Biological Conservation **67** (1994) 161–166

DYNAMICS OF A SMALL, HUNTED BROWN BEAR *Ursus arctos* POPULATION IN SOUTHWESTERN ALBERTA, CANADA

R. B. Wielgus & F. L. Bunnell

Department of Forest Sciences, University of British Columbia, 193-2357 Main Mall, Vancouver, B.C., Canada, V6T 1Z4

(Received 28 August 1992; revised version received 15 January 1993; accepted 3 March 1993)

Abstract

We studied population dynamics of brown bears Ursus arctos *in the Kananaskis Park and Bow Crow Forest of southwestern Alberta, Canada to evaluate effects of hunting. Twenty-four bears were captured and 20 were radio-monitored from 1980 to 1984. Estimated density was 1.6 bears/100 km², for a population size of 38 bears. Mean annual sex and age composition was 30% adult males, 22% adult females, 22% subadult males, 11% subadult females, and 15% cubs. Mean litter size of new cubs was 1.40 and mean birth or breeding interval was 3.00 years. The reproductive rate was estimated at 0.46 cubs/adult female/year. Adjusted annual survival rates were 0.70 for adult males, 0.93 for adult females, 0.89 for subadult males, 0.89 to 0.93 for subadult females, and 0.78 for cubs. Combined, these rates yield population growth rates of* $r_s = -0.01$ *to* $r_s = +0.01$. *Increased hunting mortality of older adult males coincided with an influx of younger immigrant males, which apparently contributed to low reproductive rate and population decline.*

Keywords: Canada, Alberta, brown bear, *Ursus arctos*, population dynamics, hunting.

INTRODUCTION

Brown bears are declining throughout most of their range and are considered vulnerable, threatened, or endangered in many countries (Servheen, 1990). They are still hunted in most countries because many wildlife managers believe that hunting of adult males has little or no negative impact on population growth or actually increases production and survival of young (see Miller, 1990). In the contiguous United States, brown bears declined from an estimated 100,000 in the 1850s to less than 900 at present. The future of the species in North America can only be assured in Canada and Alaska where the bears are managed as game animals (Servheen, 1990). In Canada, brown bears are listed as vulnerable and are restricted to parts of Alberta, British Columbia (BC), Northwest Territories, and the Yukon. In Alberta, there are an estimated 780 brown bears and numbers are declining (Servheen, 1990). Nagy and Gunson (1990) estimated 62 brown bears in southwestern Alberta, at the edge of the species' range. In 1970 hunting of brown bears was closed there because numbers were declining, but increased sightings led to reopened hunting in the Bow Crow Forest in 1982 and in adjacent Kananaskis Park in 1987. Hunting was closed again in 1988 because of public concern. Carr (1989) estimated numbers and mortality of brown bears in the Bow Crow and Kananaskis and recommended continued hunting of bears. Nagy and Gunson (1990) reviewed harvest statistics and recommended against hunting in Kananaskis but advocated limited hunting of males in the Bow Crow. The objective of this paper is to report the effects of hunting on population dynamics of brown bears in Kananaskis Park and the Bow Crow Forest of southwestern Alberta.

Biological Conservation 0006-3207/94/$07.00

STUDY AREA

The Kananaskis Provincial Park and Bow Crow Forest cover 9000 km² in southwestern Alberta, Canada (Fig. 1). Elevation ranges from 1300 m to 2700 m in rugged mountainous terrain. Bedrock is sedimentary and climate is continental with long, cold winters and short, cool summers. Forests are comprised of lodgepole pine *Pinus contorta*, Engelmann spruce *Picea engelmannii*, and alpine fir *Abies lasiocarpa* (Rowe, 1972). Common vegetative foods of bears were *Carex* spp., *Hedysarum* spp., *Equisetum* spp., *Erythronium* spp., *Heracleum lanatum*, and *Shepherdia canadensis* (Wielgus, 1986).

Trapping of bears was conducted in two areas. The 254 km² Highwood trapping zone (HTZ) covered a 50-year-old burn in the mountains (1800 m) of Kananaskis and was dominated by *Shepherdia canadensis* shrubfields. Surrounding areas were largely unburnt and were relatively unproductive for bear forage. The Sheep trapping zone (STZ) was a 225 km² area about 20 km to the east in the foothills (1400 m) and was chosen primarily for capture of black bears *Ursus americanus*. It was not centered on a burned-over area and was almost never used by brown bears (Wielgus, 1986).

Fig. 1. Location of study area (•) in relation to brown bear distribution (▦) in North America.

METHODS

Trapping and monitoring

Trapping of bears took place from 1980 to 1984 using Aldrich leg snares. Bears were immobilized with Ketamine hydrochloride (Ketaset, Rojar/STB Ltd, London, Ontario) and Xylazine hydrochloride (Rompun, Chemagro Corp., Etobicoke, Ontario). Immobilized bears were sexed, weighed, ear-tagged, had a premolar tooth (Pm1) extracted for ageing (Stoneburg & Jonkel 1966), and most were fitted with activity-sensing radio-collars (Telonics Inc., Mesa, Arizona).

Radio-telemetry from fixed-wing aircraft (Whitehouse & Steven, 1977) was conducted at weekly intervals during the non-denning period (early April to early December) from 1981 to 1984 to monitor location and status of the bears. Eighteen percent of 527 locations were visual observations.

Density, numbers, and sex and age composition

We estimated mean annual density of bears by determining the mean annual number of bears present in the 97.5% multi-annual composite home range of females (Ackerman *et al.*, 1990). Intensive field work suggested that all bears, especially females with young, were accounted for in that 868 km^2 area. The method is similar to that used in most other studies (LeFranc *et al.*, 1987) and allows direct comparisons.

If female bears were captured after 1980 (the first year of study) and restricted their movements to the composite range for at least two consecutive years, their inclusion in the population was assumed back to 1980 because females tend to remain in the same area throughout their lives (Blanchard & Knight, 1992); males were not extrapolated back to 1980 because they could have been immigrants (Glenn & Miller, 1980). The presence of cubs in the composite range was extrapolated back to their assumed date of birth (1 February). This composite home range method provides a minimum density estimate of bears because all bears present in the composite range were assumed captured and known.

We estimated numbers of bears in Kananaskis and the Bow Crow Forest by extrapolating density estimates to only the 2315 km^2 mountainous region of the study area where bear use was observed (Wielgus, 1986). We estimated sex and age composition of the bear population by calculating the mean annual percentage of male and female adults (≥ 6.5 years), male and female subadults (2.5 to 5.5 years), and cubs (0.5 to 1.5 years) in the monitored sample.

Reproductive rate

Number of cubs per litter, birth or breeding interval, and age at first parturition were determined from aerial and ground observations of females and cubs. We estimated reproductive rate by dividing mean litter size of cubs of the year by mean birth or breeding interval (Craighead *et al.*, 1974). That method allowed direct comparison of reproductive rate with the nearby

Flathead population (McLellan, 1989*b*). The reproductive rate did not include cubs that could have died prior to our first observation of litters.

Survival rates

We estimated seasonal and annual survival rates for adult males and females, subadult males and females, and cubs using the Micromort program (Heisey & Fuller, 1985). That method allowed direct comparison of survival rates with the nearby Flathead population (McLellan, 1989*c*). Birth date of all bears was assigned at 1 February for survival calculations. Seasons were defined as spring (April–June, includes grizzly bear hunting season), summer (July–August), fall (September–November, includes general hunting season), and winter (December–March, includes denning season). Date and cause of death were determined by compulsory reporting of hunter kills and reports from conservation officers. This method yielded a maximum estimate of survival because only reported kills were included; radio-collared animals that stopped transmitting were assumed alive.

We adjusted survival rates for adult females and cubs by extending the sampling period to include one known death that occurred just after radio-monitoring ceased. An adult female with yearling cubs was shot in the fall of 1985. She was included in the survival calculations and her accompanying yearling cubs were assumed to have died by 1 January 1986. We assumed that all other adult females survived through 1985 and that all other unmonitored cubs survived to weaning at 2.5 years of age.

Population trend

We estimated the survival–fecundity exponential rate of increase (r_s) by iterating the Lotka equation (Caughley, 1977). That method allowed direct comparison of population growth rate with the Flathead population (McLellan, 1989*b*). Sex- and age-specific survival rates used in the equation were estimated from radio-collared bears and dependent offspring. Maximum age was set at 21.5 years based on data for 22 different populations (LeFranc *et al.*, 1987: Table 10). Age-specific reproductive rates used in the equation were one half of estimated reproductive rate, based on an assumed 1 male:1 female sex ratio of cubs (e.g. LeFranc *et al.* 1987). Female reproduction began at the mean estimated age of first parturition.

RESULTS

Trapping and monitoring

Twenty-four brown bears (18 males, six females) were captured from 1980 to 1984—14 males and six females in the HTZ, 3 males in the STZ, and 1 male in nearby Peter Lougheed Park. Annual trapping effort was 1806, 2074, 2124, 1868, and 118 trap-nights from 1980 to 1984, respectively.

Captures of new, young males increased after the hunting season was opened in 1982. The number of new males captured per year in the HTZ and STZ was four in 1980 (4.5, 9.5, 12.5, and 14.5 years old), three in 1981 (4.5, 5.5, and 15.5 years old), two in 1982 (3.5, and 5.5 years old), and eight in 1983 (3.5, 3.5, 3.5, 3.5, 5.5, 6.5, 7.5, and 15.5 years old). No new males were captured in 1984 when trapping effort was greatly reduced. Mean age of captured males was 9.5 years for 1980 to 1981 (SE = 1.8, n = 7) and 5.8 years for 1982 to 1983 (SE = 1.1, n = 10). Mean ages were statistically different at $p = 0.09$ (t = 1.80, 15 d.f.).

Most females were captured when unaccompanied by young. A single 6.5-year-old died at capture in 1980. A 14.5-year-old with two yearlings was captured in 1981; her two female offspring (2.5 years old) and an adult (6.5 years old) in 1982. Another adult (10.5 years old) was captured in 1983. No new females were captured in 1984.

Density, numbers, and sex and age composition

Mean annual density, sex and age composition, and estimated population size are given in Table 1. Between 10 and 20 bears were known to reside annually in the female composite range. Numbers of subadult and young, adult male bears increased after the hunting season was opened in 1982. Numbers of females appeared more stable. Numbers of cubs may have been underestimated from 1980 to 1982 because the reproductive status of one adult female was unknown at that time.

Reproductive rate

Mean litter size for cubs of the year was 1.40 (SE = 0.24, $n = 5$) and mean birth or breeding interval was 3.00 years (SE = 0, $n = 3$). Combined, these values yield an estimated reproductive rate of 0.46 cubs/adult female/year or 0.23 female cubs/adult female/year. One female bred at 3.5 years of age and gave birth at 4.5 years; her sister bred at 3.5 and 4.5 years and likely gave birth at 5.5 years. Another female was nursing when captured at 6.5 years. This small sample yields a mean age at first parturition of 5.50 years.

Table 1. Annual number of bears in the female composite home range, percent composition (%), estimated density (bears/100 km²), and estimated population size for sex and age classes of brown bears in Kananaskis Park and the Bow Crow Forest of southwestern Alberta, 1980–1984

Year	Cubs	Subadult males	Subadult females	Adult males	Adult females	Total
1980	2 (20)	1 (10)	1 (10)	3 (30)	3 (30)	10
1981	2 (20)	2 (20)	1 (10)	3 (30)	2 (20)	10
1982	0 (0)	3 (27)	2 (19)	3 (27)	3 (27)	11
1983	2 (10)	6 (30)	2 (10)	7 (35)	3 (15)	20
1984	5 (26)	4 (21)	1 (5)	5 (26)	4 (21)	19
Annual mean	2·2 (15)	3·2 (22)	1·4 (11)	4·2 (30)	3·0 (22)	14·0
Density	0·25	0·39	0·16	0·48	0·34	1·62
Population Size[a]	5·78	9·02	3·70	11·11	7·87	37·50

[a] Population estimate based on application of density estimate to bear-occupied portion (2315 km²) of Kananaskis and Bow Crow Forest.

FWS_LIT_032293

Table 2. Seasonal and annual survival rates, number of bear-years monitored, and number of bear deaths/number of radio-instrumented bears for sex and age classes of brown bears in Kananaskis Park and the Bow Crow Forest of Alberta, 1980–1984

Age/sex class	Survival rate						Bear years	Deaths/ bears
	Spring	Summer	Fall	Winter	Annual	(95% CI)		
Adult males	0·70	1·00	1·00	1·00	0·70	(0·46–1·00)	8·29	3/9
Subadult males	1·00	1·00	0·89	1·00	0·89	(0·72–1·00)	6·80	1/9
Adult females	1·00	1·00	0·93	1·00	0·93	(0·83–1·00)	14·92	1/5
Subadult females	1·00	1·00	1·00	1·00	1·00	(1·00)	2·40	0/2
Cubs	1·00	1·00	0·78	1·00	0·78	(0·56–1·00)	7·02	2/5

Survival rates

Three of nine adult males were legally shot during the spring brown bear seasons in Alberta (1) and adjacent BC (2), for an annual survival rate of 0.70 (Table 2). One of nine subadult males was shot in Alberta during the fall general season for an annual survival rate of 0.89. Of 18 male bears captured from 1980 to 1984, eight were reported shot by 1987 and seven went unaccounted for by 1984. Of the eight known deaths, five were legally shot in Alberta and three were legally shot in adjacent BC. Mean age of killed males was 11.1 years (SE = 1.76, n = 8).

One radio-collared adult female with yearlings was shot in self defense by a hunter in the fall of 1985, one year after radio-monitoring ceased. If we include that death and assume that all other adult females survived through 1985 we get one death in 14.92 bear-years for an annual survival rate of 0.93 (Table 2). We assume that the cubs of the killed adult female died by 1 January 1986 and that all other cubs survived to weaning at 2.5 years of age for an estimated cub survival rate of 0.78. No subadult females died during 2.40 bear-years for a rate of 1.00.

Population trend

Age-specific reproductive rates used in the Lotka equation were 0.23 female cubs/adult female/year, starting at 5.5 years of age, and age-specific survival rates were 0.93 for adult females and 0.78 for cubs. We substituted the estimated rates of subadult males (0.89) and adult females (0.93) for subadult females because their estimated rate (1.00) was unreasonable and based on a small sample (Table 2). The calculated exponential rate of change was $r_s = -0.01$ for the subadult female survival rate of 0.89 and $r_s = +0.01$ for the subadult female survival rate of 0.93.

DISCUSSION

Density, numbers, and sex and age composition

The high trapping intensity and absence of unknown females in the composite range suggest that all females and most bears were known. The estimated density (62 km^2/bear) was similar to other interior brown bear populations (LeFranc *et al.*, 1987), but lower than in the nearby Flathead Valley of BC (16 km^2/bear; McLellan, 1989*a*). Proportions of females were lower, and of males higher, in this population than in most other brown bear populations (LeFranc, *et al.* 1987; McLellan, 1989*a*).

There is a reasonable explanation for the atypical sex and age composition of our sample. The high annual mortality (30%) of older adult males (mean age = 11.12 years) apparently allowed high rates of immigration by younger males (Bunnell & Tait, 1981). We observed that 10 new, younger males (mean age = 5.8 years) occupied the composite range after the hunting season was opened in 1982 and mortality of older adult males increased. Only one male was reported shot from 1977 to 1981 in Kananaskis and the Bow Crow but seven males were reported shot there from 1982 to 1987 (Nagy & Gunson 1990). Three other collared males were reported shot in adjacent BC between 1982 to 1986. Another five collared males went unaccounted for from 1982 to 1984. These data show that many older resident males were removed by hunting after 1981. Trapping effort remained similar from 1980 to 1983 so changes in effort could not account for the increased numbers of younger males captured after 1982. Kemp (1976) and Young and Ruff (1982) documented a three-fold increase in subadult males after removing 30% of adult male black bears. LeCount (1987) also suggested that high mortality of adult male black bears resulted in an increase of immigrant subadult males in his study area.

Our density estimates were higher than those of Carr (1989) (1.6 vs 1.2 bears/100 km^2) but our population estimates were lower (38 vs 77), especially for females (12 vs 28). Carr (1989) used the Chapman-Robson mark–recapture technique to estimate number of males then assumed a 1:1 sex ratio to estimate number of females. He also assumed population closure (no immigration) for males. We observed a sex ratio skewed towards males and evidence of immigration by males; both suggest that our population estimates are more reliable than Carr's.

Reproductive rate

The estimated reproductive rate of 0.46 was considerably lower than in the nearby Flathead (0.85; McLellan, 1989*b*). The mean birth interval (3.00 years) is similar to that of the Flathead (2.67 years, McLellan, 1989*b*) and is the average for brown bear populations in North America (LeFranc *et al.*, 1987). The estimated mean age at first parturition (5.5 years) is younger than for most other populations (6.5 to 7.5 years, Lefranc *et al.*, 1987; McLellan, 1989*b*).

Mean cub litter size (1.40) was smaller than in the Flathead (2.26) and is among the smallest reported in North America (LeFranc *et al.*, 1987; range = 1.6 to 2.66). The small litter size contrasts with the apparent early age at first parturition, since both are influenced by nutrition (Bunnell & Tait, 1981), and could be related to the abundance of immigrant males. LeCount (1987) found high rates of infanticide in a heavily hunted black bear population with many immigrant males. Hrdy and Hausfater (1984) reviewed infanticide in many species and found that most killing of young is by immigrant males. We did not observe any instances of infanticide but it may have occurred prior to our first observation of cubs. Wielgus (1993) observed that adult females avoided food-rich, immigrant male-occupied habitats and suggested that cub litter sizes suffered as a result. Subadult females did not avoid the food-rich habitat and that could explain the early age at first parturition.

Survival rates

The estimated annual survival rate for adult males (0.70) appears to be considerably lower than in the Flathead (0.92; McLellan, 1989*c*) and is among the lowest survival recorded in North America (Bunnell & Tait 1980, 1981, 1985). The rate of 0.89 for subadult males is similar to the Flathead (0.92; McLellan 1989*c*) and is consistent with hunter's avoidance of smaller, subadult animals (Bunnell and Tait 1980, 1981, 1985). Adult and subadult male survival rates could be overestimates because seven known males went unaccounted for and could have been killed.

The adjusted adult female (0.93) and subadult female (0.89–0.93) survival rates are similar to those in the Flathead (0.94 for adult and subadult females; McLellan, 1989*c*). These estimates could be optimistic because they apply only to animals that resided in Kananaskis, which was protected from hunting during the period of study. Six other uncollared females were reported shot in the study area from 1974 to 1981 (Nagy and Gunson, 1990). The adjusted survival estimate of 0.78 for cubs is also similar to that observed in the Flathead (0.82; McLellan, 1989*c*).

Our estimates of male survival contrast with those of Carr (1989). He estimated mean annual survival rates of 0.90 for males by calculating the percentage of bears marked and present on 1 January and reported killed by 31 December of that year. He counted only bears that were subject to at least one full year of mortality—one male bear was not included in his analysis because that bear died only 2.5 months after capture.

Population trend

The estimated rates of change for the female segment of the population (r_s = −0.01 to +0.01) appear lower than in the Flathead (r_s = +0.07 to +0.08; McLellan, 1989*b*). Our estimates again contrast with Carr (1989). He back-dated the population age structure to 1980 and concluded that many bears were being born into the population, but his recruitment largely comprised subadult males that were not produced by the resident females. None of the 10 captured subadult males were observed as offspring of resident females and all were ≥ 3.5 years of age at capture, suggesting that they were probably immigrants (e.g. Glenn & Miller, 1980; Blanchard & Knight, 1992).

Differences in survival of females generally contribute more to variation in population growth than do differences in reproduction (Knight & Eberhardt, 1985; McLellan, 1989*b*). Our estimates of adult female, subadult female, and cub survival are very similar to the rates in the Flathead yet the Flathead population showed a high rate of population growth (+0.08). Because mean age at first parturition appears younger and mean interbirth interval is similar to the Flathead population, the smaller litter sizes in Kananaskis caused the comparatively low estimate of population growth.

CONCLUSIONS

Hunted brown bear populations continue to decline (e.g. Servheen, 1990; Aoi, 1991) yet many wildlife managers assume that hunting of adult males has little or no detrimental effect on population growth, or that it actually increases production and survival of young (Miller, 1990). Our findings suggest the opposite. Increased numbers of younger male bears were interpreted as a growing population (Carr, 1989), but actually reflected increasing numbers of immigrant males associated with high mortality of older, adult males. Female brown bears were few in number and probably declining because of low reproductive rate. Small litters caused the low reproduction and were apparently due to either direct mortality by immigrant males (e.g. LeCount, 1987) or poor nutrition of adult females because adult females avoided numerous immigrant males and their food-rich habitats (Wielgus, 1993). Adult females should avoid immigrant males because such males should kill cubs to bring females into estrus (Hrdy & Hausfater, 1983). Subadult females did not avoid immigrant males, possibly because they offered no such reproductive opportunities (Wielgus, 1993).

The observed pattern suggests that hunting of adult males is not always compensatory for reproduction as suggested by McCullough (1981, 1986), Stringham (1983), and McLellan (1989*b*). Our data suggest that hunting of adult males can actually be depensatory for reproduction as suggested by Stringham (1980) and Lecount (1987). Such a relation could hasten the demise of small populations, especially if populations are at the edge of their range and subject to high rates of male immigration.

ACKNOWLEDGEMENTS

Field research was funded by Alberta Forestry, Lands, and Wildlife–Fish and Wildlife Branch; Alberta Recreation, Parks, and Wildlife Foundation; Boreal Institute; Carthy Foundation; Home Oil Ltd; Natural Sciences and Engineering Research Council of Canada; and the

World Wildlife Fund (Canada). Funding for population analysis was provided by James Robert Thompson Foundation, Natural Sciences and Engineering Research Council of Canada, Science Council of British Columbia, University of British Columbia, and the World Wildlife Fund (Canada).

C. Mamo and T. Manning were responsible for trapping and radio-collaring bears. Field and technical assistance was provided by J. Bicknell, R. Foreman, and L. Meszaros. H. Carr provided logistical support. B. O. Pelchat initiated the fieldwork and encouraged Wielgus's participation. Comments of reviewers improved the manuscript. The late O. Pall helped train Wielgus in aerial telemetry and conducted many grizzly telemetry flights prior to Wielgus's participation; we lost him during one of his flights and remember him fondly.

REFERENCES

Ackerman, B.B., Leban, F.A., Samuel, M.D. & Garton., E.O. (1990). User's manual for Program Home Range, 2nd edition. *Univ. Idaho, For., Wildl. and Range Exp. Stn, Tech. Rep.*, No. 15. Moscow, Idaho.

Aoi, T. (1991). Population trends of brown bear related to hunting and habitat change in northern Hokkaido, Japan. In *Wildlife Conservation, Proc. Int. Symp. Wildlife Conserv.*, ed. N. Maruyama. Japan Wildlife Research Center, Yushima, Japan, pp. 153–5.

Blanchard, B.M. & Knight, R.R. (1992). Movements of Yellowstone grizzly bears. *Biol. Conserv.*, **58**, 41–67.

Bunnell, F.L. & Tait, D.E.N. (1980). Bears in models and in reality—implications to management. *Int. Conf. Bear Res. & Manage.*, **4**, 15–23.

Bunnell, F.L., & Tait, D.E.N. (1981). Population dynamics of bears—implications. In *Dynamics of large mammal populations*, eds. C.W. Fowler & T.D. Smith. John Wiley, New York, pp. 75–98

Bunnell, F.L., & Tait, D.E.N. (1985). Mortality rates of North American bears. *Arctic*, **38**, 316–23.

Carr, H.D. (1989). Distribution, numbers, and mortality of grizzly bears in and around Kananaskis Country, Alberta. *Wildlife Research Series*, No. 3. Alberta Forestry, Lands, and Wildlife. Fish and Wildlife Division, Edmonton, Alberta.

Caughley, G. (1977). *Analysis of vertebrate populations*. John Wiley, New York.

Craighead, J.J., Varney, J.R. & Craighead, F.C. (1974). A population analysis of the Yellowstone grizzly bears. *Montana For. Conserv. Exp. Stn Bull.*, No. 40.

Glenn, L.P. & Miller, L.H. (1980). Seasonal movements of an Alaska Peninsula brown bear population. *Int. Conf. Bear Res. and Manage.*, **4**, 307–12.

Heisey, D.M. & Fuller, T.K. (1985). Evaluation of survival and cause-specific mortality rates using telemetry data. *J. Wildl. Manage.*, **49**, 668–74.

Hrdy, S.B. & Hausfater, G. (1984). Comparative and evolutionary perspectives on infanticide: Introduction and overview. In *Infanticide—comparative and evolutionary perspectives*, ed. G. Hausfater & S.B. Hrdy. Aldine Publishing Co., New York, pp. xiii–xxxv.

Kemp, G.A. (1976). The dynamics and regulation of black bear *Ursus americanus* populations in northern Alberta. *Int. Conf. Bear Res. & Manage.*, **3**, 191–8.

Knight, R.R. & Eberhardt, L.L. (1985). Population dynamics of the Yellowstone grizzly bears. *Ecology*, **66**, 323–34.

LeCount, A.L. (1987). Causes of black bear cub mortality. *Int. Conf. Bear Res. & Manage.*, **7**, 75–82.

LeFranc, M.N., Moss, M.B., Patnode, K.A. & Sugg, W.C. (1987). *Grizzly bear compendium.* US Fish and Wildlife Service, Missoula, Montana.

McCullough, D.R. (1981). Population dynamics of the Yellowstone grizzly. In *Dynamics of large mammal populations*, ed. C.W. Fowler & T.D. Smith. John Wilely, New York, pp. 173–96.

McCullough, D.R. (1986). The Craighead's data on Yellowstone grizzly bear populations: Relevance to current research and management. *Int. Conf. Bear Res. & Manage.*, **6**, 21–32.

McLellan, B.N. (1989*a*). Dynamics of a grizzly bear population during a period of industrial resource extraction, I. Density and age–sex composition. *Can. J. Zool.*, **67**, 1856–60.

McLellan, B.N. (1989*b*). Dynamics of a grizzly bear population during a period of industrial resource extraction, III. Natality and rate of increase. *Can. J. Zool.*, **67**, 1865–8.

McLellan, B.N. (1989*c*). Dynamics of a grizzly bear population during a period of industrial resource extraction, II. Mortality rates and causes of death. *Can. J. Zool.*, **67**, 1861–4.

Miller, S.D. (1990). Impacts of increased bear hunting on survivorship of young bears. *Wildl. Soc. Bull.*, **18**, 462–7.

Nagy, J.A. & Gunson, J.R. (1990). Management plan for grizzly bears in Alberta. *Wildlife Management Planning Series*, No. 2. Alberta Forestry, Lands, and Wildlife, Fish and Wildlife Division, Edmonton, Alberta.

Rowe, J.A. (1972). Forest regions of Canada. *Can. For. Serv.* Publs., No. 1300. Ottawa, Ontario.

Servheen, C. (1990). The status and conservation of the bears of the world. *Int. Conf. Bear Res. & Manage.*, **8**, Monogr. Ser., No. 2.

Stoneburg, R.P. & Jonkel, C.J. (1966). Age determination of black bears by cementum layers. *J. Wildl. Manage.*, **30**, 411–14.

Stringham, S.F. (1980). Possible impacts of hunting on the grizzly/brown bear, a threatened species. *Int. Conf. Bear Res. & Manage.*, **4**, 337–49.

Stringham, S.F. (1983). Roles of adult males in grizzly bear population biology. *Int. Conf. Bear Res. & Manage.*, **5**, 140–51.

Whitehouse, S. & Steven, D. (1977). A technique for aerial radio tracking. *J. Wildl. Manage.*, **41**, 771–5.

Wielgus, R.B. (1986). Habitat ecology of the grizzly bear in the southern Rocky Mountains of Canada. MS thesis, University of Idaho.

Wielgus, R.B. (1993). Causes and consequences of sexual habitat segregation in grizzly bears. PhD thesis, University of British Columbia.

Young, B.F. & Ruff, R.L. (1982). Population dynamics and movements of black bears in east central Alberta. *J. Wildl. Manage.*, **46**, 845–60.