

Estimating effects of adult male mortality on grizzly bear population growth and persistence using matrix models

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Received 28 October 1999; received in revised form 17 July 2000; accepted 22 August 2000

Abstract

We radio monitored a hunted, sexually segregated grizzly bear (*Ursus arctos*) population and an unhunted, unsegregated population for demographics and constructed a stage- and age-classified matrix model to test for the effects of adult male mortality and resulting sexual segregation on population growth and persistence. Population parameters in the model were adult female survival, subadult female survival, offspring survival, probability of litter sizes, and probability of unsuccessful pregnancy. The last three parameters were affected by adult male mortality and segregation, the others were not. We compared population growth with and without effects of hunting by holding adult female and subadult female survival constant and by using hunted and unhunted values for offspring survival, litter size, and pregnancy. Population growth (λ) showed the greatest elasticity for adult survival, subadult survival, offspring survival, litter size, and unsuccessful pregnancy, in that order. This corresponds with observed anti-infanticide tactics (sexual segregation) by adult females to maximize their fitness. The hunted population decreased at a rate of 0.99 whereas the simulated, unhunted population increased at a rate of 1.05. The hunted population was much more susceptible to population extinction. Under demographic stochasticity mean time to extinction was 32 years in the hunted population and 110 years in the unhunted population. Under environmental stochasticity mean time to extinction was 21 years in the hunted population and 43 years in the unhunted population. We suggest that sexual segregation caused by hunting resident adult males can result in population decline and can even contribute to rapid population extinctions when numbers are small. © 2001 Elsevier Science Ltd. All rights reserved.

Keywords: Mortality; Population growth; Adult; Offspring; Grizzly bears

1. Introduction

Many species of animals are declining towards extinction because of a combination of human-induced habitat loss and mortality (Wilson, 1988). This situation is exacerbated for large mammalian carnivores (Belovsky, 1987) because, being at the top of the food web, they often exhibit relatively low densities, reproductive rates, and population growth rates. As such, their populations are unusually sensitive to increases in mortality and decreases in reproduction (Gittleman, 1986, 1989). For example, grizzly bears are considered threatened or endangered and are declining in many

parts of their range (Servheen, 1990). Despite these declines, adult male grizzlies are hunted in many jurisdictions, even in small, low density populations at the edge of the species' range (Wielgus and Bunnell, 1994a; Wielgus et al., 1994), because trophy hunting is believed beneficial or benign for population growth (Dood et al., 1986; Nagy and Gunson, 1990; Smith, 1990; British Columbia Ministry of Environment, 1995). Many wildlife managers assume trophy hunting results in reduced numbers of competitive or cannibalistic adult males with consequent increases in cub production, survival, and population growth (see review by Miller, 1990). This "increased reproduction" hypothesis serves as the justification for trophy hunting and/or adult male-biased removal in grizzly bears and likely justifies trophy hunting of other carnivores as well (e.g. cougars, *Felis concolor*; Dixon, 1983; Ross and Jalkotzey, 1992;

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Dolbeer et al., 1994; Strickland et al., 1994; Spreadbury et al., 1996).

Garshelis (1994), McLellan (1994) and Derocher and Taylor (1994) reviewed the literature for black (*U. americanus*), brown, and polar bears (*U. maritimus*) respectively, and found little or no evidence for such compensatory density dependent effects, although most studies they reviewed were not designed to test the effects of hunting adult males. These reviews were interpreted as support for the “increased reproduction” hypothesis (British Columbia Ministry of Environment, 1995). More recently, Wielgus and Bunnell (1994a, 2000), and Swenson et al. (1997, 2000) tested the hypothesis by comparing reproduction and cub survival in hunted and unhunted populations and controlling for confounding factors. Their results showed a decrease in cub litter size and cub survival, respectively, in the hunted populations. Mortality of older resident males coincided with increased immigration and settling by younger, potentially infanticidal nonsire males in both study areas. Swenson et al. (1997, 2000) found that cub survival decreased, ostensibly because of sexually selected infanticide by immigrant males. Wielgus and Bunnell (1994a,b, 1995) found that adult females responded to increased numbers of potentially infanticidal immigrants by segregating into food-poor, male-unoccupied areas and that this appeared to result in smaller litter sizes (Wielgus and Bunnell, 2000).

Wielgus and Bunnell (1994a, 2000) suggested that the small litter sizes associated with sexual segregation may have contributed to an estimated population decline in their study area, but they did not assess the effects of segregation on population growth. In this paper we present a matrix model of grizzly bear population demography to examine the potential significance of adult male mortality and related sexual segregation on population growth and persistence. We compare population growth of a hunted, segregated population to that of an unhunted, unsegregated population using empirical data obtained from both. The putative causal chain is as follows: higher mortality of older resident males — higher immigration by potentially infanticidal new males — increased infanticide and/or avoidance of new males and sexual segregation by resident adult females into food-poor environments — smaller litter sizes and reduced reproductive success. The model can be adapted for other potentially infanticidal carnivores with similar proposed causal chains (brown bears, Swenson et al., 2000; black bears, LeCount, 1987; cougars, Ross and Jalkotzey, 1992).

2. Study Areas

The Kananaskis (hunted population) study area covers 6300 km² in the Kananaskis Provincial Park (3400

km²) and Bow-Crow Forest (2900 km²) of southwestern Alberta (50–51° lat, 115–116° long). Elevation ranges from 1300–2700 m in mountainous terrain. Climate is continental. Vegetation is in the subalpine fir-Engelmann spruce (*Abies lasiocarpa*/*Picea engelmanni*) forest region (Rowe, 1972). Hunting of grizzly bears was closed from 1970–1981, but was reopened in the Bow Crow forest from 1982–1988 because the population was believed increasing (Carr, 1989; Nagy and Gunson, 1990). Grizzly hunting seasons took place from 1 April–15 June, 1982–1988. For details on this study area see Wielgus and Bunnell (1994a). This population was classified as vulnerable (Banci, 1991).

The unhunted Selkirk Mountains Grizzly Bear Ecosystem (SMGBE) covers 5700 km² in northern Idaho, northeastern Washington (3000 km²), and southern British Columbia (2700 km²) (48–49° lat, 116–117° long). Physiography is mountainous with elevations from 550–2500 m. Climate is Pacific maritime/Continental. Vegetation is in the Engelmann spruce/subalpine fir and cedar/western hemlock (*Thuja plicata*/*Tsuga heterophylla*) biogeoclimatic zones (Pojar et al., 1987). Hunting of grizzly bears was not allowed in the US SMGBE under the Endangered Species Act and hunting in the B.C. SMGBE did not occur during research (1985–1990). For details on this study area see Wielgus et al. (1994). This population was classified as threatened in the U.S. (Servheen, 1990) and vulnerable in Canada (Banci, 1991), and is now classified as threatened in both countries.

3. Methods

3.1. Trapping and monitoring

We trapped bears in two areas of Kananaskis (Highwood and Sheep trapping zones) and two areas of the SMGBE (Idaho and British Columbia trapping zones) (Wielgus, 1993). We used Aldrich leg snares to trap bears and immobilized them with Ketamine hydrochloride and Xylazine hydrochloride in both study areas. All bears were immobilized, weighed, ear-tagged, had a premolar tooth extracted for aging (Stoneburg and Jonkel, 1966) and were fitted with mortality-sensing radio-collars. We handled bears according to protocol of the Canadian Council on Animal Care, University of British Columbia Animal Care Certificate 890105. We monitored bears using fixed-wing radiotelemetry (Whitehouse and Steven, 1975) once every week or two during the non-denning period (Early April–early November) from 1981–1984 in Kananaskis and from 1985–1990 in the SMGBE. Details on trapping, monitoring of bears, and habitat use are given in Wielgus (1993), Wielgus and Bunnell (1994a,b, 1995) and Wielgus et al. (1994).

3.2. Estimates of survival and reproduction

We estimated annual mortality rates for radiocollared females using the Micromort Program (Heisey and Fuller, 1985), which calculates the number of deaths recorded during the number of radio-days monitored. Details on mortality estimates are given in Wielgus and Bunnell (1994a) and Wielgus et al. (1994). We determined mean number of cubs per litter, birth interval, and age at first parturition from aerial and ground observations of females and their cubs. Reproductive rates and cub litter sizes include cubs <1 year of age observed during June and July and do not incorporate any offspring that could have died in the den or shortly after leaving the den (e.g. February–May). We estimated reproductive rate for each population as average litter size of new cubs divided by average birth interval (Craighead et al., 1974). Details on effects of hunting on female reproduction are given in Wielgus and Bunnell (2000).

3.3. Modeling population growth

We constructed a post-breeding (Jenkins, 1988; Akcacaya et al., 1999) stage- and age-classified matrix model (Caswell, 1989; Ebert, 1999) to estimate annual population growth (λ) and elasticity of λ to parameters such as survival rates and litter sizes. We used the Unified Life Models (ULM) program (Legendre and Clobert, 1995) to run our model and to estimate population dynamics and elasticities (Ferriere et al., 1996). Our deterministic model to estimate λ and elasticities assumed density independent population growth because we do not know how density dependence affects grizzly bear population growth and what form any putative density dependent function should take (McLellan, 1994; Mills et al., 1996). Furthermore, both hunted and unhunted populations were very small and far below carrying capacity (Wielgus and Bunnell, 1994a; Wielgus et al., 1994) so both would be expected to exhibit exponential growth.

Our model takes the form: $n(t) = L * n(t-1)$, where n = number of individuals, t = time in years, and L = the population growth multiplier (λ). Within the full stage-class life cycle graph (Fig. 1) there are nine stage-classes: 2 and 3 year-old female subadults (F2, F3), 4 and older estrus females (Fe), 5 and older females with 1–3 cubs (Fc1, Fc2, Fc3), and six and older females with 1–3 yearlings (Fy1, Fy2, Fy3). Transition probabilities from F2 to Fe are simply based on survival rates of subadult females (Ssf). Transition probabilities from Fe back to Fe, Fe to Fc_i, Fc_i to Fy_i, Fc_i to Fe, and Fy_i to Fe are based on the product of survival rates of adult females (Saf), probability of unsuccessful pregnancy (Pu), probability of cub litter size (Pl), and survival rates of cubs (Sc; Table 1). Survival of littermates, or prob-

ability of mothers moving from one stage-class to another was calculated using factorial probabilities (Feller, 1968). For example, there are three probabilities for two cubs surviving out of a three cub (A,B,C) litter based on survival rates, ($Sc_A \times Sc_B \times 1 - Sc_C$, $Sc_A \times Sc_C \times 1 - Sc_B$, $Sc_B \times Sc_C \times 1 - Sc_A$). We summed these probabilities to arrive at the overall probability of a female moving from Fc₃ to Fy₂ (e.g. see Table 1).

In the full stage-class life cycle graph there are no age-classes (Fig. 1) so maximum life span depends entirely on female survival. In this case (Saf=0.93) females lived for over 50 years, an unrealistic approximation (Eberhardt, 1990; Eberhardt et al., 1994; Wielgus et al., 1994) that overestimated λ (1.04) compared to the standard Lotka equation with maximum age at 20 years for this population (0.99; Wielgus and Bunnell, 1994a).

We considered solving this problem by building a full stage- and age-classified model. That would result in seven adult stage-classes (Fe, Fc_i, Fy_i; Fig. 1) multiplied by 16 adult age-classes (5–20 years), for a total of 112 adult stage- and age-classes or a matrix of 112 rows and 112 columns (12,544 cells). Because of the large cell size, we collapsed the seven stage-classes into three stage-classes (Fe, Fc, Fy; Fig. 2). We collapsed females with one, two, or three cubs (three stages) and females with one, two, or three yearlings (three stages) into Fc (one stage) and Fy (one stage) respectively. We maintained the integrity and reality of the full model in our collapsed version by formulating probability equations for each full stage (Fc_i–Fy_i, Table 1) and applying algebraically reduced summations of these equations to each collapsed stage (Fc, Fy, Table 2). For example, the total

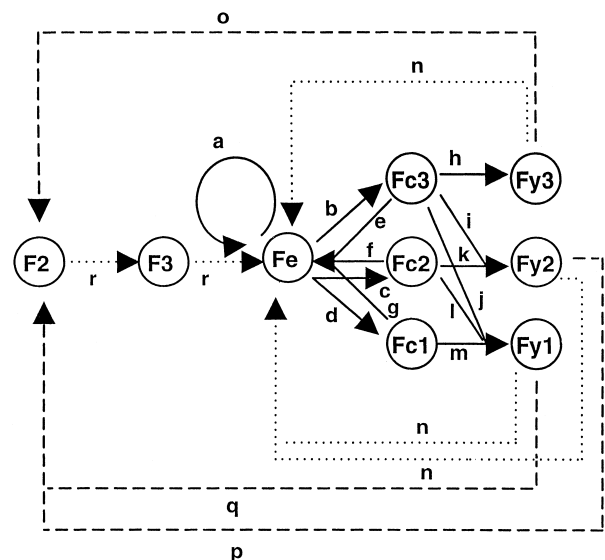


Fig. 1. Life cycle graph of grizzly bear population growth corresponding to the full stage-class matrix model (see text). Definition of stage classes (F2 to Fy₁) and transition probabilities (a to r) are given in Table 1.

number of F_2 at $t+1$ is the summation of $n F_{y_i} \times P F_{y_i} \times S_{sf}$. Similarly, the total number of F_e is the summation of $n F_{c_i} \times P F_{c_i}$ losing one cub, $P F_{c_2}$ losing two cubs, etc. This mathematical manipulation allowed us to calculate population growth based on the realistic full model while using the collapsed matrix. We then com-

bined the collapsed stage-class model with the full age-class model to produce our final stage- and age-class model given in Table 2 and Fig. 2. This resulted in a matrix of 51 rows and 51 columns (three subadult age classes + 16 adult age classes \times three reproductive stages) or 2601 cells.

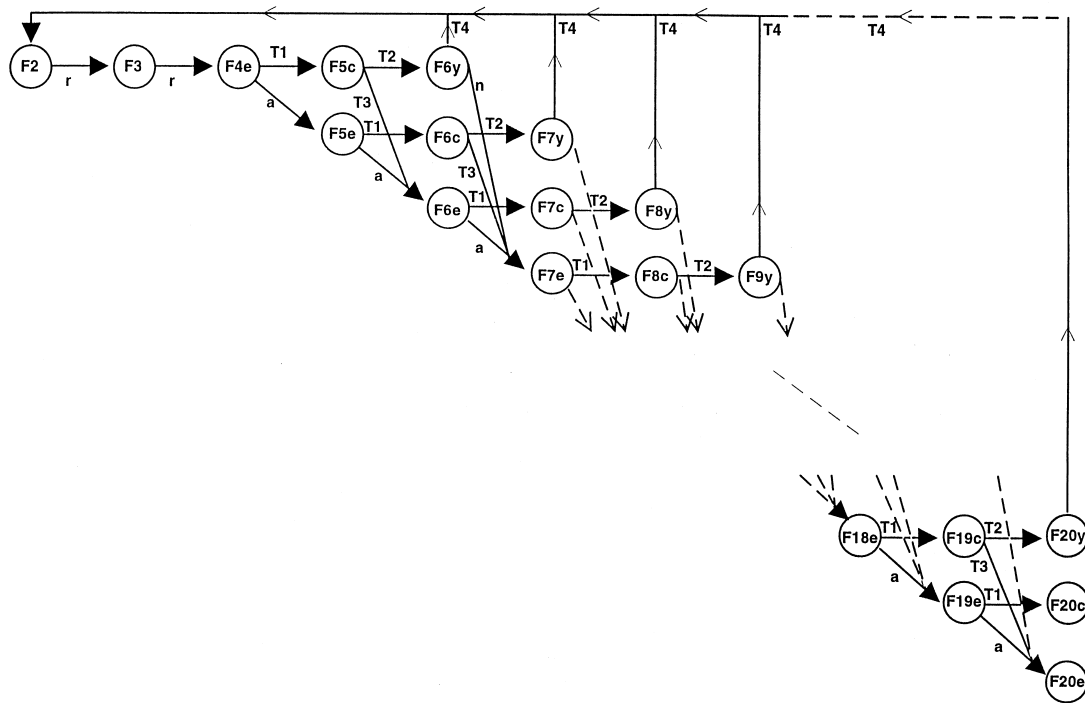


Fig. 2. Life cycle graph of grizzly bear population growth corresponding to the reduced stage and full age-class matrix model (see text). Definition of stage and age-classes (F_2 to F_{ij}) and transition probabilities (T_1 to T_4) are given in Table 2.

Table 1

Transition probability equations corresponding to the life cycle graph given for the full stage-class model given in Fig. 1^a

P for transition of estrus females (F_e) to F_e and females with cubs (F_c)	P for transition of F_c to F_e and females with yearlings (F_y)	P for transition of F_{y_i} to F_e and F_2 , and F_2 to F_e
F_e to F_e $a = S_{af} \times P_u + S_{af} \times (1 - P_u) \times ((P_{trip} \times M_c^3) + (P_{twin} \times M_c^2) + (P_{sing} \times M_c))$	F_{c_i} to F_e $e = S_{af} \times M_c^3$ $f = S_{af} \times M_c^2$ $g = S_{af} \times M_c$	F_{y_i} to F_e $n = S_{af}$
F_e to F_{c_i} $b = S_{af} \times (1 - P_u) \times (P_{trip} \times S_c^3)$ $c = S_{af} \times (1 - P_u) \times (P_{trip} \times 3(M_c \times S_c^2) + (P_{twin} \times S_c^2))$	F_{c_i} to F_{y_i} $h = S_{af} \times S_c^3$ $i = S_{af} \times 3(M_c \times S_c^2)$ $j = S_{af} \times 3(M_c^2 \times S_c)$ $k = S_{af} \times S_c^2$ $l = S_{af} \times 2(M_c \times S_c)$ $m = S_{af} \times S_c$	F_{y_i} to F_2 $o = S_{sf} \times S_r \times 3$ $p = S_{sf} \times S_r \times 2$ $q = S_{sf} \times S_r \times 1$
$d = S_{af} \times (1 - P_u) \times (P_{trip} \times 3(M_c^2 \times S_c) + (P_{twin} \times 2(M_c \times S_c) + (P_{sing} \times S_c)))$		F_2 to F_e $r = S_{sf}$

^a S_{af} , survival adult females; S_{sf} , survival subadult females; P_u , P unsuccessful pregnancy; P_{trip} , P triplets; P_{twin} , P twins; P_{sing} , P singletons; S_c , survival cubs; M_c , $1 - S_c$; S_r , sex ratio.

3.4. Effects of adult male mortality on population growth

We tested for the effects of adult male mortality by comparing Lambda of an actual hunted population to that of a simulated unhunted population. We modeled the two populations based on empirical data taken from two studies; a hunted population affected by segregation (Kananaskis, Wielgus and Bunnell, 1994a) and an unhunted, unaffected population (Selkirks, Wielgus et al., 1994). Pu, Pl, and Sc appeared affected by hunting and segregation because post-estrous adult females avoided males and food-rich habitats, and this appeared to result in greater unsuccessful pregnancies, smaller litters, and marginally lower survival of cubs (Wielgus and Bunnell, 1995, 2000). In the hunted population we calculated lambda using the observed empirical parameter values for Pu, Pl, Sc, Ssf, and Saf taken from Kananaskis. In the unhunted population we replaced those parameter values affected by segregation (Pu, Pl, Sc) with values from the Selkirks. Any difference in lambda should be due solely to effects of hunting because we set Ssf and Saf at the same observed rate from Kananaskis for both the real and simulated populations, and because differences in Pu, Pl, and Sc between the hunted and unhunted populations did not appear to be due to other effects (Wielgus and Bunnell, 1995, 2000). In fact, the Kananaskis population had a superior overall diet quality and should have exhibited greater reproduction than the Selkirks had it not been for effects of adult male mortality and segregation (Wielgus and Bunnell, 2000). In this sense, our test for the effects of hunting may be conservative since parameter values for the simulated unhunted population incorporates inferior diet quality relative to the hunted population.

Table 2
Transition (T) equations corresponding to the life cycle graph of the reduced stage- and full age- class model given in Fig. 2^a

Fe to Fc

$$T1 = T Fe_i \text{ to } Fc_{(i+1)} \\ = b + c + d$$

Fc to Fy

$$T2 = T Fc_i \text{ to } Fy_{(i+1)} = (T Fe_{(i-1)} \text{ to } Fy_{(i+1)}) / (T Fe_{(i-1)} \text{ to } Fc_i) \\ = (bh + bi + bj + ck + cl + dm) / (b + c + d)$$

Fc to Fe

$$T3 = T Fc_i \text{ to } Fe_{(i+1)} = (T Fe_{(i-1)} \text{ to } Fe_{(i+1)}) / (T Fe_{(i-1)} \text{ to } Fc_i) \\ = (be + cf + dg) / (b + c + d)$$

Fy to F2

$$T4 = T Fy_i \text{ to } F2 = (T Fe_{(i-2)} \text{ to } F2) / (T Fe_{(i-2)} \text{ to } Fy_i) \\ = (bho + bip + bjg + ckp + clq + dm) / (bh + bi + bj + ck + cl + dm)$$

^a Fe_i=females estrous at age *i*; Fc_i=females with cubs at age *i*; Fy_i=females with yearlings at age *i*; F2=2 year-old females, *b* to *r*= transition *P* equations from Table 1, Fig. 1.

Probability of unsuccessful pregnancy was 0.12 for the unhunted population and 0.20 for the hunted population because one of eight and one of five prime age (<20 years) breeding estrous females showed unsuccessful pregnancy in the Selkirks and Kananaskis, respectively (Wielgus, unpublished data). This is the same proportional difference (60%) as observed for litter sizes (1.4 vs. 2.2, Wielgus and Bunnell, 2000). Probability of one, two, or three cub litters was 0.60, 0.39, and 0.01 for Kananaskis and 0.01, 0.79, and 0.20 for the Selkirks. Cub survival was 0.78 in Kananaskis and 0.84 in the Selkirks. Age at first birth was set at 5 years for both populations because segregation appeared to have no effect on that parameter (Wielgus and Bunnell, 1995, 2000) and because grizzly bears can and do give birth at that age for many populations (McLellan, 1989a; Eberhardt, 1990; Eberhardt et al., 1994; Wielgus and Bunnell, 1994a; Wielgus et al., 1994).

3.5. Effects of adult male mortality on population persistence

Effects of hunting on short-term population extinction were estimated by observing the total number of females present after model runs of 20 and 40 years, one and two life spans, respectively, and by calculating mean time to extinction under stochastic effects. Number and age of animals entered into the model at time *t* were obtained from empirical estimates for the Kananaskis population (Wielgus and Bunnell, 1994a). There were 38 bears consisting of 12 females, six cubs, and 20 males. The 12 females entered into the model were more or less evenly distributed across ages 2–17 years. This stochastic model assumes population closure for females (no immigration by females) — a not unreasonable assumption given that we observed no female emigration/immigration in either study area (Wielgus and Bunnell, 1994a; Wielgus et al., 1994) and the generalized paucity of female movements from one area to another (IGBC, 1987; Blanchard and Knight, 1991).

We considered two stochastic factors, demographic and environmental stochasticity, because they are likely to exert a major influence on the risk of extinction in small populations (Shaffer, 1981; Belovsky, 1987; Goodman, 1987; Lande, 1993). We measured extinction risk by the average time \bar{t}_{ext} to extinction (Lande, 1993), and examined how sensitive to λ this risk is under either demographic or environmental stochastic effects. For demographic stochasticity we used the analytical model of Leigh [1981, Eq. (8)] with extinction occurring at a population size of $n = 1$ [also see Lande, 1993, Eq. (3)] to compute the average time to extinction. The equations are given in Appendix A. Our stochastic model to estimate population persistence incorporates a population ceiling (exponential growth to upper limit, Akcacaya et al., 1999), but not a density-dependent function because

we do not know what form a density dependent function should take for grizzly bears and because a ceiling model appears consistent with a very high density population observed by Hovey and McLellan (1996), whereby density dependence appears manifested through emigration, not reduced reproduction or survival. This model relies on the diffusion approximation of the density-independent growth up to carrying capacity K of a structured population. In this context, \bar{t}_{ext} depends in part on carrying capacity K , which we bounded at $K=30$ and 80 , respectively, equivalent to unimpeded exponential growth for model runs of 20 and 40 years (see Results). The lower bound is equal to double the estimated population size (from 15 to 30) and density (from 0.63 females/100 km² to 1.26 females/100 km²) of females in Kananaskis and is similar to density estimated for the protected portion of the Selkirks population in Canada (1.46 females/100 km², Wielgus et al., 1994). The upper bound is equal to $5 \times$ the estimated population size (from 15 to 75) and density (from 0.63 to 3.15 females/100 km²) and is similar to the density estimated for one of the densest populations recorded (3.53 females/100 km², McLellan, 1989b; Hovey and McLellan, 1996).

For environmental stochasticity, we applied Ewens et al.'s [1987, Eq. (14)] and Lande's [1993, Eqs. (A15a) and (A16b)] analytical results. The equations are given in Appendix A. We set environmental stochastic effects as mortality events affecting 10% of the population, or approximately one mortality event at $n=12$ (see Results). We bounded frequency of stochastic effects or waiting time between mortality events between 1 and 4 years. This frequency is similar to the observed rate of six unexpected female mortalities in 8 years (frequency of mortality events = 1.3 years) during the period 1974 to 1981 when hunting was prohibited in Kananaskis and adjacent Bow-Crow Forest (Wielgus and Bunnell, 1994a).

4. Results

4.1. Population growth

Parameter values and their elasticities are given in Table 3. In both populations survival of adult females (Saf) showed the largest elasticity, followed by survival of subadult females (Ssf), survival of offspring (Sc), probability of cub litter sizes (Pl), and probability of unsuccessful pregnancy (Pu). Elasticities for all parameters were similar between the two populations. Comparing those parameters affected by adult male mortality (Pu, Pl, Sc), survival of cubs had a considerably larger elasticity than probability of litter sizes and unsuccessful pregnancy.

The effects of hunting on reproductive parameters and on lambda was not inconsequential (Table 3). The

Table 3

Values for population parameters, elasticities, and finite rates of population growth for hunted and unhunted populations

Parameter ^a	Hunted population		Unhunted population	
	Value	Elasticity	Value	Elasticity
Pu	0.20	-0.011	0.12	-0.005
Ptrip	0.01	0.001	0.20	0.016
Ptwin	0.39	0.031	0.79	0.026
Psing	0.60	0.014	0.01	-0.000
Sc	0.78	0.140	0.84	0.184
Ssf	0.89	0.292	0.89	0.328
Saf	0.93	0.707	0.93	0.671
Lambda	0.99		1.05	
<i>n</i> 20 years	10		28	
<i>n</i> 40 years	9		75	

^a Pu, P unsuccessful pregnancy; Ptrip, P triplets; Ptwin, P twins; Psing, P singleton; Sc, survival cubs; Ssf, survival subadult females; Saf, survival adult females.

hunted population was decreasing at a rate of 0.99, whereas the simulated, unhunted, population was increasing at a rate of 1.05. Total number of females decreased from 12 to 10 at 20 years and from 12 to nine at 40 years in the hunted population. Total number of females increased from 12 to 28 at 20 years and from 12 to 75 at 40 years in the simulated, unhunted population.

4.2. Population persistence

The hunted population appears to face a greater risk of extinction than the unhunted population because of negative growth and resulting small population size. Under demographic stochasticity, we find that \bar{t}_{ext} remains low and increases linearly with the logarithm of K when $\lambda=0.99$, whereas \bar{t}_{ext} increases exponentially with K when $\lambda=1.05$ (Fig. 3). For example, at $n_0=12$ and $K=30$, we obtain $\bar{t}_{\text{ext}}=32$ years for the hunted population ($\lambda=0.99$) and $\bar{t}_{\text{ext}}=110$ years for the unhunted population ($\lambda=1.05$). At $K=80$ the hunted population goes extinct in 41 years, but the unhunted population persists for 4577 years.

Under environmental stochasticity, the average time to extinction \bar{t}_{ext} is critically affected by the frequency of mortality events and whether λ is less or greater than one (Fig. 4). For a given magnitude of mortality (in our case a 10% reduction in total population size every time a mortality event occurs), the increase of \bar{t}_{ext} with the average waiting time W between mortality events is low at $\lambda=0.99$, but very steep (exponential) at $\lambda=1.05$. If deaths occur every year ($W=1$), we find an average time to extinction as short as $\bar{t}_{\text{ext}}=21$ years for the hunted population ($\lambda=0.99$) and $\bar{t}_{\text{ext}}=43$ years for the unhunted population ($\lambda=1.05$). Even though the difference in λ caused by adult male mortality and segregation appeared relatively small (dif. = 0.06), mean time to

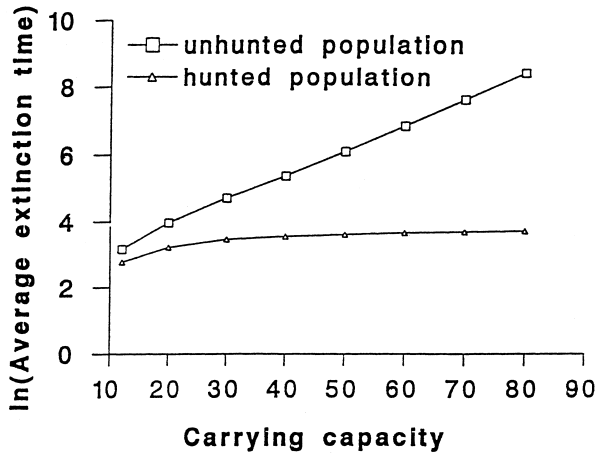


Fig. 3. Average time to extinction, \bar{t}_{ext} , in log-transformed years, as a function of carrying capacity, K , for a hunted ($\lambda=0.99$) and unhunted ($\lambda=1.05$) population subject to demographic stochasticity. In both cases, population size is initially $n_0=12$. Extinction occurs when $n=1$. See text for methods.

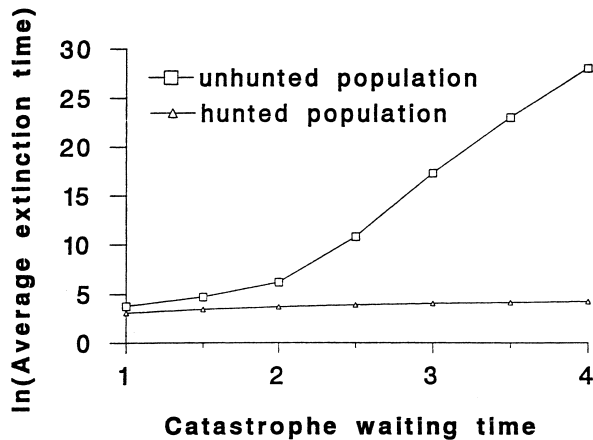


Fig. 4. Average time to extinction, \bar{t}_{ext} , in log-transformed years, as a function of waiting time (years) between mortality events (random catastrophes) for a hunted ($\lambda=0.99$) and unhunted ($\lambda=1.05$) population. The magnitude of mortality events is set at a 10% reduction in total population size. In both cases, population size is initially $n_0=12$. Extinction occurs when $n=1$. When $\lambda < 1$, \bar{t}_{ext} is independent of carrying capacity K ; when $\lambda > 1$, \bar{t}_{ext} very slowly increases with K and eventually stabilizes. Thus, to present conservative and comparable results, we performed the calculations with $K=n_0=12$. See text for methods.

extinction due to either demographic or environmental stochasticity always occurred much sooner in the hunted population.

5. Discussion

Our results suggest that the effects of adult male mortality: increased immigration by new males, related sexual segregation, and reduced reproduction (Wielgus and Bunnell, 1995, 2000) can result in lowered population growth and population declines and can even lead

to rapid population extinctions when numbers are very small. Swenson et al. (1997, 2000) also documented lowered recruitment and population growth because of high cub mortality in a population with higher adult male mortality, but that population was still increasing because of very high adult female survival and reproduction. We did not observe direct infanticide, but we did observe lower cub production — ostensibly because of sexual segregation by adult females into food-poor environments where infanticidal males were rare (Wielgus and Bunnell, 1994b, 1995). The larger elasticity for cub survival than for litter size or unsuccessful pregnancy suggests that the anti-infanticide tactic of sexual segregation by adult females (Wielgus and Bunnell, 1995), although resulting in smaller litters and more unsuccessful pregnancies than would otherwise be the case, is effective in maximizing fitness. The fitness costs of reduced cub survival via infanticide outweigh the fitness costs of smaller litter sizes and increased unsuccessful pregnancies via segregation. These results are consistent with, and help to explain, the observed sexual segregation in the hunted Kananaskis population (Wielgus and Bunnell, 1995).

However, even ostensibly protected populations where females reside in parks (e.g. Kananaskis) can decline ($\lambda=0.99$) and go extinct if trophy hunting of males outside of parks results in segregation and reduced reproduction within parks (Wielgus and Bunnell, 1994a,b, 1995, 2000). Unprotected, small populations may be at even greater risk because of the combined effects of segregation, infanticide, and incidental sport-hunting mortalities of females. For example, when we modeled lack of park protection in Kananaskis, and decreased female survival from 0.93 to 0.83 and cub survival from 0.78 to 0.67 (equivalent to losing one additional female and accompanying cub/year at $n=12$) the population went extinct in 20 years ($\lambda=0.88$), even without any stochastic effects.

These results should not be too surprising given the low rates of growth and small population sizes shown by many grizzly bear populations. Of the five published studies on brown bear population demography in North America (1. Knight and Eberhardt, 1985; Eberhardt et al., 1994; 2. McLellan, 1989a; Hovey and McLellan, 1996; 3. Wielgus and Bunnell, 1994a; 4. Wielgus et al., 1994; 5. Mace and Waller, 1998) only one and two were considered relatively safe from decline. A high-density population remote from human habitation and with very high adult female (0.94) and adult male (0.94) survival showed the fastest growth documented in North America ($\lambda=1.08$, McLellan, 1989a,b; Hovey and McLellan, 1996). That population had an annual reproductive rate of 0.42. Another protected population (Yellowstone — Craighead et al., 1974; Knight and Eberhardt, 1985) was declining, but now appears to be recovering only after a prolonged period of complete

protection (Eberhardt et al., 1994). Three other “ostensibly protected” populations (Kananaskis — Wielgus and Bunnell, 1994a; Selkirk — Wielgus et al., 1994; Swan Mountains — Mace and Waller, 1998) appeared to be declining. It appears that grizzly bears in North America hover near $\lambda = 1.00$ even when protected and when densities are low.

The findings that grizzly bear populations are susceptible to decreases in recruitment due to adult male mortality (Wielgus and Bunnell, 1994a, 2000; Swenson et al., 1997, 2000) are extremely controversial, but not evolutionarily surprising. Most top carnivores are unlikely to have adapted over evolutionary time to interspecific predation in general, and predation by humans in particular, and so should not be expected to compensate with increased offspring production and survival like some other herbivores or traditional game animals (e.g. Cervids). To manage potentially infanticidal carnivores as if they were cervids (e.g. trophy hunting or removal of resident, dominant males) is to ignore basic evolutionary differences. Unlike Artiodactyla, many carnivora exhibit some form of same-sex territoriality, extended parental care (> 1 year) by females but annual breeding by males, and hastened return to estrous through infanticide by weapon-bearing (teeth, claws) non-sire males (Hrdy, 1979; Packer and Pusey, 1983, 1984; Hausfater and Hrdy, 1984; MacDonald et al., 1987; Gittleman, 1989; Pusey and Packer, 1994). This life history of carnivores suggests that mortality of resident males could result in increased numbers of potentially infanticidal, immigrant males, with resulting reduced production and survival of young for females. That appears to be the case in grizzlies (Wielgus and Bunnell, 1994a, 2000; Swenson et al., 1997, 2000). However, few if any, population biologists have acknowledged the potential negative effects of adult male mortality on carnivore (and prey — via increased immigration) population growth (see reviews by Sinclair, 1989; Wolf, 1997; Sinclair et al., 1998). Even though some cervids engage in sexually selected infanticide when resident males are removed (Bartos and Madlatousek, 1994), most have relatively high reproductive rates and tend to breed annually during specific seasons regardless of offspring mortality.

Although our results suggest that adult male mortality and reduced recruitment can have a significant negative effect on population growth and persistence, we acknowledge that the empirical data (Wielgus and Bunnell, 1994a, 1995, 2000; Swenson et al., 1997, 2000) are very limited. None-the-less, we urge caution in managing small populations of grizzly bears because the empirical evidence to the contrary is even more limited (Miller, 1990; Derocher and Taylor, 1994; Garshelis, 1994; McLellan, 1994). Furthermore, theoretical predictions alone (Hrdy, 1979; Hausfater and Hrdy, 1984; Packer and Pusey, 1983, 1984), warrant caution in

removing adult male carnivores and possibly instigating infanticide by increasing immigrant males.

We also hypothesize that the occurrence of infanticide and sexual segregation may be more pronounced in small populations at the edge of the species' range because infanticide may not pay fitness dividends for males when population sizes and/or densities are high. For example, as density increases, any female induced into estrus by an infanticidal male may have an increasing probability of being bred by another competing male. Additionally, monogamous breeding by females and mate guarding by males may be replaced by promiscuity at high densities (Hornocker, 1962), confusing paternity and precluding infanticide by males. For the same reasons as above, we also speculate that “naturally occurring” infanticide and segregation (not exacerbated by human removal of resident males) may be more prevalent and important in small, low density populations and at the edge of the species' range where the potential for male-biased immigration and settling is high. Such a compensatory or inversely density dependent effect might explain apparent reproductive failures and lack of growth in some small, protected populations such as the grizzly bears in the North Cascades of British Columbia and Washington State and in the Pyrenees of France and Spain.

Regardless of our last two hypotheses, we argue that the empirical evidence (Wielgus and Bunnell, 1994a,b, 1995, 2000; Wielgus et al., 1994; Swenson et al., 1997, 2000; this paper) for negative effects of trophy hunting on small populations of grizzly bears is sufficient to question the advisability of hunting such populations, at least until evidence to the contrary is forthcoming. We advise caution in managing such populations. We also urge other researchers to test for effects of adult male mortality on cub production and survival and population growth and persistence in other areas.

Acknowledgements

Funding was provided by the Alberta Fish and Wildlife Branch; Alberta Recreation, Parks, and Wildlife Foundation; B.C. Ministry of Environment; B.C. Ministry of Forests; B.C. Ministry of Parks; Boreal Institute; Carthy Foundation; CNRS Lab D'Ecologie; Crestbrook Forest Industries; Darkwoods Forestry; Ecole Normale Superieure; Forest Renewal B.C.; James Robert Thompson Foundation; Home Oil Ltd.; Idaho Department of Fish and Game; Natural Sciences and Engineering Research Council of Canada; Science Council of B.C.; Trail Wildlife Assoc.; University of British Columbia; Universite Pierre et Marie Curie; U.S. Fish and Wildlife Service; U.S. Forest Service; Washington Department of Fish and Wildlife; Washington State

University; and World Wildlife Fund (Canada). Fieldwork and technical assistance were provided by J. Almack, J. Bicknell, K. Chambers, B. Compton, R. Dice, H. Carr, R. Foreman, D. Johnson, S. Knick, C. Mamo, T. Manning, L. Meszaros, B. Pelchat, G. Servheen, R. Steiner, M. Super, W. Wakkinen, and P. Zager. The late O. Pall helped train Wielgus in aerial telemetry and conducted many telemetry flights prior to Wielgus's participation. We lost him during one of his flights in Kananaskis and remember him fondly. The manuscript benefited from the comments and discussion of E. Danchin, D. Mattson, J. Weaver, G. Wright, and anonymous reviewers.

Appendix A.

Average time to extinction under demographic stochasticity

Following on from Leigh [1981, Eq. (8)] and Lande [1993, Eq. (3)], given carrying capacity K , the average time to extinction for a population of size n_0 is

$$\bar{T}_{\text{ext}} = 2 \int_l^{n_0} e^{-G(z)} \int_z^K \frac{e^{G(y)}}{y} dy dz$$

where

$$G(y) = 2 \int_1^y \ln \lambda dN = 2(y - 1) \ln \lambda.$$

Integrating by parts then yields

$$\bar{T}_{\text{ext}} = \frac{1}{2 \ln \lambda} [I(1) - I(n_0) - \ln n_0]$$

with

$$I(x) = e^{-2x \ln \lambda} \int_x^K \frac{e^{-2y \ln \lambda}}{y} dy.$$

Numerical computations of integrals were performed using MATHEMATICA software (Wolfram Research Inc.).

Average time to extinction from catastrophes

The risk of extinction from random catastrophes is influenced by the frequency and magnitude of catastrophes, in a different way depending on λ . Let us assume that each catastrophe reduces instantaneously

the population by a proportion δ . The waiting time for a catastrophe has an exponential distribution with mean w . According to Lande [1993, Eq. (A16b)], if $\lambda < 1$, average time to extinction is

$$\bar{T}_{\text{ext}} = \frac{\ln n_0}{-\ln \lambda - w^{-1} \ln(1 - \delta)}.$$

If $\lambda > 1$ [Lande, 1993, Eq. (15a)], \bar{T}_{ext} is given by

$$\bar{T}_{\text{ext}} = \frac{\ln n_0}{-\ln \lambda - w^{-1} \ln(1 - \delta)} e^{\frac{\beta n_0 K}{\ln(1 - \delta)}} \times \left[1 + \frac{\ln(1 - \delta) \left(1 - n_0^{\frac{\beta}{\ln(1 - \delta)}} \right)}{\ln n_0 \beta} \right]$$

where β is the solution of a transcendental equation

$$\frac{\beta}{e^\beta - 1} = -\frac{\ln(1 - \delta)}{w \ln \lambda}$$

that we could solve numerically using MATHEMATICA again.

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