

University of Nebraska - Lincoln

DigitalCommons@University of Nebraska - Lincoln

USDA National Wildlife Research Center - Staff
Publications

U.S. Department of Agriculture: Animal and Plant
Health Inspection Service

2014

Modeling black bear population dynamics in a human-dominated stochastic environment

D. L. Lewis

Colorado State University

S. W. Breck

USDA/APHIS/WS National Wildlife Research Center, stewart.w.breck@aphis.usda.gov

K. R. Wilson

Colorado State University, kenneth.wilson@colostate.edu

C. T. Webb

Colorado State University, Colleen.Webb@ColoState.EDU

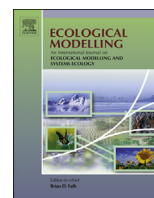
Follow this and additional works at: https://digitalcommons.unl.edu/icwdm_usdanwrc

 Part of the [Life Sciences Commons](#)

Lewis, D. L.; Breck, S. W.; Wilson, K. R.; and Webb, C. T., "Modeling black bear population dynamics in a human-dominated stochastic environment" (2014). *USDA National Wildlife Research Center - Staff Publications*. 1531.

https://digitalcommons.unl.edu/icwdm_usdanwrc/1531

This Article is brought to you for free and open access by the U.S. Department of Agriculture: Animal and Plant Health Inspection Service at DigitalCommons@University of Nebraska - Lincoln. It has been accepted for inclusion in USDA National Wildlife Research Center - Staff Publications by an authorized administrator of DigitalCommons@University of Nebraska - Lincoln.



Modeling black bear population dynamics in a human-dominated stochastic environment



D.L. Lewis^{a,*}, S.W. Breck^b, K.R. Wilson^a, C.T. Webb^c

^a Department of Fish, Wildlife, and Conservation Biology, Colorado State University, 1474 Campus Delivery, Fort Collins, CO 80523-1474, USA

^b USDA-WIS-National Wildlife Research Center, 4101 Laporte Avenue, Fort Collins, CO 80521, USA

^c Department of Biology, Colorado State University, Fort Collins, CO 80523, USA

ARTICLE INFO

Article history:

Received 15 February 2014

Received in revised form 29 July 2014

Accepted 26 August 2014

Keywords:

Black bear

Elasticity

Sensitivity

Stochastic population growth

Ursus americanus

ABSTRACT

Many large carnivore populations exist in human-influenced stochastic environments where availability of natural food sources vary annually and anthropogenic food sources can supplement energetic demands, but at a potential demographic cost due to human–wildlife conflict and subsequent conflict management. Understanding how these competing factors influence a population is complex and difficult to study, but here we demonstrate the utility of using a stochastic projection matrix model and perturbation analysis to gain insight into this problem. We modeled a black bear population subjected to stochastic failures of fruiting and masting species, but with access to garbage in urban environments. We parameterized our model with data from a 6-year study on black bears in Aspen, Colorado and data synthesized from other research studies. Using computer simulation, we investigated the effect that different levels of conflict–bear removal can have on a bear population by comparing a “reference” scenario where bears did not benefit from human food sources or experience conflict–bear removals with two urban scenarios where bears had varying access to human foods, but conflict bears were removed. We used perturbation analyses to evaluate consequences for changing population vital rates and to estimate the impact each vital rate change had on population growth. Simulations were used to identify how much variation in each vital rate influenced variation in the population growth rate. We identified the survival rate of breeding adult females during good natural food years as having the highest elasticity value. We found that the benefit of increased cub production from available human food sources during natural food failure years was quickly negated if management of conflict bears through removal reduced adult female survival. Increasing the frequency of years when natural food production fails resulted in disproportionate impacts from available urban food and conflict–bear removals, where population growth rates in a High Removal scenario declined 1.5 times faster than in the reference scenario. Our findings suggest that for regions where changing climates will increase the frequency of natural food failures, managers may need to utilize non-lethal practices in managing conflict bears and municipalities will need to secure human food sources to reduce the need for conflict–bear removals and potential population declines.

© 2014 Elsevier B.V. All rights reserved.

1. Introduction

For most wildlife, natural food sources vary over time and space, thereby directly impacting the behavior, population dynamics, and ecology of animals. In ecosystems where wildlife coexist with people, natural food shortages can lead to increased use of anthropogenic food sources (e.g., livestock and garbage) that can

positively impact the demographics (e.g., survival and reproduction) of animals utilizing these resources (Fedriani et al., 2001; Webb et al., 2004). In other cases, lack of tolerance to wildlife conflict by humans and subsequent wildlife removal can lead to negative demographic impacts and population decline (Linnell et al., 2001; Mech, 1995). Thus, knowing how a wildlife population responds to availability of anthropogenic food requires understanding of natural food production variability, the intensity of management of conflict wildlife, and the resulting demographic response. The complexity of this issue is global, and particularly relevant to the management and conservation of large carnivores as more large carnivores are forced to exist in human dominated

* Corresponding author. Tel.: +1 970 274 9578.

E-mail addresses: dsiwellewis@gmail.com, David.Lewis@state.co.us (D.L. Lewis).

systems. However, studying the impacts that humans have on large carnivores is challenging, because of the long life spans of many carnivores and the corresponding expense and challenge of monitoring them.

Population models can provide insight about population responses under complex environmental scenarios (Conner et al., 2008; Heppell et al., 2000). In particular, perturbation analyses can be used to predict how changes in population vital rates, e.g., survival and reproduction, influence population growth or abundance (Caswell, 2001). Newer perturbation analyses can now be used to evaluate scenarios where stochastic environments are modeled (Caswell, 2005), allowing for a more realistic evaluation of how changing management actions impact a population. Our goal was to utilize these demographic tools to explore how variation in natural food sources, availability of anthropogenic resources, and management of human–wildlife conflicts can impact a carnivore population.

We used black bears (*Ursus americanus*) as a model species for this exercise because they are well studied across their range (see Beston (2011) for summary of population studies), will readily take advantage of anthropogenic resources, and wildlife managers are challenged with trends of increasing human–bear conflict rates and maintaining productive bear populations (Hristienko and McDonald, 2007). Bear populations that use urban food sources potentially have vital rates that differ in comparison to populations relying solely on natural food sources that vary seasonally and annually (Beckmann and Lackey, 2008; Elowe and Dodge, 1989; Inman and Pelton, 2002; Rogers et al., 1976). For example, natural food production can fail from environmental factors, e.g., spring freeze, drought, disease, insect infestation (Kasbohm et al., 1995; Neilson and Wullstein, 1980; Pierre, 1989; Sharp and Sprague, 1967; Tomback and Achuff, 2010). During these food failure years adult survival is thought to remain high (Kasbohm et al., 1996; Noyce and Garshelis, 1994; Schrage and Vaughan, 1995), but cub production declines (Beck, 1991; Beckmann and Lackey, 2008; Bridges et al., 2011; Elowe and Dodge, 1989; Rogers et al., 1976). But bears in urban environments can supplement their diets to include available urban food, eliminating seasonal and annual variation in food resources resulting in cub production when natural foods are not available (Baruch-Mordo et al., 2014; Beckmann and Lackey, 2008). While urban food sources can provide the benefit of stable cub production, to prevent property damage and for human safety, wildlife managers often remove or destroy bears that use the urban environment and cause conflict. For example, Aspen, Colorado (USA), experienced two natural food failure years during a 6-year study from 2005 to 2011 (Baruch-Mordo et al., 2014). During these poor natural food years, annual mortalities of adult females increased 2–3 times, with the majority of mortalities being attributed to removal of conflict bears. Unlike non-urban studies that observed declines in reproduction after food failure years (Beck, 1991; Bridges et al., 2011; Elowe and Dodge, 1989; Jonkel and Cowan, 1971; Rogers et al., 1976), the Aspen population exhibited normal cub production.

We developed a population projection matrix model that included survival and reproduction as a function of variation in natural food production, use of urban food resources, and conflict–bear management. We parametrized our models using demographic data from a 6-year study of urban bears (Aspen study), supplemented with vital rates from a meta-analysis of Western black bear populations (Beston, 2011). We developed a Baseline scenario where the bear population did not have access to urban food sources or experience management removal of conflict bears and used computer simulation to compare this with two management scenarios where bears utilized human foods and managers removed conflict bears. We evaluated how an increase in the

number of natural food failure years could impact the population by calculating population growth rates at six different natural food failure year frequencies. We quantified the potential impact that vital rate changes can have on the stochastic population growth rate using prospective perturbation analyses to calculate vital rate elasticity values. Additionally, we used elasticity values in conjunction with changes to vital rates between scenarios to assess overall cost and benefit of each management scenario and to show the impact each vital rate change had on the population growth rate. We then used additional simulations to assess how much each vital rate contributed to variation in the population growth rate over 50-year projections. Our modeling effort is unique because we model changing environmental conditions, allowing a more realistic understanding of the influence that changes in vital rates will have when management actions respond to changing environmental conditions.

2. Methods

2.1. Study area

We used data from a bear study (2005–2011) in and around the cities of Aspen and Snowmass, Colorado, USA within Pitkin County (combined human population size of approximately 17,100) to develop the bear population model parameters. Aspen and Snowmass are surrounded by a variety of important natural foods for bears including oak brush (*Quercus gambelli*), service berry (*Amelanchier alnifolia*), chokecherry (*Prunus virginiana*) and other fruiting and masting species. Annual variation in natural food production can directly affect bear behavior, in particular whether bears come into town to forage for anthropogenic foods (Baruch-Mordo et al., 2013). Bears are a game species in Colorado and are managed by Colorado Parks and Wildlife (CPW). CPW managers responded to human–bear conflicts with a two-strike policy, where upon first capture (1st strike) bears deemed to pose a low threat to human safety were ear tagged and translocated, and if recaptured (2nd strike) were euthanized (administrative directive W-2, CPW).

2.2. Population model

We used a projection matrix to model the female portion of the bear population through time using

$$\mathbf{n}(t+1) = \mathbf{A}_t \mathbf{n}(t), \quad (1)$$

where $\mathbf{n}(t)$, a vector of stage densities at time t , and \mathbf{A}_t , a 4×4 stochastic projection matrix that varied at each time step depending on good or poor natural food production, are used to compute $\mathbf{n}(t+1)$, the stage densities in the next year. We assumed the following: a post-birth census in late March, litter sex ratio of 0.5, male densities do not affect breeding success, and equal immigration and emigration rates. We used a projection matrix similar in structure to those used for other bear populations (Freedman et al., 2003; Hunter et al., 2010), where the adult stage classes are distinguished by the developmental state of offspring still under maternal care. We separated females into four distinct life stages: cubs (age 0–1), subadults (not mature enough to breed), adults available to breed (i.e., adult females that did not successfully produce a litter at the previous census, produced and lost the entire litter from the previous census soon enough to breed prior to the next census, and females that separated from yearlings to breed after the previous census), and adults with yearlings (see Table 1 for parameter descriptions and Fig. 1 for a life cycle

Table 1

Vital rates used to model the female portion of black bear populations. Additional subscripts *g* and *b* are used to indicate if the vital rate is associated with good or poor natural food years.

Symbol	Description
s_c	Survival of cubs to 1 year of age.
s_s	Survival of subadults not yet mature enough for breeding.
s_a	Survival of adults available to breed in the previous year.
s_r	Survival of adults that raised cubs the previous year.
τ_{sa}	Transition rate of subadult to breeding adult.
τ_{ar}	Transition rate of breeding adult to adult with newborn cubs. ^a
L	Average number of female cubs per litter.

^a Transition probability τ_{ar} is estimated as the proportion of adult females which rear cubs through the next full census period or at least long enough to hinder production of cubs in consecutive years.

diagram). The projection matrix had the form (see Table 1 for definitions).

$$\mathbf{A}_t = \begin{bmatrix} 0 & 0 & s_a \tau_{ar} L & 0 \\ s_c & s_s(1 - \tau_{sa}) & 0 & 0 \\ 0 & s_s \tau_{sa} & s_a(1 - \tau_{ar}) & s_r \\ 0 & 0 & s_a \tau_{ar} & 0 \end{bmatrix}, \quad (2)$$

This model structure incorporated the following life history traits: ~16 months maternal investment in offspring leading to a 2-year litter production cycle (Lee and Vaughan, 2004), age of primiparity ranging from 3 to 7 years (Beston, 2011), and litter production in consecutive years is possible when females breed after loss of an entire litter (Barber and Lindzey, 1986).

We developed a sequence of stochastic matrices in two steps. First, we defined ρ as the frequency of good natural food years and generated an independent identically distributed (iid) environmental sequences of good and poor natural food years using random draws from a binomial distribution. Second, we used vital rate estimates from Aspen (Baruch-Mordo et al., 2014) in conjunction with mean and 95% credible intervals for Western bear populations determined by Beston (2011) as a guide for selecting vital rate means and standard deviations for good and poor natural food years in the three scenario described in Section 2.3. We used these vital rate means and standard deviations to calculate parameters for beta and gamma distributions (see Appendix A). We used random draws from beta distributions to generate stochastic survival rates and stage transition probabilities (White, 2000) and random draws from a gamma distribution for the average number of female cubs per litter. All computations were performed using program R version 2.12.2 (R Development Core Team, 2012).

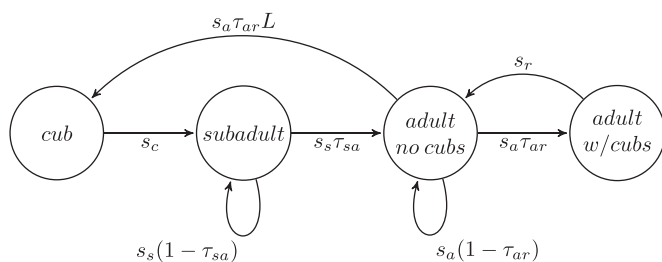


Fig. 1. Four stage classes in the female black bear life cycle are represented by circles; arrows indicate possible transitioning between stages or staying in the same stage class; s_i are survival probabilities for stage i : s_c (cubs), s_s (subadults), s_a (adults available to breed), and s_r (adults with cubs); τ_i are transition probabilities τ_{sa} (subadults to adults without cubs) and τ_{ar} (adults without cubs to adults with cubs); L is the average number of female cubs per litter.

2.3. Scenario development

We used three scenarios to evaluate the influence that frequency of poor natural food production years, available human food sources, and conflict-bear management in urban environments could have on a bear population. We created a Baseline scenario to establish a reference for comparing a population free from the influence of urban food sources and conflict-bear management with two urban removal scenarios (see Table 2 for vital rate values used in simulation). There was little information about vital rates calculated during good and poor natural food years in the literature; we thus parameterized the Baseline scenario vital rates such that the vital rate mean taken across good and bad years was near values calculated in a meta-analysis for Western black bears (Beston, 2011). We assumed that poor natural food production more negatively influenced younger stage class survival rates than adult survival (Eiler et al., 1989; Schrage and Vaughan, 1995; Noyce and Garshelis, 1994; Kasbohm et al., 1996). During good natural food years transition from subadult to breeding adult was assumed to occur on average at age 4 such that bears typically would give birth to their first litter at age 5 (Baruch-Mordo, 2012; Beston, 2011). We assumed a decrease in the transition rate from subadult to adult during poor food years, even though literature supporting this was sparse (Eiler et al., 1989). We also assumed a decrease in the transition rate of breeding adults to adult with cub(s) during poor natural food years as litter production depends on body condition (Noyce and Garshelis, 1994) and has been observed to decrease when natural foods are not available (Beck, 1991; Bridges et al., 2011; Rogers et al., 1976).

We developed two urban scenarios where vital rates were changed to reflect the influence of urban food resources and conflict-bear removal. For both urban scenarios (Low and High Removal), we assumed that available anthropogenic food sources resulted in normal cub production during poor natural food years (Baruch-Mordo et al., 2014; Beckmann and Lackey, 2008). During the Aspen study all adult females consistently gave birth on a two year cycle and the number of cubs/litter remained steady regardless of good or poor natural food availability, i.e., $\tau_{ar} = 1$ and 2.21 total cubs/litter (Baruch-Mordo et al., 2014). Because fewer than 10 adult females were monitored annually, we conservatively set $\tau_{ar} = 0.95$ and $L = 1.15$ female cubs/litter for good and poor natural food years. For the Low Removal scenario vital rates during good years essentially mimicked the Baseline scenario; the difference being that we assumed bears with a consistent food source during poor natural food years would have residually higher transition probabilities and cub production during good food years. During poor natural food years cub and sub-adult survival increased along with the transition probabilities and cub production, but adult survival dropped. For the High Removal scenario, during good forage years vital rates were the same as the Low Removal scenario, and during poor forage years, we reduced cub and subadult survival rates to be less than and equal to survival for the Baseline scenario and set adult survival rates near empirical estimates from the Aspen study (Baruch-Mordo et al., 2014) (Table 2). We assumed that vital rate values were normally distributed around a central value and set the standard deviation for good and poor natural food year vital rate distributions as follows: cub and subadult survival ($\sigma = 0.05$), adults with and without cubs survival ($\sigma = 0.025$), transition probabilities ($\sigma = 0.02$), and number of female cubs/litter ($\sigma = 0.10$).

2.4. Stochastic long-term projections

We used the stochastic projection matrix model framework developed by Tuljapurkar (1990) and analysis methods derived in

Table 2
Female bear population vital rates for Baseline, Low Removal, and High Removal scenarios. Baseline scenario represents a population with no access to urban food sources and no conflict-bear removals. Low and High Removal scenarios represent populations that use urban environments to forage during poor natural food years benefiting from urban food, but experiencing reduced survival from conflict-bear removals. Percent changes in population vital rates from the Baseline scenario to Low and High Removal scenarios are shown as • for no difference, + for an increase, and – for a decrease. Bold-faced text indicates vital rates similar to those estimated for Aspen, Colorado 2005–2010.

Vital rate	Baseline		Low Removal				High Removal			
	Good	Poor	Good		Poor		Good		Poor	
	Value	Value	Value	% change	Value	% change	Value	% change	Value	% change
s_c	0.60 ^a	0.40 ^a	0.60	• 0.0%	0.45	+ 12.5%	0.60	• 0.0%	0.35	– 12.5%
s_s	0.75 ^a	0.60 ^a	0.75	• 0.0%	0.65	+ 8%	0.75	• 0.0%	0.60	• 0.0%
s_a	0.90 ^a	0.85 ^a	0.90	• 0.0%	0.80	– 6%	0.90	• 0.0%	0.70	– 18%
s_r	0.90 ^a	0.85 ^a	0.90	• 0.0%	0.80	– 6%	0.90	• 0.0%	0.70	– 18%
τ_{sa}	0.33	0.25 ^b	0.33	• 0.0%	0.33	+ 32%	0.33	• 0.0%	0.33	+ 32%
τ_{ar}	0.90 ^b	0.60 ^b	0.95	+ 5.5%	0.95	+ 58%	0.95	+ 5.5%	0.95	+ 58%
L	1.10 ^b	0.60 ^b	1.15	+ 4.5%	1.15	+ 130%	1.15	+ 4.5%	1.15	+ 130%

^a At good natural food year frequencies of 75% the mean vital rate values of good and poor natural food years are near values calculated for Western black bears (Beston, 2011).

^b Data was not available in the meta-analysis of Western black bears (Beston, 2011) to parameterize these vital rates for the reference scenario.

Caswell (2005) to calculate stochastic population growth rates and elasticities. The stochastic population growth rate is defined as

$$\log(\lambda_s) = \lim_{t \rightarrow \infty} \frac{1}{t} \log \|\mathbf{A}_{t-1} \cdots \mathbf{A}_0 \mathbf{n}_0\|, \tag{3}$$

which can be approximated with

$$\log(\lambda_s) \approx \frac{1}{T} \sum_{t=1}^T \log(\|\mathbf{R}_t\|), \tag{4}$$

when T , the number of time steps is large ($T = 100,000$). The annual population growth between time step t and $t + 1$ is $\mathbf{R}_t = \frac{\mathbf{A}_t \mathbf{n}(t)}{\|\mathbf{n}(t)\|}$ (Caswell, 2001), $\|\cdots\|$ is a sum of the vector elements. We calculated elasticity of $\log(\lambda_s)$ for good and poor year vital rates by forward projecting a stage vector $\mathbf{n}(t)$ and setting $\|\mathbf{n}(0)\| = 1$, and back projecting a reproductive value vector $\mathbf{v}(t)$ and setting $\|\mathbf{v}(T)\| = 1$ (Caswell, 2005). Elasticities were calculated using

$$\frac{\partial \log(\lambda_s)}{\partial \log \theta_i} = \lim_{T \rightarrow \infty} \frac{1}{T} \sum_{t=1}^{T-1} \frac{J_i \theta_i(t) \mathbf{v}^T(t+1) \frac{\partial \mathbf{A}_t}{\partial \theta_i(t)} \mathbf{n}(t)}{\mathbf{R}_t \mathbf{v}^T(t+1) \mathbf{n}(t+1)}, \tag{5}$$

where J_i is an indicator variable having a value of 1 when time-steps match the year-type specific elasticity being calculated and 0 for other time steps, $\theta_i(t)$ is a vector of vital rates, and $\frac{\partial \mathbf{A}_t}{\partial \theta_i(t)}$ is a differentiation of the projection matrix with respect to the vital rate vector $\theta_i(t)$. We discarded the first 30,000 time steps in the projection sequence and used only the remaining 70,000 time steps for calculating population growth rates and elasticity values.

For each scenario, we determined stochastic population growth rates and elasticity of these population growth rates to vital rates at six different frequencies of good natural food years $\rho = \{0.45, 0.55, 0.65, 0.75, 0.85, 0.95\}$. Records of natural food failure years and their causes were limited, so we used this range of good natural food year's frequencies to better understand the impact this model parameter had on population growth. We then determined the influence that a set of vital rate changes had on population growth. The increase or decrease in a population growth rate due to a different set of vital rates was determined with

$$\Delta \log(\lambda_s) = \sum_i e_{\theta_i} \delta_i, \tag{6}$$

where e_{θ_i} is the elasticity value of vital rate θ_i and δ_i is a proportional change in the vital rate calculated with

$$\delta_i = \frac{\theta'_i - \theta_i}{\theta_i}, \tag{7}$$

where θ'_i and θ_i are the new and original vital rate values, respectively (Caswell, 2001). A positive value determined from Eq. (6) can be interpreted as a beneficial set of vital rate changes, i.e., increased population growth, while a negative value suggests a decline in population growth due to the changes. We calculated the percent change in each vital rate from the Baseline scenario to the Low and High Removal scenarios (Table 2). We then compared the predicted population growth rates based on those changes (Eq. (7)) with the population growth rates calculated for the Low and High Removal scenarios (Eq. (4)).

2.5. Simulation: 50-year projections

Elasticity values do not show how much vital rate variations contribute to variation in population growth, so we used a different simulation to evaluate how temporal variation in vital rates influenced variation in population growth for 50-year projections. We used a mark-recapture population estimate of 94 individuals from the Aspen study (P.M. Lukacs, Colorado Parks and Wildlife, Personal Communication) to set the initial stage densities for the three older stage classes and calculated the number of cubs so that each simulation began at a stable stage distribution (SSD). We used the R package popbio version 2.4 (Stubben and Milligan, 2007) to calculate a SSD for each scenario determined from the eigen-vector associated with the dominate eigen-value of a projection matrix populated with good year vital rate means. Natural food failures in Aspen are often attributed to late spring freezes, so we used 30 years of minimum daily temperatures during the month of June and assumed temperatures below -2.2°C caused a failure of the main natural food sources (Neilson and Wulstein, 1980; Pierre, 1989). Good years occurred 75% of the time so we created 200 iid environmental sequences of good and poor years where $\rho = 0.75$. For each environmental sequence and scenario, we ran one hundred 50-year stochastic projections and calculated the median, 10th percentile, and 90th percentile of population totals at each time step. For each 50-year projection, we determined the standard deviation of annual population growth ($\lambda_{sim} = \frac{N_{t+1}}{N_t}$) over the 50 years and the coefficient of variation of each vital rate. We then used linear regression to determine the relationship between standard deviation of population growth ($\sigma_{\lambda_{sim}}$) to vital rate coefficient of variation.

3. Results

3.1. Stochastic long-term projections

The stochastic population growth rate $\log(\lambda_s)$ in the High Removal scenario was 1.5 times more sensitive to the frequency

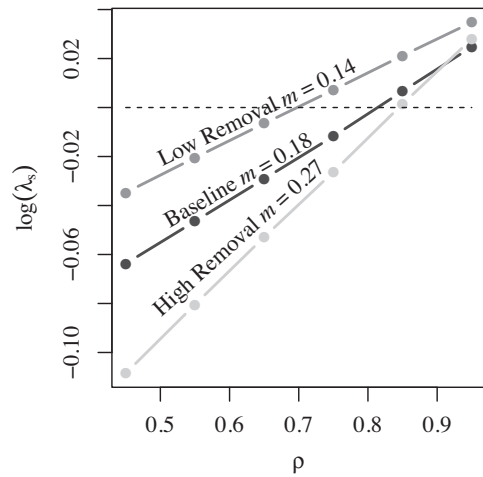


Fig. 2. Stochastic population growth rate for a female black bear population (y -axis) with respect to the frequency of good natural food years, ρ (x -axis). Horizontal dotted line indicates no increase or decrease in the population and m is the slope of $\log(\lambda_s)$ with respect to ρ . Baseline scenario represents a bear population without access to urban food and no conflict-bear removals, Low and High Removal scenarios represent populations that benefit from urban food, but have reduced survival rates from conflict-bear removals.

of good natural food years (ρ) than in the Baseline scenario and 1.9 times more sensitive than in the Low Removal scenario as indicated by the steeper slope for the High Removal scenario (Fig. 2). Relative to the Baseline scenario, increased cub production and survival rates in Low Removal scenario were more beneficial to the population than the cost of a 6% decline in adult survival. For the Low Removal scenario, reduction in adult survival was fully offset by normal litter sizes during poor natural food years (L_b). In the High Removal scenario, the negative influence of reduced survival for just breeding adult females during poor years (s_{ab}) was higher than the benefit of poor year cub production (see Table 3).

In each scenario for all frequencies of good food years considered, elasticities were always higher for survival of both adult stages (s_a and s_r) even with elasticity being partitioned between these two stage classes (Fig. 3). Considering all vital rates from both good and poor years, elasticities of subadult survival and litter size during poor natural food years (Fig. 3). When $\rho = 0.75$, elasticity values and proportional vital rate changes predicted an increase of $\log(\lambda_s)$ from -0.0118 in Baseline scenario to 0.0112 in Low Removal scenario and a decrease to -0.0228 in High Removal scenario, near approximations to Eq. (4), where $\log(\lambda_s)$ was 0.0072 and -0.0263 for Low and High Removal scenarios respectively (see Table 3 for

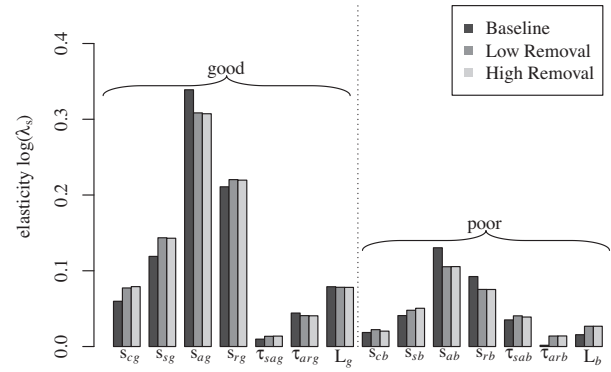


Fig. 3. Elasticity values of long-term stochastic population growth $\log(\lambda_s)$ for three black bear management scenarios (y -axis) separated by vital rates of good and poor natural food years (x -axis). Proportion of good years was $\rho = 0.75$ for this set of elasticity values. Baseline scenario represents a bear population without access to urban food and no conflict-bear removals, Low and High Removal scenarios represent populations that benefit from urban food, but have reduced survival rates from conflict-bear removals. See Table 1 for variable definitions.

proportional vital rate changes, elasticity values, and changes in population growth due to changes in each parameter). Positive contributions to the population growth rates of the Low and High Removal scenarios came mostly from consistent litter size during poor natural food years, while reductions in population growth were mainly from reduced survival of available breeding adults.

3.2. Simulation: 50-year projections

Trends in median population totals declined for both Baseline and High Removal scenarios, and increased for the Low Removal scenario (Fig. 4). At year 50, positive population growth occurred in 12%, 78%, and 3% of the Baseline, Low Removal, and High Removal scenario iterations, respectively. The vital rates with the most influence on variation in population growth differed between scenarios. For the Baseline scenario, variance in population growth could mostly be attributed to variance in τ_{ar} and average litter size (L), while for Low and High Removal scenarios variation in these vital rates contributed little to variation in population growth as they remained more constant between good and poor natural food years. For the two removal scenarios, s_a was responsible for most of the variation in population growth, followed by variation in cub survival. The pattern between the Low and High Removal scenarios was similar, but with greater differences in regression coefficients for the High Removal scenario (Fig. 5). We estimated a negative regression coefficient for the coefficient of variation of the transition rate from subadult to breeding adult (τ_{sa}) in the Baseline

Table 3

Contributions that vital rates had on stochastic population growth ($\Delta \log(\lambda)$) when vital rates of the baseline scenario (θ_{BL}) were changed to match vital rates of the Low and High removal scenarios. In the baseline scenario the bear population did not benefit from urban foods and had no conflict-bear removals and in the Low and High removal scenarios human food sources were available and removal of conflict bears occurred. Changes in the population growth rate were determined from proportional changes in vital rates (δ) and elasticity values from the baseline scenario (e_{BL}) calculated when the frequency of good natural food years was $\rho = 0.75$.

	θ_{BL}	e_{BL}	Baseline to Low Removal			Baseline to High Removal			
			θ_{LR}	δ	$\Delta \log(\lambda)$	θ_{HR}	δ	$\Delta \log(\lambda)$	
τ_{arg}	0.90	0.044	0.95	0.056	0.002	0.95	0.056	0.002	
L_g	1.10	0.079	1.15	0.045	0.004	1.15	0.045	0.004	
s_{cb}	0.40	0.019	0.45	0.125	0.002	0.35	-0.125	-0.002	
s_{sb}	0.60	0.041	0.65	0.083	0.003	0.60	0.000	0.000	
s_{ab}	0.85	0.130	0.80	-0.059	-0.008	0.70	-0.176	-0.023	
s_{rb}	0.85	0.092	0.80	-0.059	-0.005	0.70	-0.176	-0.016	
τ_{sab}	0.25	0.010	0.33	0.333	0.003	0.33	0.333	0.003	
τ_{arb}	0.60	0.002	0.95	0.583	0.001	0.95	0.583	0.001	
L_b	0.50	0.016	1.15	1.300	0.020	1.15	1.300	0.020	
			$\sum \Delta \log(\lambda):$			0.023			-0.011

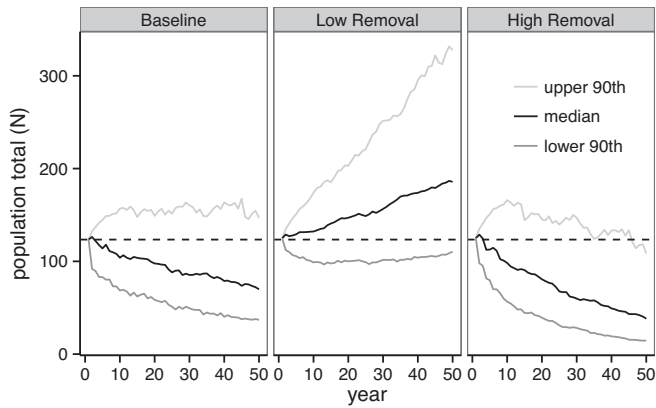


Fig. 4. Female black bear population totals (y-axis) summarized over 50 years (x-axis) where the frequency of good food years was $\rho \approx 0.75$. At each time step the median, lower 90th, and upper 90th percentile population totals summarize 20,000 iterations. Baseline scenario represents a bear population without access to urban food and no conflict-bear removals, Low and High Removal scenarios represent populations that benefit from urban food, but have reduced survival rates from conflict-bear removals.

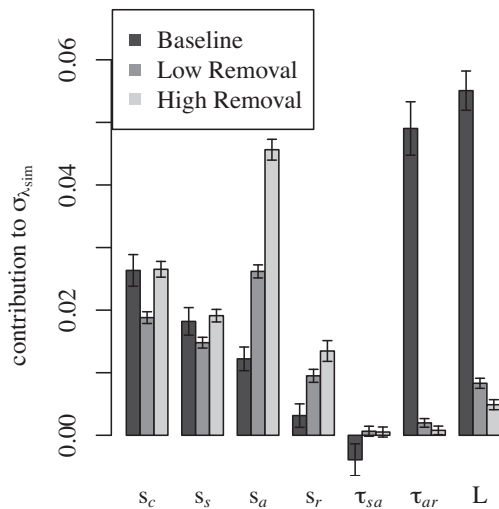


Fig. 5. Modeled contributions to the standard deviation of the population growth rate of a female black bear population (y-axis) with respect to each vital rate. Baseline scenario represents a bear population without access to urban food and no conflict-bear removals, Low and High Removal scenarios represent populations that benefit from urban food, but have reduced survival rates from conflict-bear removals. See Table 1 for variable definitions.

scenario. The relationship between variation in population growth and the coefficient of variation for this vital rate was positive, but covariance between τ_{sa} and τ_{ar} resulted in a negative regression coefficient for τ_{sa} .

4. Discussion

Using bears as a model species, our approach demonstrates how available human food sources, natural food sources influenced by changing climate, and management of conflict animals can be important when determining the impact anthropogenic resources could have on large carnivore populations. First, our model supports the idea that a high removal rate of individuals in response to human–carnivore conflict can result in anthropogenic resources being the bait of an ecological trap, i.e., the benefit of higher birth rates from anthropogenic foods is lower than the cost of conflict animals being removed from the population (Schlaepfer et al., 2002). Our model also supports the notion that carnivore populations

can benefit from anthropogenic food sources when management response includes a certain level of tolerance to wildlife conflict. However, tolerance of carnivore conflict and failure to limit anthropogenic food resources will likely support population densities that are beyond the natural carrying capacity, e.g., bears in Lake Tahoe (Beckmann and Berger, 2003b) and coyotes in California (Fedriani et al., 2001).

Our model helps identify critical variables that should be considered for measurement and manipulation when management involves similar human–wildlife dynamics. The impacts frequency of natural food failures had on the population growth rate indicate how important it is for wildlife managers to anticipate potential changes populations may encounter. For example, more frequent food failures would likely increase the impacts available anthropogenic foods and conflict management have on bear populations. Consequently it becomes important to measure the impact these factors have on vital rates, particularly rates with high elasticity values like survival of breeding adults.

Our simulations showed that temporal variation in litter size and the transition of breeding adults to adults with cubs were responsible for most variation in the Baseline scenario population growth rate. This differed from the removal scenarios where temporal variation in survival of breeding adults contributed most to the variation in the population growth rate. Life history patterns of many other species typically follows a pattern where vital rates with high elasticity values have low variation, while vital rates with low elasticity values tend to be more variable (Pfister, 1998). Removal of conflict bears artificially increases the variability of adult survival the vital rates with the high elasticity values, so will have far greater long-term repercussions than bears forgoing a reproductive cycle and/or cubs starving during poor food years.

Natural food failures and their impacts on population vital rates are mentioned in several bear studies (Beck, 1991; Bridges et al., 2011; Powell et al., 1996; Rogers et al., 1976), but our study explicitly incorporated them into the population model. We found that increasing the frequency of poor natural food years increased the differences between population growth rates of the Baseline scenario and both Removal scenarios. Many climate models predict warming and increased drought in the Rocky Mountains (Rangwala et al., 2012; Strzepek et al., 2010) that could lead to an increase in the frequency of poor natural food years. Although the pattern of food failure under a drought could be different than the spring-freeze scenarios that we simulated, our modeling approach has the benefit of easily being modified to incorporate such variations. We assumed no correlation in the sequence of good and poor years, but acknowledge that correlated poor years may have compounding impacts that were not addressed with our model. For example, weather patterns can occur over several years (e.g., the North Atlantic Oscillation, Hurrell, 1995), and could result in grouped good or poor natural food years. Under such scenarios, which are predicted to increase in some climate models (Seager et al., 2007), even the survival rate of adults in the Baseline scenario may decline after several poor natural food years, resulting in both of our urban scenarios having an overall benefit to the population. Additional scenarios having different natural food failure year patterns and continued availability of urban food sources can be incorporated into our model framework, regardless our results suggest that management efforts will need to ensure that fewer adult females are killed from urban conflict or accept that cities are potentially ecological traps that will result in smaller bear populations in the vicinity of cities. While there is currently limited concern for black bear populations, similar dynamics may occur where available anthropogenic foods may be causing ecological traps for species of greater conservation concern like grizzly bears (*Ursus arctos*) and polar bears (*Ursus maritimus*).

Prospective bear population models typically assume stable stage or age class distributions, i.e., constant vital rates through time (Beston, 2011; Freedman et al., 2003; Hebblewhite et al., 2003). We relaxed this assumption allowing vital rates to change with respect to good and poor natural food years and found that elasticity values were highest for survival of breeding adults during good years until the frequency of good years dropped below 0.55, where elasticity was then highest for survival of breeding adults during poor years. Calculating elasticities for vital rates during good and poor natural food years allows for a more realistic understanding of the influences that year specific management actions could have on the population. Previous bear studies have also identified adult survival as having the highest elasticity (Beston, 2011; Freedman et al., 2003; Hebblewhite et al., 2003). The high elasticity value for adult survival suggests that managers need to focus on understanding how different management responses to conflict affect this vital rate.

Manipulating the vital rates with the highest elasticity values may not always provide the best overall solution to broader management goals. For example, the most efficient short-term solution for suppressing a bear population that has become too large due to access to urban food sources would be to reduce survival of adult females by increasing hunting and management removals. Unfortunately, increased harvest rates near urban areas may not be practical, and management removals are not always supported by the public (Campbell, 2013) and can be expensive (Hristienko and McDonald, 2007). Although litter size during poor natural food years has a low elasticity value, it is higher when urban foods are available and made positive contributions to changes in the stochastic population growth rate that were enough to offset reduced adult survival in the Low Removal scenario. A long-term solution to maintaining a stable bear population and public support would be to limit the availability of anthropogenic foods to reduce cub production and subsequently the number of conflict bears that would need to be removed in the future. In Yellowstone and Yosemite National Parks, management action aimed at securing available human food sources were thought to have reduced bear conflicts and subsequently the role that conflict removals and human food sources were having on these populations (Gunther, 1994; Keay and Webb, 1987).

We based our model structure on observations from the Aspen region where bears switched from using human food sources in poor natural food years to using natural foods when available (Baruch-Mordo et al., 2014). This flexible foraging behavior differs from the Lake Tahoe, Nevada, region where bears primarily remained in either urban or wildland areas regardless of natural food production (Beckmann and Lackey, 2008). Additionally, removal of conflict bears was a major source of mortality for adult females in Aspen (Baruch-Mordo et al., 2014), while mortality in Lake Tahoe's urban areas was primarily from vehicle collisions (Beckmann and Lackey, 2008). Comparing bear movements and sources of mortality for the Lake Tahoe and Aspen studies demonstrates the importance of understanding region specific dynamics, management practices, and bear behavior for parameterizing, structuring, and interpreting model results. Applying our model to Lake Tahoe would thus not work without restructuring and reparameterizing our model, but this could readily be accomplished for Lake Tahoe and other systems.

A major challenge with modeling systems like these is parameterizing the model. Often baseline vital rate data are lacking and even further speculation is required to anticipate how vital rates will be changed by future events. Small changes in vital rates with high elasticity can have substantial impact on some results thus interpretation of model results will need to be limited. For example, the poor year survival rate of adults in the High Removal scenario are similar to estimates from the Aspen study. However, these

estimates were calculated from a small sample size and should not be used as conclusive evidence that Aspen's bear population was declining. We can say that a population growth rate declining 1.5 times faster in the High Removal scenario than the Baseline scenario indicates that a high removal rate of adult females would likely have negative impacts on the population. Additionally some results are robust to rough estimates during parameterization, e.g., even though vital rates are quite different between scenarios there is still a distinct vital rate elasticity pattern.

The Aspen study lacked information on whether females permanently migrated from more remote areas to forage in Aspen during poor natural food years. Our model does not account for migration between a wildland and urban population. However, the possibility of a distinct wildland population that bears are immigrating to or from was not well supported in the Aspen region. First, female home range sizes in Aspen were 5–10 km² (Baruch-Mordo et al., 2014) and wildland bears typically utilize larger areas (Beckmann and Berger, 2003a). In the Aspen region, large areas of undeveloped land between adjacent cities is lacking and the habitat of more remote areas primarily consisted of coniferous forests, high alpine tundra, and talus, which do not produce abundant fall food sources for bears in this region. Second, seasonal movement distances observed by Noyce and Garshelis (2011) suggest that even bears located in more remote areas of Colorado may be within a reasonable distance to supplement their diets in the nearest urban environment.

4.1. Conclusions

Population models are a critical tool for understanding potential challenges that wildlife populations face. Our model provides managers with a more informed perspective of how conflict-bear management strategies and changing climates could impact bear populations. As a generalist species, black bears inhabit a variety of North American habitats, and climate change scenarios underscore the need for managers to better understand future challenges of maintaining viable populations. Ultimately, management plans will need to rely more on proactive measures of reducing human–bear conflicts (Hopkins et al., 2010), if bear populations are to be sustained in and near urban areas in the future. This means that in cities like Aspen, where cub production and adult survival rates are more similar to the High Removal scenario, communities will need to better secure human food sources like garbage; a method that has been successfully implemented in many of our national parks (Gunther, 1994; Keay and Webb, 1987; Schirokauer and Boyd Hilary, 1995) and some municipalities (Peine, 2001).

Acknowledgments

We thank our funding sources Colorado Parks and Wildlife (CPW), National Wildlife Research Center (NWRC), and The Berryman Institute. We thank personnel from CPW, NWRC, City of Aspen and Pitkin County, Aspen Ranger district of the U.S. Forest Service, Aspen Field Biology Lab, Aspen Center for Environmental Studies, and field technicians. We also thank K. Crooks of Colorado State University for advice during the development of this manuscript.

Appendix A. Beta and gamma shape parameter calculation

Mean of vital rate (μ) and standard deviation (σ) were used to calculate shape parameters of beta and gamma distributions (White, 2000):

Beta distribution:

$$\alpha = \frac{\mu^2 - \mu^3 - \sigma^2}{\sigma^2} \quad (\text{A.1})$$

$$\beta = \frac{\mu - 2\mu^2 + \mu^3 - \sigma^2 + \mu\sigma^2}{\sigma^2} \quad (\text{A.2})$$

Gamma distribution:

$$\text{shape} = \frac{\mu^2}{\sigma^2} \quad (\text{A.3})$$

$$\text{scale} = \frac{\sigma^2}{\mu} \quad (\text{A.4})$$

Appendix B. Supplementary data

Supplementary data associated with this article can be found, in the online version, at <http://dx.doi.org/10.1016/j.ecolmodel.2014.08.021>. These data include Google maps of the most important areas described in this article.

References

- Barber, K.R., Lindzey, F.G., 1986. Breeding behavior of black bears. *Int. Conf. Bear Res. Manag.* 6, 129–136.
- Baruch-Mordo, S., 2012. Black Bear Ecology and Human–Bear Interactions in an Urban System. Colorado State University (Ph.D. thesis).
- Baruch-Mordo, S., Webb, C.T., Breck, S.W., Wilson, K.R., 2013. Use of patch selection models as a decision support tool to evaluate mitigation strategies of human–wildlife conflict. *Biol. Conserv.* 160, 263–271.
- Baruch-Mordo, S., Wilson, K.R., Lewis, D.L., Broderick, J., Mao, J.S., Breck, S.W., 2014. Stochasticity in natural forage production affects use of urban areas by black bears: implications to management of human–bear conflicts. *PLoS ONE* 9 (1), e85122.
- Beck, T.D.I., 1991. Black bears of west-central Colorado. Tech. Rep. No. 39. Colorado Division of Wildlife, Fort Collins, CO, USA.
- Beckmann, J.P., Berger, J., 2003a. Rapid ecological and behavioural changes in carnivores: the responses of black bears (*Ursus americanus*) to altered food. *J. Zool.* 261 (2), 207–212.
- Beckmann, J.P., Berger, J., 2003b. Using black bears to test ideal-free distribution models experimentally. *J. Mammal.* 84 (2), 594–606.
- Beckmann, J.P., Lackey, C.W., 2008. Carnivores, urban landscapes, and longitudinal studies: a case history of black bears. *Human Wildl. Confl.* 2 (2), 168–174.
- Beston, J.A., 2011. Variation in life history and demography of the American black bear. *J. Wildl. Manag.* 75 (September (7)), 1588–1596.
- Bridges, A.S., Vaughan, M.R., Fox, J.A., 2011. Reproductive ecology of American black bears in the Alleghany Mountains of Virginia, USA. *J. Wildl. Manag.* 75 (5), 1137–1144.
- Campbell, M.O., 2013. The relevance of age and gender for public attitudes to brown bears (*Ursus arctos*), black bears (*Ursus americanus*), and cougars (*Puma concolor*) in Kamloops, British Columbia. *Soc. Anim.* 21 (4), 341–359.
- Caswell, H., 2001. *Matrix Population Models: Construction, Analysis, Interpretation*, 2nd ed. Sinauer Associates, Sunderland, MA.
- Caswell, H., Mar. 2005. Sensitivity analysis of the stochastic growth rate: three extensions. *Aust. N. Z. J. Stat.* 47 (1), 75–85.
- Conner, M.M., Ebinger, M.R., Knowlton, F.F., 2008. Evaluating coyote management strategies using a spatially explicit, individual-based, socially structured population model. *Ecol. Model.* 219 (1–2), 234–247.
- Eiler, J.H., Wathen, W.G., Pelton, M.R., 1989. Reproduction in black bears in the southern Appalachian Mountains. *J. Wildl. Manag.* 53 (2), 353–360.
- Elowe, K.D., Dodge, W.E., 1989. Factors affecting black bear reproductive success and cub survival. *J. Wildl. Manag.* 53 (4), 962–968.
- Fedriani, J.M., Fuller, T.K., Sauvajot, R.M., 2001. Does availability of anthropogenic food enhance densities of omnivorous mammals? An example with coyotes in southern California. *Ecography* 24 (3), 325–331.
- Freedman, A.H., Portier, K.M., Sunquist, M.E., 2003. Life history analysis for black bears (*Ursus americanus*) in a changing demographic landscape. *Ecol. Model.* 167 (1–2), 47–64.
- Gunther, K.A., 1994. Bear management in Yellowstone National Park, 1960–93. In: Claar, J., Schullery, P. (Eds.), *Bears – Their Biology and Management*, vol. 9, pp. 549–560.
- Hebblewhite, M., Percy, M., Serrouya, R., 2003. Black bear (*Ursus americanus*) survival and demography in the Bow Valley of Banff National Park, Alberta. *Biol. Conserv.* 112 (3), 415–425.
- Heppell, S.S., Caswell, H., Crowder, L.B., 2000. Life histories and elasticity patterns: perturbation analysis for species with minimal demographic data. *Ecology* 81 (March (3)), 654–665.
- Hopkins III, J.B., Herrero, S., Shideler, R.T., Gunther, K.A., Schwartz, C.C., Kalinowski, S.T., 2010. A proposed lexicon of terms and concepts for human–bear management in North America. *Ursus* 21 (2), 154–168.
- Hristienko, H., McDonald, J.E., 2007. Going into the 21st century: a perspective on trends and controversies in the management of the American black bear. *Ursus* 18 (1), 72–88.
- Hunter, C.M., Caswell, H., Runge, M.C., Regehr, E.V., Amstrup, S.C., Stirling, I., 2010. Climate change threatens polar bear populations: a stochastic demographic analysis. *Ecology* 91 (October (10)), 2883–2897.
- Hurrell, J.W., 1995. Decadal trends in the north Atlantic oscillation: regional temperatures and precipitation. *Science* 269 (5224), 676–679.
- Inman, R.M., Pelton, M.R., 2002. Energetic production by soft and hard mast foods of American black bears in the Smoky Mountains. *Ursus* 13 (2002), 57–68.
- Jonkel, C.J., Cowan, I.M., 1971. The black bear in the spruce–fir forest. *Wildl. Monogr.* (27), 3–57.
- Kasbohm, J.W., Vaughan, M.R., Kraus, J.G., 1995. Black bear home range dynamics and movement patterns during a gypsy moth infestation. *Ursus* 10, 259–267.
- Kasbohm, J.W., Vaughan, M.R., Kraus, J.G., 1996. Effects of gypsy moth infestation on black bear reproduction and survival. *J. Wildl. Manag.* 60 (2), 408–416.
- Keay, J.A., Webb, M.G., 1987. Effectiveness of human–bear management at protecting visitors and property in Yosemite National Park. In: Bromely, M. (Ed.), *Bear–People Conflicts: Proceedings of a Symposium on Management Strategies*. Northwest Territories Department of Renewable Resources, Yellowknife, Northwest Territories, Canada, pp. 145–154.
- Lee, D.J., Vaughan, M.R., 2004. Black bear family breakup in western Virginia. *North-east. Nat.* 11, 111–122.
- Linnell, J.D.C., Swenson, J.E., Andersen, R., 2001. Predators and people: conservation of large carnivores is possible at high human densities if management policy is favourable. *Anim. Conserv.* 4, 345–349.
- Mech, L.D., 1995. The challenge and opportunity of recovering wolf populations. *Conserv. Biol.* 9 (2), 270–278.
- Neilson, R.P., Wullstein, L.H., 1980. Catkin freezing and acorn production in Gambel Oak in Utah, 1978. *Am. J. Bot.* 67 (3), 426–428.
- Noyce, K.V., Garshelis, D.L., 1994. Body size and blood characteristics as indicators of condition and reproductive performance in black bears. *Int. Conf. Bear Res. Manag.* 9, 481–496.
- Noyce, K.V., Garshelis, D.L., 2011. Seasonal migrations of black bears (*Ursus americanus*): causes and consequences. *Behav. Ecol. Sociobiol.* 65 (4), 823–835.
- Peine, J.D., 2001. Nuisance bears in communities: strategies to reduce conflict. *Hum. Dimens. Wildl.* 6 (3), 223–237.
- Pfister, C.A., 1998. Patterns of variance in stage-structured populations: evolutionary predictions and ecological implications. *Proc. Natl. Acad. Sci. U. S. A.* 95 (1), 213–218.
- Pierre, R.G.S., 1989. Magnitude, timing, and causes of immature fruit loss in *Ame-lanchier alnifolia* (Rosaceae). *Can. J. Bot.* 67 (February), 726–731.
- Powell, R.A., Zimmerman, J.W., Seaman, D.E., Gilliam, J.F., 1996. Demographic analyses of a hunted black bear population with access to a refuge. *Conserv. Biol.* 10 (1), 224–234.
- R Development Core Team, 2012. R: A Language and Environment for Statistical Computing. R Foundation for Statistical Computing, Vienna, Austria <http://www.R-project.org>
- Rangwala, I., Barsugli, J., Cozzetto, K., Neff, J., Prairie, J., 2012. Mid-21st century projections in temperature extremes in the southern Colorado Rocky Mountains from regional climate models. *Clim. Dyn.* 39 (7), 1823–1840.
- Rogers, L.L., Kuehn, D.W., Erickson, A.W., Harger, E.M., Verme, L.J., Ozoga, J.J., 1976. Effects of mast and berry crop failures on survival, growth, and reproductive success of black bears. 3rd Int. Conf. on Bear Res. and Mgmt, vol. 41. IUCN, Morges, Switz., pp. 431–438.
- Schirokauer, D.W., Boyd Hilary, M., 1995. Bear–human conflict management in Denali National Park and Preserve, 1982–94. *Ursus* 10, 395–403.
- Schlaepfer, M.A., Runge, M.C., Sherman, P.W., 2002. Ecological and evolutionary traps. *Trends Ecol. Evol.* 17 (10), 474–480.
- Schrage, M.W., Vaughan, M.R., 1995. Population responses of black bears following oak mortality induced by gypsy moths. *Ursus* 10, 49–54.
- Seager, R., Ting, M., Held, I., Kushnir, Y., Lu, J., Vecchi, G., Huang, H.-P., Harnik, N., Leetmaa, A., Lau, N.-C., et al., 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316 (5828), 1181–1184.
- Sharp, W.M., Sprague, V.G., 1967. Flowering and fruiting in the white oaks. Pistillate flowering, acorn development, weather, and yields. *Ecology* 48 (2), 243–251.
- Strzepek, K., Yohe, G., Neumann, J., Boehlert, B., 2010. Characterizing changes in drought risk for the United States from climate change. *Environ. Res. Lett.* 5 (4), 044012.
- Stubben, C.J., Milligan, B.G., 2007. Estimating and analyzing demographic models using the popbio package in R. *J. Stat. Softw.* 22 (11).
- Tombac, D.F., Achuff, P., 2010. Blister rust and western forest biodiversity: ecology, values and outlook for white pines. *For. Pathol.* 40 (August (3–4)), 186–225.
- Tuljapurkar, S., 1990. *Population Dynamics in Variable Environments*. Springer, New York, NY.
- Webb, W.C., Boarman, W.I., Rotenberry, J.T., 2004. Common raven juvenile survival in a human-augmented landscape. *Condor* 106 (3), 517–528.
- White, G.C., 2000. *Population Viability Analysis: Data Requirements and Essential Analyses*. Columbia University Press, New York, NY, USA.