

Black bear (*Ursus americanus*) survival and demography in the Bow Valley of Banff National Park, Alberta

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Abstract

We studied survival and demography of black bears, *Ursus americanus*, in Banff National Park (BNP) from 1994 to 2000 to test the efficacy of National Park protection. We monitored 25 radiocollared bears an average of 1.9 years each for a total of 51.8 bear-years. Eighty-two percent of all mortality ($n = 11$) was human-caused, composed of highway mortality (36%), management mortality (27%) and management relocation (18%). Survival was influenced by season and management status. Once bears became a management problem, survival (0.66) was lower than several hunted populations. Adult (0.84) survival was comparable to other unprotected or partly protected populations. Cub (0.64) and yearling (0.67) survival, and reproductive rate ($m_x = 0.47$ female cubs/inter-birth interval), was slightly lower than other populations in western North America. We combined survival and reproductive rates in a preliminary post-birth pulse age-class Leslie matrix model and estimated population growth rate as 0.95 (95% simulated C.I. 0.79–1.10). Sensitivity analyses showed λ was most sensitive to changes in adult female survival. Responsible management agencies should reduce adult female highway mortality and the likelihood of becoming a management problem, while continuing monitoring to refine demographic analyses to adequately protect this population.

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1. Introduction

Large carnivores are sensitive to human-caused extirpation and extinction due to their large home-ranges, low population densities and reproductive rates, and life-history characteristics that put them in conflict with humans (Noss et al., 1996; Weaver et al., 1996; Gittleman et al., 2001). Among carnivores, Ursids have been identified as particularly susceptible to human-caused extirpation due to their potential for direct aggressive conflict with humans, overlap in habitat, and broad food habits (Weaver et al., 1996; Purvis et al., 2001). Protected areas can play an important role in maintaining populations of carnivores where natural processes and population dynamics can occur unhindered, often providing a source population for adjacent sink habitat (Doak, 1995; Noss et al., 1999). However, even within

protected areas, human-caused mortality and habitat displacement occurs for many carnivore species (Noss et al., 1996; Woodroffe and Ginsberg, 1998; Woodroffe, 2001).

In the Bow Valley (BV) of Banff National Park (BNP), Canada's oldest National Park, carnivores must contend with over five million visitors per year, the National highway and railway systems, and towns with ~10,000 inhabitants (Green et al., 1996). Recent research on grizzly bears, *Ursus arctos* (Gibeau, 1998; Gibeau et al., 2002), gray wolves, *Canis lupus* (Callaghan, 2002), and lynx, *Lynx canadensis* (Apps, 2000) suggests the negative effects of human-caused mortality and habitat fragmentation may threaten population viability (e.g. Herrero et al., 2000; Callaghan, 2002). Black bears are thought to be more resilient to human-caused mortality and habitat fragmentation than other carnivores (Weaver et al., 1996; Bunnell and Tait, 1981). This resilience is due to higher reproductive rates and younger age at first reproduction than grizzlies (Bunnell and Tait, 1981), higher resultant population densities

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(Pelton, 1982), and a greater overall tolerance to human disturbance (Kasworm and Manley, 1990).

Despite their higher apparent tolerance to human activities, black bears may be vulnerable if mortality rates exceed some critical threshold (Eberhardt, 1990). Although population status of black bears in the BV has not been quantitatively examined, the cumulative effects of human activity may be causing mortality to approach this threshold. For example, fencing the Trans-Canada Highway (TCH) to reduce highway-caused wildlife mortality is unsuccessful for black bears (Clevenger et al., 2001), because bears simply climb over fencing. Despite wildlife crossing mitigation (Clevenger and Waltho, 2000), and black bears' fence-climbing ability, the fenced TCH was still a partial barrier to movement, potentially alienating bears from important habitat (Serrouya, 1999). Furthermore, black bears are frequently relocated and destroyed because of habituation to humans (Parks Canada, unpublished data). A preliminary population estimate suggested the BV black bear population size was 20–30 during 1997 (Serrouya, 1999). During the same year, 12 black bears were killed by humans (Parks Canada, unpublished data), suggestive of high mortality. Finally, black bears in BNP are restricted to lower elevation valleys, and the human-dominated Bow Valley contains the majority of the black bear habitat and population of BNP (Holroyd and Van Tighem, 1982).

Due to the cumulative effects of human activity, the status of black bear populations in BNP is uncertain despite formal protection in a National Park. Federal legislation mandates the maintenance of ecological integrity as the primary mandate of National Parks, which includes maintaining populations of animals free from major human disturbance (Government of Canada, 2000). Since 1994, black bears have been radiocollared in the BV, providing a post-hoc (i.e. survival was not a primary research objective) opportunity to investigate survival and demography with respect to the management objectives of Parks Canada. Our main objective was to estimate overall survival and cause-specific mortality of black bears in the BV of BNP over a 7-year period from 1994 to 2000 to test efficacy of National Park protection. Our secondary objectives were to use an information-theoretic approach to (1) test for the effects of broad management and ecological factors on survival (Burnham and Anderson, 1998), and (2) to combine survival rates with reproductive data to infer potential consequences to population dynamics. Based on knowledge of bear biology and management issues, we tested for effects of season, age and sex-class, and management status (i.e. management problem bear vs. research bear, see methods) on survival. We determined reproductive rate, and cub and yearling survival by monitoring radiocollared female reproduction. We combined these vital rates in a Leslie matrix model to

estimate population growth rate (λ). Finally, we assessed sensitivity of λ to changes in vital rates to explore potential management options for this population.

2. Study area

BNP (6641 km²) is located in the front and main ranges of the Canadian Rocky Mountains 120 km west of Calgary, Alberta, Canada, in rugged mountainous topography (1400–3400 m). The climate is characterized by long cold winters with infrequent warming Chinook winds, and short, dry summers. Our study area included a 2500 km² area of BNP centered on the Bow Valley, a wide (2–6 km width) and low elevation (1350–1600 m) valley containing the highest quality black bear habitat within BNP (Holroyd and Van Tighem, 1983). Habitats were divided into the montane, subalpine, and alpine ecoregions, corresponding with increasing elevation and decreasing productivity (Holland and Coen, 1983). Black bears primarily use the montane ecoregion in BNP, 80% of which is contained within the BV. The montane consists of lodgepole pine (*Pinus contorta*), interspersed with infrequent aspen (*Populus tremuloides*) and grasslands (Holroyd and Van Tighem, 1983). Important bear foods in BNP include buffaloberry (*Sherperdia canadensis*), graminoids, crowberries (*Empetrum nigrum*), horsetail (e.g., *Equisetum* spp.), bearberry (*Arctostaphylos uva-ursi*), ants (*Formicidae*), and seasonally important ungulates during spring (Holcroft and Herrero, 1991). Other large mammals include grizzly bears, wolves, elk (*Cervus elaphus*), and Bighorn sheep (*Ovis canadensis*). Two towns, the national railway (Canadian Pacific Railway, CPR) and highway (Trans-Canada Highway, TCH) systems, a golf course, outlying hotels, and numerous secondary roads and other human developments are located in the study area.

3. Methods

3.1. Capture and monitoring

Black bears were captured between May and October of each year from 1994 to 1999 using Aldrich foot snares (Aldrich Animal Trap Co., Clallham Bay, WA) and culvert traps. Bears were immobilized using Telazol at an intended dosage of 5 mg/kg under veterinary direction. All bears were captured under approval by Parks Canada. Bear ages were determined from cementum annuli of extracted premolars (Stoneberg and Jonkel, 1966) at a commercial laboratory (Mattson's Lab, Milltown, MT). Bears were fitted with VHF radio-telemetry collars (LOTEK Engineering Ltd, Aurora, ON) or VHF eartag transmitters (Advanced Telemetry Systems, Isanti, MN), with mortality sensors when

bears were inactive ≥ 4 h. Radiocollars were fitted with a breakaway device to release the collar in ~ 3 –4 years (Hellgren et al., 1988). Bears were relocated weekly during the non-denning period using ground triangulation (White and Garrott, 1990), or from the air if bears were not relocated from the ground for > 1 week. Direct observations of bears by researchers and reliable observers (Park employees, Wardens, etc.) were also used to supplement monitoring when radiocollars were still active on bears.

3.2. Estimating survival (ϕ) of black bears

We estimated black bear survival (ϕ) rates using known-fate (Pollock et al., 1989; White and Garrott, 1990) mark–recapture models in program MARK (White and Burnham, 1999) using a staggered entry design (Pollock et al., 1989). Some bears dropped collars and were re-collared later in life. Including the intervening periods following Eberhardt et al. (1994) introduces a positive bias in survival rate noted by White and Garrott (1990: p. 224) because only surviving bears can be recaptured. Therefore, we estimated survival only when black bears had functioning radiocollars.

We included bears tracked over 30-days in length, and ensured ≥ 4 black bears were radiocollared at any point in the study (White and Garrott, 1990). Similar to Sorenson and Powell (1998), we estimated survival in monthly intervals, allowing sufficient detail to explore seasonal effects, yet approximate enough to meet the assumption of constant survival within a month. If bears were relocated due to management reasons outside of BNP and did not return, we counted these as management mortality within the context of National Parks policy (Government of Canada, 1998) because bears were lost to the BNP population.

3.3. Factors affecting survival (ϕ) of black bears

Using an information theoretic approach (Burnham and Anderson, 1998), we tested for the effect of age-class, sex, season (spring, summer, fall), and management status (problem, non-problem bear) on black bear survival because of the potential importance of these factors to management. Age-classes were subadult (2 and 3 years old) or adult (≥ 4 years old); survival of cub and yearlings are described later. We modeled seasonal effects on survival by dividing the year into denning (November–March), spring (April–June), summer (July, August), and fall (September, October) periods, following denning dates (unpublished data) and seasonal occurrence of foods in the Canadian Rockies (Hollcroft and Herrero, 1991).

We defined management status following Pease and Mattson (1999). Bears were considered to be non-management bears until the first date that they were trapped due to management related problems (i.e. campground

feeding, aggression towards humans, entering town-sites). Similar to McLellan et al. (1999), we estimated survival only for bears originally collared for research purposes, or “research” bears to avoid biasing survival low. Some “research” bears later became management problems, and we estimated survival separately for such bears during their non-management and management states. We compared the fates of management and non-management bears. We also estimated the management–status transition rate following Pease and Mattson (1999) as the mean of the monthly proportion of radiocollared bears that became a problem bear during that month, not including denning periods.

3.4. Statistical methods

We modeled survival (ϕ) using generalized linear models (GLMs) as a function of independent variables (age, sex, etc.) bound by the logit (logistic) link function in program MARK (White and Burnham, 1999). Survival models were of the form $\text{logit}(\phi) = \beta_0 + \beta_1 X_1 + \dots + \beta_n X_n + \varepsilon$, where β_0 is the intercept, $\beta_1 \dots \beta_n$ are the coefficients of survival effects $X_1 \dots X_n$, and ε is random error. To derive real values for survival, we back-transformed using $\phi = e^u / (1 + e^u)$, where u = the linear form of the GLM above. We used an information theoretic approach to guide survival model selection and inference (Burnham and Anderson, 1998). This approach ensures results are robust to model selection uncertainty, providing reliable inferences about survival factors despite biological variation (Lebreton et al., 1992; Burnham and Anderson, 1998; Anderson et al., 2000). We developed an a-priori set of all first-order (no interactions) candidate models of black bear survival from factors listed above (i.e. 24 base models + 1 intercept only model, + 1 global model for 26 total models). We used Akaike Information Criteria (AIC) adjusted for small sample size (AIC_c) (Anderson et al., 2000), and overdispersion, if necessary (QAIC) (Anderson et al., 1994), to select the best candidate model(s). We considered all models within 0–4 ΔAIC_c in the top model set, and incorporated model selection uncertainty by deriving unconditional parameter estimates for survival effects from this top model set (Burnham and Anderson, 1998: pp 139). We used Akaike weights to gauge relative importance of survival factors (Burnham and Anderson, 1998), and used the evidence ratio of the ΔAIC weights for model i and model j as the likelihood that model i was better than model j (Burnham and Anderson, 1998).

Current theory is lacking in addressing goodness of fit testing and correcting for overdispersion in known-fate models (K. Pollock, North Carolina University, personal communication, G. White, Colorado State University, personal communication). We conducted a preliminary test of goodness of fit by estimating \hat{c} for the global model in program MARK (Anderson et al., 1994). We

used the global model \hat{c} as a guideline to indicate if the family of models was adequate. We corrected for overdispersion in the top model set using this naïve estimate of \hat{c} (K. Pollock, G. White, personal communication) using quasi-likelihood methods to derive QAIC_c if \hat{c} was > 1 (Anderson et al., 1994).

3.5. Cause-specific mortality

We determined cause-specific mortality rates by determining the proportion of total mortality in the following categories: (a) highway, (b) management mortality, (c) removal/translocation, and (d) natural mortality. No hunting or railway mortality occurred for collared black bears during our study. We determined cause-specific mortality by multiplying mean overall annual mortality rate $(1-\phi)$ for all black bears in the BV by the proportion of mortalities in each class to estimate cause-specific mortality rate.

3.6. Reproduction and cub survival

We estimated reproductive data from radiocollared black bears with and without active radiocollars because there were few reproductive females ($n=5$) in our sample. We estimated annual survival of cubs of the year and yearlings similar to Hovey and McLellan (1996) and Mace and Waller (1998), where cub survival (S_c) is $S_c = 1 - [(\text{cub deaths})/(\text{total number of cubs born})]$, and survival of yearlings is $S_{\text{YLY}} = 1 - [(\text{recorded YLY deaths})/(\text{YLY bear-years})]$. This assumes yearlings that survived to the late summer survived the whole year, potentially biasing our yearling survival high if mortality occurred after family break-up. However, we were unable to address this bias, therefore our estimates of yearling survival should be considered optimistic. We estimated variance in cub and yearling survival using binomial confidence intervals (Sokal and Rohlf, 1995).

Following Eberhardt et al., (1994) and Hovey and McLellan (1996) we estimated reproductive rate (m_x) as the mean number of female cubs born per inter-birth interval from adult females tracked ≥ 1 inter-birth interval [$m_x = (\text{number of cubs born})/(\% \text{ female cubs})/(\text{inter-birth interval})$]; we assumed sex-ratio of parity (50:50) at birth. We defined inter-birth interval as the period between subsequent litters, including a recovery year where females did not have cubs, if any (Hovey and McLellan, 1996). We determined age at first parturition from the literature. We used annual age-specific survival rates in demographic analyses for cub, yearling, and adult age-classes combined across sexes.

3.7. Population demography

To explore potential effects of survival and reproductive rates on demography, we estimated finite rate of

increase, or population growth rate (λ) using a post-birth pulse, age-class Leslie matrix population model (Caswell, 2001) in Ramas Ecolab (Akçakaya et al., 1997). Eberhardt (1985) developed a condensed version of an age-based Leslie-matrix population model, reformulated as a discrete version of the Lotka-Volterra growth equation, to estimate grizzly bear λ yet the two approaches are equivalent (Caswell, 2001: p. 74) except for flexibility in incorporating age at first parturition (see Hovey and McLellan, 1996; Oli and Zinner, 2001). However, we decided to use the matrix formulation because of the management difficulty in influencing this vital rate.

We combined all adults ≥ 4 years old into one composite age-class following Akçakaya et al. (1997) and Caswell (2001) as this had little influence on population growth rates (see Appendix). Similar to Wiegus et al. (2001) we assumed stable age distribution. We estimated adult fecundity (f_{ADULT}) by multiplying reproductive rate by adult survival following post-birth pulse models (Caswell, 2001). Age at first parturition was set at 5 (see results), resulting in a corresponding 5 age-class matrix. See Appendix for full details on the matrix population model. We estimated variation in black bear population growth rate using the series approximation, or delta method (Caswell, 2001: p. 300), which incorporates vital rate uncertainty into uncertainty in population growth rate. This approach assumes normally distributed vital rates, and coefficients of variation in vital rates that are $< 50\%$ (Alvarez-Buylla and Slatkin, 1993).

3.8. Sensitivity analysis

We derived sensitivity, the contribution of each vital rate to variation in λ (Caswell, 2001), for each vital rate using the matrix formulation to derive the analytical sensitivity (Caswell, 2001, p. 210) to give insight into future additive changes in vital rates. We explored effects of varying age at first parturition on λ independent of survival rates by setting age at first parturition to 3 and 7 (maximum age reported in Garshelis (1994) for western North American black bears).

4. Results

4.1. Capture and monitoring

We captured a total of 25 individual black bears (11 F:14 M) from August 1994 to September 1999 for research purposes on 33 different occasions (e.g. bears dropped collar and were re-collared at a later date). Six bears were radiocollared as subadults. We monitored an average of 7.4 radiocollared bears per month (range 4–14), and each bear was monitored for an average of 1.9 years (range 0.2–4.0 years), totaling 51.8 bear-years

of monitoring. We recorded 11 deaths of radiocollared bears during the study. There were broad differences in the fates of black bears in the two different management states. Approximately 24% of all non-management bears died, compared to 55% of all management bears that died or were relocated outside of BNP (Table 1). Similarly, 28% of all bears became management problems during the study (Table 1).

4.2. Estimating survival (ϕ) of black bears

The estimate of \hat{c} from the global survival model was 1.711, within the range for adequate global model fit (Anderson et al., 1994), yet suggestive of overdispersion. Therefore, despite small sample sizes, there was biological and statistical support for considering the effects of some factors on survival. We adjusted AIC_c for overdispersion using \hat{c} to derive $QAIC_c$. Using the criteria of 0–4 $\Delta QAIC_c$ for defining the top model set suggested up to 6 models should be considered (Table 2). The top

Table 1
Fates of radiocollared black bears in the Bow Valley of Banff National Park, 1994–2000

Fate	Non-management bear		Management bear	
	n	%	n	%
Alive	6	0.24	1	0.11
Dead	6	0.24	3	0.33
Relocated	0	0	2	0.22
Censored	6	0.24	1	0.11
Move to management bear state	7	0.28	–	–
Total	25	–	7	–

Fate includes bears that were alive, dead (for causes see text), censored (dropped collar, left study area), relocated outside of study area, and for non-management bears, those that transitioned to the problem management bear state.

Table 2
Model selection results for monthly black bear survival (ϕ) analysis in the Bow valley of Banff National Park, 1994–2000

Model Structure	K^a	Log Likelihood	d.f.	$\Delta QAIC_c$	$\Delta QAIC_c (w_i)$
1. (ϕ) = Season + Status + Age	9	–39.15	27	0	0.255
2. (ϕ) = Season + Status	7	–41.47	29	0.39	0.210
3. (ϕ) = Season + Status + Sex	7	–40.47	27	1.38	0.129
4. (ϕ) = Season + Status + Age + Sex	11	–38.63	26	1.51	0.120
5. (ϕ) = Status + Sex	5	–47.09	30	2.21	0.084
6. (ϕ) = Season	5	–45.75	29	2.84	0.061

Shown are the top candidate set of black bear survival models, with the model structure, number of parameters (k), Log-likelihood, $\Delta QAIC_c$ (corrected for overdispersion, $\hat{c} = 1.711$), and $QAIC_c$ weights (w_i). Parameter estimates for individual models are given in Table 3.

^a Includes parameter for estimating overdispersion, \hat{c} (Anderson and Burnham, 2002).

ranked model, (ϕ) = Season + Status + Age, was only ~1.2 times as likely to be the best candidate model as the second ranked model, (ϕ) = Season + Status. Despite substantial model selection uncertainty, several main survival effects were consistent across top models (Table 2), supporting their importance to bear survival in the BV of BNP. Management status was a main effect in 5 of the top 6 models ($\Sigma QAIC_c$ weights for models in the top set with season = 0.80), as were the effects of season ($\Sigma QAIC_c$ weights = 0.78), and both had consistent effects on survival (Table 3). Other variables were present in the top model set, but with lower Akaike weights (Table 2). Furthermore, parameter estimates for

Table 3
Unconditional parameter estimates from the top model set (from Table 2) for monthly survival rates from black bear survival (ϕ) models in the Bow Valley of Banff National Park, 1994–2000

Variable	Monthly survival rate (ϕ)	Monthly S.E. ^a	$\Delta QAIC_c$ weight ^b	Annual survival rate ^c	Annual S.E. ^a
Overall mean survival rate (intercept)	0.981	0.007	–	0.796	0.088
<i>Management status</i>			0.85		
Non-management (0)	0.976	0.032	–	0.848	0.127
Management (1)	0.942	0.022	–	0.660	0.113
<i>Seasonal survival rates</i>			0.83		
Denning	1.0	0	–	1.0	0
Spring Mngt	0.982	0.014	–	0.948	0.028
Spring Non-Mngt	0.993	0.035	–	0.980	0.070
Summer Mngt.	0.867	0.051	–	0.752	0.102
Summer Non-Mngt	0.945	0.080	–	0.892	0.160
Fall Mngt.	0.962	0.015	–	0.926	0.030
Fall Non-Mngt	0.985	0.021	–	0.971	0.042
<i>Age^d</i>			0.49		
Subadult (0)	0.978	0.031	–	0.765	0.149
Adult (1)	0.985	0.011	–	0.835	0.106
<i>Sex^d</i>			0.20		
Male (0)	0.967	0.022	–	0.769	0.247
Female (1)	0.985	0.069	–	0.836	0.153

Shown are real estimates, backtransformed through the logit link, with the Akaike weight ($\Delta QAIC_c w_i$) for the independent variables age, sex, and combined season + status on black bear survival, with S.E.s, and annual survival rates where appropriate.

^a Standard errors' are linear in the logit transformation.
^b $\Delta QAIC_c$ weight is calculated from the top model set only, with a total $\Delta QAIC_c$ weight = 0.85.

^c Annual survival rate = (monthly survival rate)¹², or for seasonal survival rates, equal the cumulative survival over that season (i.e. during summer = monthly survival rate ϕ^2 for July and August).

^d We did not test for an Age x Sex interaction effect due to small sample size (i.e. subadult Female, subadult male).

other factors indicated factors had small effect sizes on survival (e.g. Sex, Table 3).

Overall monthly survival (across all factors) for black bears originally collared as research bears was 0.981, for an annual rate of $(0.981)^{12} = 0.796$ (S.E. 0.088, Table 3). The parameter estimates for season and management status were consistent and biologically significant among the top model set (unconditional parameter estimates in Table 3). Adult black bear survival was 1.0 over the denning period, and then declined during the spring and summer, increasing in the fall (Table 3). For non-management problem bears monthly spring survival was $\phi = 0.993$, summer monthly survival rate was $\phi = 0.945$, and fall monthly survival rate was $\phi = 0.985$, resulting in a joint annual survival rate of $\phi = 0.845$ (S.E. = 0.127) [a product of the seasonal survival rates raised to the number of months per season, i.e., $(1)^5(0.993)^6 (0.945)^2 (0.985)^2$]. For management-problem bears, monthly spring survival was $\phi = 0.982$, summer monthly survival rate was $\phi = 0.867$, and fall monthly survival rate was $\phi = 0.962$, resulting in an annual survival rate of $\phi = 0.660$ (S.E. 0.113). Subadults ($\phi_{\text{SUBADULT}} = 0.765$) had lower survival than adults ($\phi_{\text{SUBADULT}} = 0.835$), and although estimates were not statistically different (Table 3), these were biologically meaningful differences.

The monthly management transition rate from non-management status to management problem status was 0.014 /month (S.E. 0.007). This monthly rate summed to an annual rate of 0.101 (not including denning season); in other words, there was an additive 10% chance/year of each individual bear becoming a problem bear.

4.3. Cause-specific mortality

From the radiocollared sample, 82% ($n = 9$) of the mortalities were human caused, and 18% ($n = 2$) were predation by grizzly bears (one adult female and one younger adult male). Of the human-caused mortality, 44% ($n = 4$) were highway caused, 33% ($n = 3$) were caused by management mortality, and 22% ($n = 2$) were caused by management removal. Annual cause-specific mortality rates were 0.167 due to human causes, composed of 0.08 from highways, 0.06 from management mortality, and 0.04 from management removals. Annual natural mortality rate due to grizzly predation was 0.037.

4.4. Reproduction and cub survival

We estimated reproductive rates from five different adult females. A total of 28 cubs were born in 15 litters during the study, yielding mean litter size of 1.87 (S.E. = 0.009, $n = 15$). Some of these female bears were not monitored for ≥ 1 inter-birth interval, therefore we used 22 cubs for cub survival estimation. Cub survival

was 0.64 (S.E. 0.107, $n = 22$), and yearling survival was 0.67 (S.E. = 0.142, $n = 12$). Average inter-birth interval was 2 ($n = 5$, no variation). Assuming a 50:50 sex ratio at birth, the reproductive rate (m_x) was 0.467. Adult fecundity (f_{ADULT}), the product of reproductive rate and adult survival, was 0.390 (S.E. = 0.09). Age at first breeding for female black bears was 4 for 2 known-age subadult females, resulting in a minimum age at first parturition of 5 in BNP, comparable to other western black bear populations (Table 4). Demographic data are summarized in Table 4.

4.5. Population demography

We constructed a five age-class, post-breeding birth-pulse Leslie matrix model for black bears in BNP (see Appendix for details). We calculated a finite population growth rate of $\lambda = 0.953$, with S.E. = 0.079 using the series approximation. The maximum CV for our vital rates was 21.1% (Table 3), satisfying this assumption of the series approximation (Alvarez-Bullya and Slatkin, 1993). Our assumption of normally distributed vital rates for the series approximation appeared robust because results from stochastic simulations from a uniform distribution did not differ (unpublished data). The 95% confidence interval for lambda (0.79–1.10) overlapped 1.0, and

Table 4
Annual black bear survival and reproductive parameters used in demographic analyses in the Bow valley of BNP, 1994–2000

Parameter	<i>n</i>	Estimate	S.E. ^b	Lower ^b 95% C.I.	Upper ^b 95% C.I.	Western North America ^c
Adult Survival ^d	19	0.835	0.106	0.627	0.982	0.826 ^e
Cub survival ^f	22	0.640	0.107	0.438	0.849	0.623
Yly survival ^f	12	0.670	0.142	0.392	0.948	
Subadult Survival ^d	6	0.765	0.149	0.472	0.992	
Litter size	15	1.87	0.09	1.667	2.060	2.05
Inter-birth Interval	5	2.00	–	–	–	2.43
Reproductive rate, m_x	5	0.465	0.09	0.289	0.642	0.43
Fecundity ^a F_{AD}	5	0.390	0.09	0.213	0.566	–
Age first parturition	2	5	–	–	–	5.3

Survival and reproductive parameters from black bear populations in western North America for comparison.

^a Fecundity was calculated as breeding adult survival multiplied by the reproductive rate (m_x), the mean number of female cubs born per adult female per inter-birth interval. See text and Appendix for details.

^b Survival rate S.E.s are linear in the logit transformation. 95% Confidence intervals are transformed from the logit values.

^c From reviews in Garshelis (1994), and in Alberta Fish and Wildlife (1993) for Alberta populations.

^d Estimated from survival models. Adult female and male survival, and subadult survival were set equal due to small sample size and low support for Program MARK survival models with different age + sex survival rates.

^e Adult male survival rate (from Garshelis, 1994).

^f Estimated from observational data. See text.

while this corresponded with a 70% chance of decline, was statistically indistinguishable from a stable population.

4.6. Sensitivity analysis

Population growth rate was most sensitive to changes in adult female survival (analytical sensitivity=0.75), followed by subadult survival (0.206), fecundity (0.21), and then by either cub survival (0.13) or yearly survival (0.12). We did not decompose fecundity into its component vital rates, but λ increased with decreasing age at first parturition using matrix simulations (unpublished data).

5. Discussion

Our analysis suggests National Park protection is not adequately protecting black bears in Banff National Park. Management caused mortality, highway mortality, and management removal were the dominant causes of black bear mortality in the BV of BNP. Natural mortality was rare despite park protection. Survival was lower across all seasons for black bears that had become management problems, and was lowest during summer. Because the reasons for becoming management problems in BNP were related to habituation to humans and human food, we suggest lower summer survival results from high human use. The results of our demographic analyses based on these vital rates suggest this bear population may be declining, although population growth rate was not statistically different from 1. However, even modest declines in difficult to study carnivore populations (such as 5% in our study) may take decades to detect with reasonable statistical confidence (Gerrodette, 1987). Furthermore, we followed the typical scientific approach of minimizing the probability of falsely claiming there was a population decline (Type I error, α) instead of minimizing the probability of failing to detect a real decline (Type II error, β) a more costly conservation error. Considering the cumulative effects of human activities on black bears in BNP (e.g. Serrouya, 1999, Clevenger et al., 2001), waiting to detect statistically significant declines may not be desirable from a Parks Management perspective. Therefore, Park managers may want to adopt a conservative approach given this population's protected status (Mattson et al. 1996) and Parks Canada policy (Government of Canada, 2000).

Despite λ suggestive of a declining population, this population may be stable or increasing, if supported by high immigration. This hypothesis is partially supported by the consistently high numbers of black bears killed in the BV year-after-year (minimum of $n=34$ bears over our 7-year study, unpublished data). Future research in BNP should test whether this population is a true sink

population by determining if immigration offsets population declines, possibly using genetic methods. Despite our uncertainty in λ and the possibility that immigration may offset mortality, maintaining a sink population in BNP is in direct contravention of National Parks legislation (Government of Canada, 2000).

Vital rates of carnivores are difficult to estimate (Gese, 2001), possibly precluding management action by default because of uncertainty (Mattson et al., 1996). However, black bear survival and reproductive rates in BNP were comparable to those across western North America [see Table 4 including reviews by Garshelis (1994) and Alberta Fish and Wildlife (1993)]. For example, adult survival rate (0.835) during our study was comparable to adult male survival across western North American populations (Table 4). Mean litter size across western North America was 2.05 (Table 4) and in non-mountain environments in Alberta, litter size averaged 2.34 (Alberta Fish and Wildlife, 1993). Age at first parturition in BNP was similar to other populations (Table 4). Furthermore, changing age at first parturition to an optimistic 4 in our stage-matrix still resulted in a $\lambda < 1$ (unpublished data). Inter-birth interval was shorter than other western North American populations (Table 4). Thus, reproductive rates in BNP were similar to those reported for black bear populations in western North America, lending support to our population modeling. Furthermore, estimates of survival based on small sample sizes may be accurate and therefore useful for population modeling (Mayer et al., 2002).

Further support for our population modeling comes from comparison to other protected populations in North America. Black bear survival in BNP was marginally higher than a hunted bear population in a protected area in North Carolina where Powell et al. (1996) and Sorenson and Powell (1998) estimated an overall survival rate for all age- and sex-classes of 0.76. Powell et al. (1996) did not report cub survival estimates, but based on Monte-Carlo simulations, found that population growth rate would exceed one if cub survival was greater than 0.7. However, as this was the upper limit for cub survival in their study, they concluded the Pisgah bear sanctuary did not provide enough protection to maintain a viable breeding population within its boundaries. Alternately, Beringer et al. (1998) found the Harmon Den bear sanctuary in North Carolina provided some refuge from human caused mortality for black bears. They found adult male survival rates were 0.89 ± 0.105 (S.E.), adult female 0.82 ± 0.096 , subadult female 0.53 ± 0.218 , and subadult male 0.27 ± 0.129 (Beringer et al., 1998). BNP black bears had survival rates intermediate to these two black bear populations, yet reproductive rates that were likely lower than those in the productive American southeast, therefore our results of potential population declines are consistent with these two cases.

Sensitivity analysis further supported the use of our parameter estimates in demographic analysis, as survival rates with the most uncertainty (i.e. cub, subadult) contributed the least to variation in λ . Sensitivity analysis revealed the most effective method of increasing λ is to improve adult female survival, similar to studies of grizzly bears across western North America (Hovey and McLellan, 1996; Wiegus et al., 2001). Further, sensitivity analysis allowed exploration of management scenarios for improving management. For example, from our matrix model, reducing adult female human-caused mortality by > 50% (equivalent to increasing survival to ~ 0.90) will be necessary to increase population growth rates to > 1 in BNP black bears. Other vital rates may not be as easy or cost-effective to increase, with most of the variation in age at first reproduction, litter size, inter-birth interval, and cub survival coming from natural processes that are difficult to manipulate. The management implication of the sensitivity analysis is clear: park managers should adopt aggressive measures to reduce human-caused mortality to adult females to restore natural processes in this protected black bear population. Such measures may include campground fencing, improvements to bear-proof food storage facilities, heavy fines for improper food storage, reducing the potential for habituation to humans through temporal (seasonal or daily) area closures, regulated public transit along slow-moving scenic highways, and increased tourist education. Such management approaches are currently practiced in National Parks in the USA such as Yosemite, Yellowstone, and Denali. Furthermore, such management actions would benefit other imperiled carnivores in BNP (Herrero et al., 2000; Callaghan, 2002; Gibeau et al., 2002).

In conclusion, despite small sample size common in studies of difficult to study carnivores, using an information-theoretic approach (Burnham and Anderson, 1998) resulted in biologically meaningful inferences that black bear survival in BNP was negatively affected by management status and was related to season. Combining these estimates of survival and reproductive rates in a matrix model suggests this black bear population may be declining despite National Parks protection. Despite our statistical uncertainty for λ , management interpretation is aided by Parks Canada policy and legislation (Government of Canada, 2000), which states native species should be maintained at viable population sizes. Waiting for enough statistical evidence to be marshaled to reduce uncertainty in λ may lead to potential population declines (Gerrodette, 1987). However, managers should note our research was a post-hoc exploratory analysis (i.e. not designed to estimate survival), and our management recommendations for improving adult female survival should be viewed as management experiments. Actions aimed to improve survival should be combined with continued research to refine survival

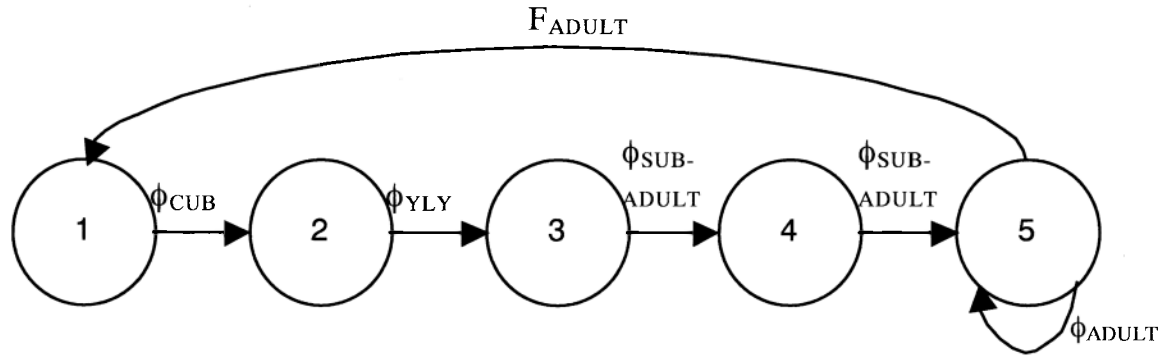
and reproductive rates, while testing results of management actions.

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Appendix. Matrix population model for black bear demographic analysis in the Bow Valley of Banff National Park

Vital rates from Table 3 were used to construct a post-birth pulse Leslie age-class matrix (Caswell, 2001, pp 57) for black bears in the Bow valley of BNP. Age at first parturition was estimated at a minimum of 5 from $n=2$ known age subadults, which was similar to literature values (Garshelis, 1994). This resulted in a 5 age-class matrix, cubs, yearlings, subadults age 2 and 3, and a composite adult age-class including all individuals ≥ 4 -years old. Survival rates for subadults aged 2 and 3 were set at equal, and adults did not breed until their fourth year, giving birth during their fifth year. We did not adjust for senescence by truncating the age distribution following Wiegus et al. (2001) because we felt the composite age-class for adults without senescence was appropriate in our study. For example, survival alone suggested bears survive to ~ 22 years of age less than 1% of the time (i.e. $(\phi_{YOY})(\phi_{YLY})(\phi_{Subadult}^2)(\phi_{Adult}^{18}) = 0.009$). This was very close to the average age of senescence in black bears of approximately 20 reported by Koleonosky and Strathearn (1987). In addition, we



observed one radiocollared black bear female (No. FA2) with 2 YOY at a known age of 21 years old in 1999 (unpublished data). Therefore, we did not adjust for senescence in our age-class Leslie matrix model similar to Eberhardt et al. (1994) or Wielgus et al. (2001). With these considerations, our matrix formulation corresponds with the life-cycle diagram:

Where ϕ_{CUB} , ϕ_{YLY} , $\phi_{SUBADULT}$, and ϕ_{ADULT} correspond with the survival rates for cubs, yearlings, sub-adults, and breeding adults respectively, and F_{ADULT} corresponds with breeding adult fecundity. All other fecundities are set at 0. Fecundity, F_{ADULT} , was calculated as the product of adult survival and reproductive rate. Reproductive rate was calculated similar to Hovey and McLellan (1995) as the number of cubs born per litter multiplied by the number of females born (assuming 50:50 sex ratio) divided by the inter-birth interval, or $F_{ADULT} = m_x \times \phi_{ADULT} = [(1.87 \times 0.5) / 2] \times 0.835 = 0.390$. The resultant population matrix is:

$$\begin{bmatrix} 0.20 \\ 0.13 \\ 0.09 \\ 0.08 \\ 0.49 \end{bmatrix} = \begin{bmatrix} 0 & 0 & 0 & 0 & 0.390 \\ 0.640 & 0 & 0 & 0 & 0 \\ 0 & 0.670 & 0 & 0 & 0 \\ 0 & 0 & 0.765 & 0 & 0 \\ 0 & 0 & 0 & 0.765 & 0.835 \end{bmatrix} = \lambda = 0.953$$

where the top row indicates reproductive rates associated with each age-class, and the sub-diagonal indicates age-class specific survival rates. The survival rate in the last column and row (Matrix element $a_{5,5}$) corresponds to the composite of breeding adults. Solving this matrix for the right eigenvalue results in the above stable age distribution, and for the dominant eigenvalue, population growth rate, or lambda. Solving this matrix for the partial derivatives of each matrix element, $a_{i,j}$, or the sensitivity, results in the following sensitivity matrix (emitting all biologically irrelevant sensitivities):

$$\begin{bmatrix} 0 & 0 & 0 & 0 & 0.203 \\ 0.124 & 0 & 0 & 0 & 0 \\ 0 & 0.118 & 0 & 0 & 0 \\ 0 & 0 & 0.103 & 0 & 0 \\ 0 & 0 & 0 & 0.103 & 0.668 \end{bmatrix}$$

Note that as sensitivities are additive (Caswell, 2001: p. 224) subadult sensitivity is the sum of both subadult age-class sensitivities, or 0.206. Using the delta method (Caswell, 2001) for estimating variance in the population growth rate uses these sensitivities to weight the variance in each matrix element, with a corresponding S.E. of 0.079, and 95% confidence interval of 0.79–1.10.

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