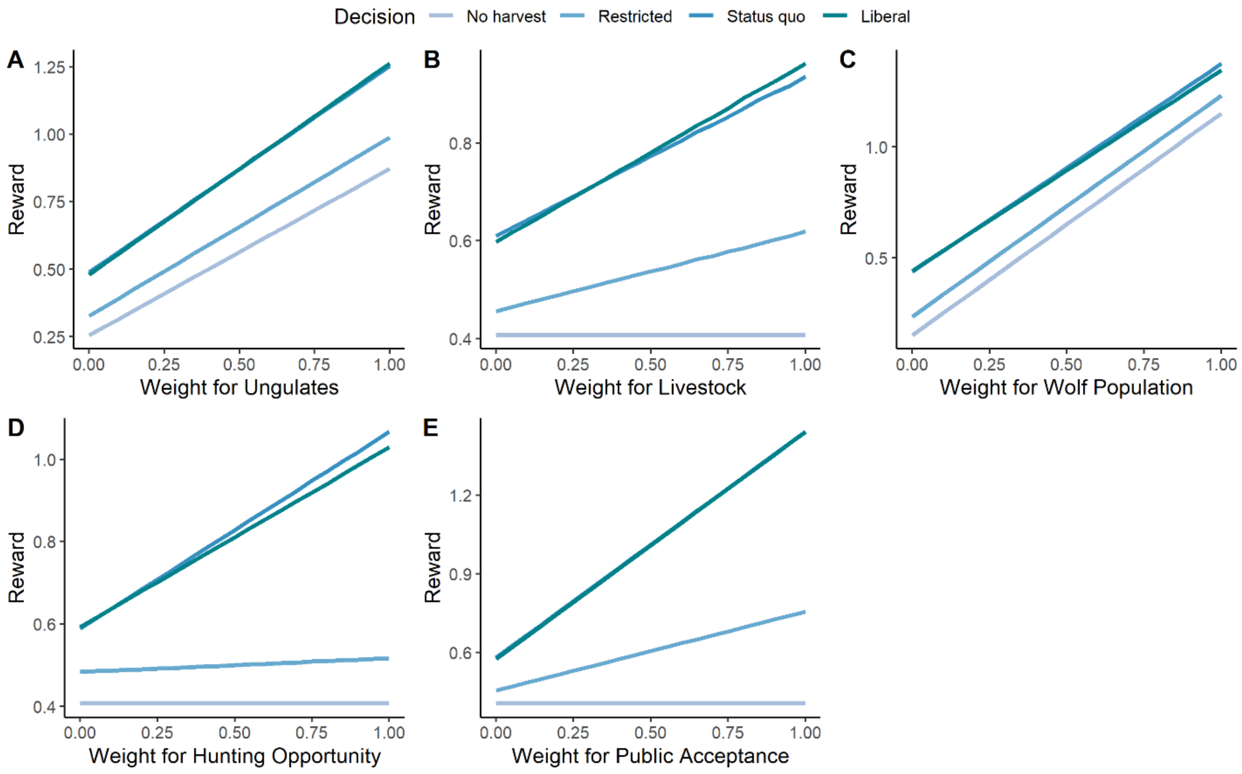

Figure 5.B.14: Indifference curves of the sensitivity of the reward value in meeting objectives to weight on objectives for an adaptive management framework for managing wolf harvest regulations in Montana when the current abundance was 810 wolves. Objectives included A) reduce wolf impacts on ungulates, B) reduce wolf impacts on livestock, C) maintain a viable and connected wolf population, D) maintain hunter opportunity for wolves, and E) increase public acceptance of wolf harvest. We varied the weight for each objective from zero to one while holding the other objective weights at their original value. The management action with the greatest reward value indicates greater support.

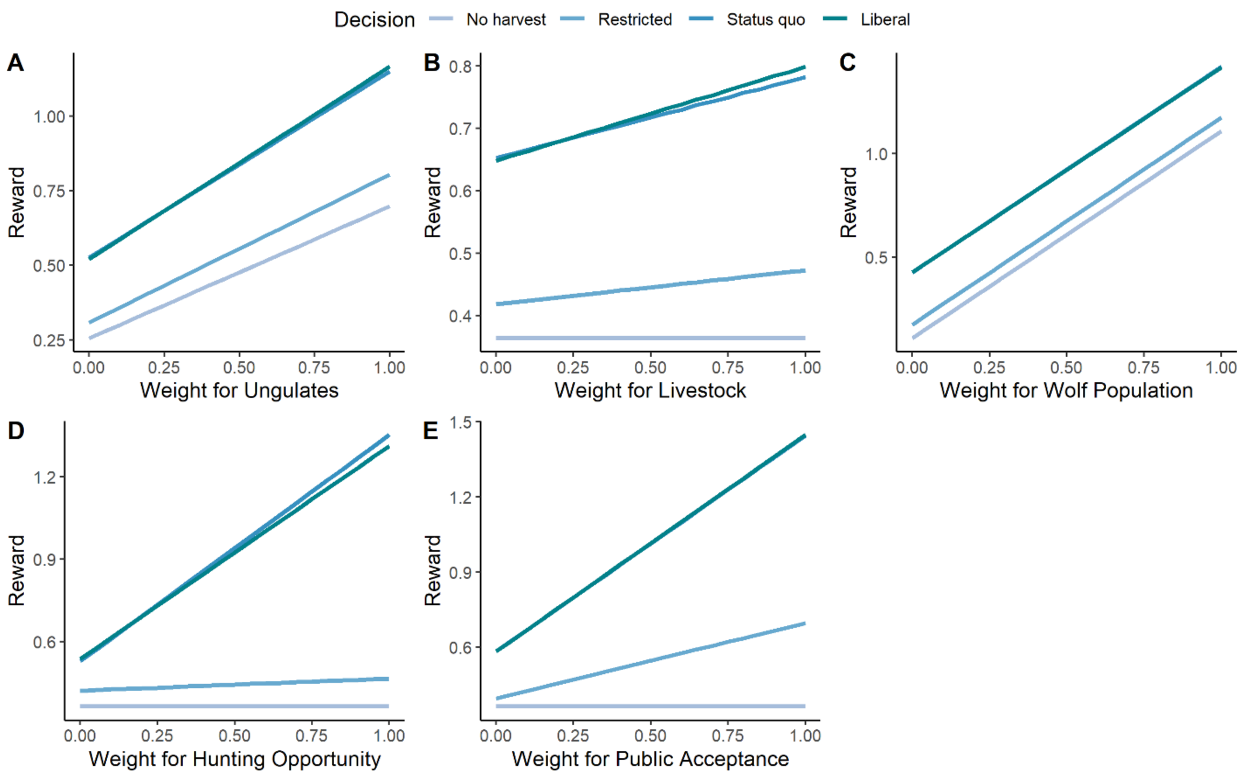

Figure 5.B.15: Indifference curves of the sensitivity of the reward value in meeting objectives to weight on objectives for an adaptive management framework for managing wolf harvest regulations in Montana when the current abundance was 1000 wolves. Objectives included A) reduce wolf impacts on ungulates, B) reduce wolf impacts on livestock, C) maintain a viable and connected wolf population, D) maintain hunter opportunity for wolves, and E) increase public acceptance of wolf harvest. We varied the weight for each objective from zero to one while holding the other objective weights at their original value. The management action with the greatest reward value indicates greater support.

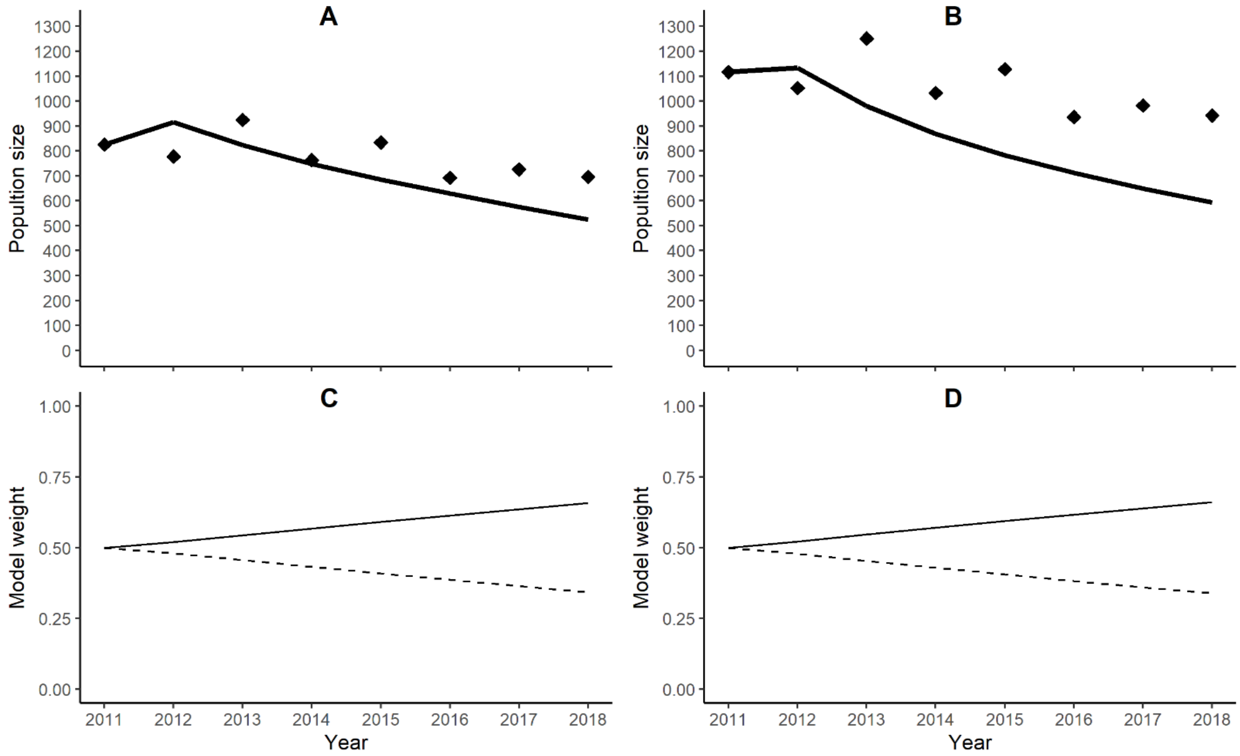

Figure 5.B.16: Sensitivity of expected performance from simulations of passive adaptive management for wolves in Montana from 2011 – 2018 to a 15% negative (A and C), or positive (B and D) bias in estimates of abundance. The expected performance metrics were predicted population size (line) compared to estimates of abundance (points; A and B), and change in model weights with no immigration (solid) and positive immigration (dashed; C and D).