Projected Future Abundance of the Yellowstone Grizzly Bear

funded by the Pa. Game Comm. Appreciation is extended to J. M. Gruttadauria, K. M. Weaver, F. W. Alt, and R. D. Buss, who provided valuable field assistance, and to G. L. Storm and M. R. Pelton for comments on the manuscript.

LITERATURE CITED

ALT, G. L. 1982. Reproductive biology of Pennsylvania's black bear. Pa. Game News 53(2):9–15.

———. 1983*a*. Timing of parturition of black bears (*Ursus americanus*) in northeastern Pennsylvania. J. Mammal. 64:305–307.

———. 1983*b*. Bear dens under interstate highway. Pa. Game News 54(8):8–10.

———, AND J. M. GRUTTADAURIA. 1984. Reuse of black bear dens in northeastern Pennsylvania. J. Wildl. Manage. 48:236–239.

BOYER, R. H. 1949. Mountain coyotes kill yearling black bear in Sequoia National Park. J. Mammal. 30:75.

ROGERS, L. L. 1977. Social relationships, movements, and population dynamics of black bears in northeastern Minnesota. Ph.D. Thesis, Univ. Minnesota, Minneapolis. 194pp.

———, AND L. D. MECH. 1981. Interactions of wolves and black bears in northeastern Minnesota. J. Mammal. 62:434–436.

Received 30 August 1983.
Accepted 20 December 1983.

PROJECTED FUTURE ABUNDANCE OF THE YELLOWSTONE GRIZZLY BEAR

R. R. KNIGHT, Interagency Grizzly Bear Study Team, Forestry Sciences Laboratory, Montana State University, Bozeman, MT 59717; and L. L. EBERHARDT, Pacific Northwest Laboratory, Battelle Memorial Institute, P.O. Box 999, Richland, WA 99352.

Low densities, secretive behavior, and high mobility make grizzlies (*Ursus arctos horribilis*) especially difficult to census. Adult females with cubs are most readily observed, and the presence of the young provides additional cues for distinguishing family groups (individuals can be identified by cataloging coat colors, scars, tags, locations, etc., as suggested by Cole 1974). Reproduction begins at age 5 and cubs are produced at an average interval of just over 3 years. Summing the numbers of different females with cubs that were counted over 3 successive years thus gives an estimate of a minimal number of fully adult females in the population during the 1st year of any 3-year period. Although intensive efforts have been made to develop other census techniques, this method appears to provide the best presently available index of grizzly abundance in Yellowstone National Park and its environs.

The Yellowstone population is isolated from the other remnant grizzly populations and occupies an area roughly double that of the National Park, or about 20,000 km^2 in total. From the 1920's to the late 1960's much of the population was seasonally concentrated at garbage dumps in and near the Park and obtained an important supplemental food supply there. Between 1968 and 1971 the Park dumps were phased out, and procedures initiated to deny access by bears to dumps outside of the Park. Recorded mortalities roughly doubled in the 2 years (1970–71) of major dump closures, and a downward trend in counts of different females with young (Fig. 1) was initiated (since the index is cumulative, reductions in population size would influence the calculated index 3 years prior to the actual reduction). Closure of the dumps was followed by a significant decline in reproductive and survival rates. In the earlier years (1959–70) litter size averaged 2.1 cubs, and 70% of the females produced their first litter at age 5. In recent years (1974–82), average litter size has been 1.9 and about 60% of

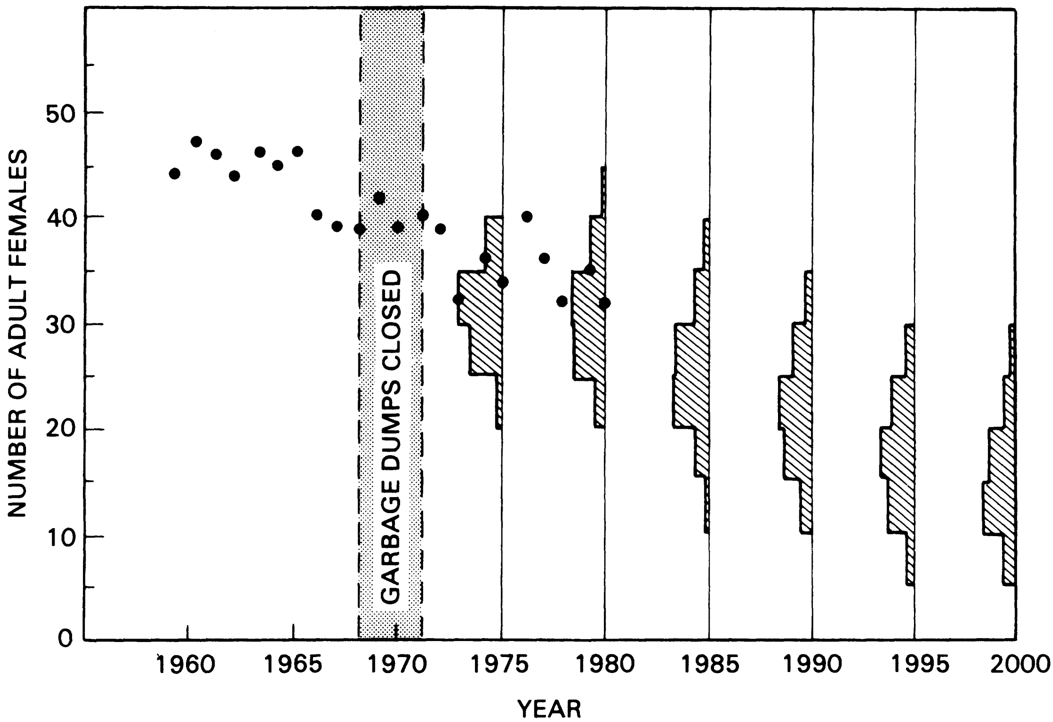

Fig. 1. Observed index of abundance (●) and projected population sizes (histograms) from a stochastic model of the adult female grizzly bear population of Yellowstone National Park and surrounding area. The index is based on 3-year sums of adult females with cubs, since these are the most visible elements of the population. A reduction in reproduction and survival rates after closure of open garbage dumps in and near the Park resulted in the observed decline in the population, and the general course of the likely future trend is illustrated by the histograms. Each histogram shows the frequency distribution of population size based on 10,000 simulations for periods of from 5 to 30 years. Each histogram was produced by an independent simulation, starting in 1970.

females produced first litters at age 6. Survival to age 6 decreased from about 38% to 23%, and annual survival rates for prime-age adult bears decreased from about 96% to about 92% (Craighead et al. 1974, 1976; Knight and Eberhardt 1985).

METHODS

In view of the declines in both population index and key population parameters, it is highly desirable to attempt a projection of the likely future course of the Yellowstone population. Such projections are usually accomplished with the Leslie matrix model, but there are two difficulties in the present situation. One is that, in the Leslie model, reproduction is expressed as a fraction of females in 1 year that produce young that are fully independent in the next year. Young grizzlies normally do not become independent of the female until about age 2, whereas reproductive rates are recorded at about 6 months of age (i.e., when females emerge from winter dens with cubs). The second problem is that the small present population may be importantly influenced by chance events. We have thus devised a stochastic model of the female bear population, implemented in repeated computer simulations.

In the model, age-specific reproductive

and survival rates are incorporated as probabilities, so that each individual's fate is decided by independent, annual random draws from a uniform probability distribution. An initial population of independent females was assigned to elements of a two-dimensional array classified according to the individual's age and reproductive status (alone, with cubs, or with yearlings). Each individual then moves through the array by way of annual determinations of survivorship (including that of any accompanying young) and reproductive success. Rates determined in the 1973–82 study period were used in the simulation and were reported by Knight and Eberhardt (1985). Only females were considered (beyond recruitment to independent status, usually at age 2), in 26 age-classes. Starting with an initial population of 61 female bears age 2 and older in 1970, corresponding to data given by Craighead et al. (1974, Table 9), independent sets of 10,000 simulations each were run in periods of 5, 10, 15, 20, 25, and 30 years. The outcomes are depicted as histograms of population size (Fig. 1) to suggest a likely range of index population sizes in future years. Inasmuch as reproductive and survival rates no doubt actually vary from year to year, the range of model outcomes may be less than would be produced if actual annual rates were known. Conversely, in the absence of human influences, compensatory responses might possibly narrow the range of outcomes. Various other techniques relevant to the study were described in detail by Knight and Eberhardt (1985).

RESULTS AND DISCUSSION

Projections from the model suggest a continuing long-term decline in approximate accord with the trend of the female population index. Other questions have been studied with the model. For example, restoring litter size to the level observed before closure of the garbage dumps has about the same impact on population trend as increasing adult female survival by 2 percentage points or reducing adult female mortality by roughly one bear per year (Knight and Eberhardt 1985). We believe adult female mortality is the key issue in maintaining the grizzly bear population of Yellowstone National Park. In fact, the likely difference between earlier years, when the population was stable or possibly increasing, and the present situation may amount to an added mortality of one or two fully adult females per year.

Very likely the population before dump closures was somewhat larger than that used to initiate the simulations. Craighead et al. (1974) and a National Academy of Sciences committee (Natl. Acad. Sci. 1974) estimated an average total population on the order of 230 bears. An estimate of about 300 bears appeared in subsequent correspondence and is cited by McCullough (1981) and Cole (1976), but unfortunately has never been documented to our knowledge. The average observed composition data (Craighead et al. 1974, Table 1) gave 43.6% adults, whereas 53.7% of the adults observed in the field (Craighead et al. 1974:6) were females. One might thus suppose that there were about $230(0.436)(0.537) = 54$ adult females in the population. Records of "unduplicated" females with cubs kept during 9 years of the present study average 12 such individuals per year. Since the interval between litters is a little more than 3 years, we propose that a likely minimum recent number of adult females may be just under 40 bears.

Further analysis of the available data is needed in an effort to refine these estimates. However, the management implications seem reasonably clear whether one

Table 1. Recorded mortalities of adult female grizzly bears in Yellowstone National Park and environs. All mortalities listed here were confirmed by retrieval of a carcass, with the exception of three denoted as "probable," for which there was strong presumptive evidence of death.

Year	Age	Location	Cause of death
1983	12	Gardiner, Mont.	Control
	6 (cubs)	W. Yellowstone, Mont.	Control
1982	Adult	YNP[a]	Research
	Adult	SNF	Shot by black bear hunter
	16	Cooke City, Mont.	Control
	Adult (yearlings)	TNF	Shot by hunter
1981	25	YNP	Old age and malnutrition
	10–12	GNF	Charged bird hunter
	22	GNF	Shot
	9	GNF	Unknown
	Adult (cubs)	BTNF	Shot (probable)
1980	Adult (cubs)	GNF	Killed by hunter
1979	10	YNP	Research
	Adult	GNF	Charged hunter (probable)
1978	Adult	GNF	Road kill
1977	10–12 (cubs)	YNP	Road kill
	Adult (cubs)	BTNF	Killed by outfitter
	Adult (cubs)	SNF	Shot (probable)
	5	TNF	Shot from residence
	Adult (yearlings)	SNF	Livestock related (?)
	6–8 (cubs)	SNF	Poacher
1976	11 (cubs)	YNP	Control
1975	Adult	TNF	Control, sheep depredation
1974	16	YNP	Control
	6	SNF	Legal harvest
	8	SNF	Legal harvest
	Adult	BTNF	Unknown
1973	22	YNP	Road kill (?)
	6	GNF	Control
	7	SNF	Legal harvest
	19	SNF	Legal harvest

[a] YNP = Yellowstone National Park; BTNF = Bridger Teton National Forest; GNF = Gallatin National Forest; SNF = Shoshone National Forest; TNF = Targhee National Forest. "Yearlings" or "cubs" after age of bear indicates that bear was accompanied by yearlings or cubs at time of death.

assumes a population of 40 or 50 adult female bears. Present evidence (Fig. 1) indicates a continuing decline in numbers, with an annual mortality of prime-age adult females of about 8%, or three to four such bears each year. Our earlier simulations (Knight and Eberhardt 1985) suggested that reducing mortality of prime-age females to about 5%/year (two or three bears) might permit the population to stabilize. Consequently, the margin between continuing decline and population stability is not likely to be much more than one or two bears per year. We emphasize that this calculation pertains to total losses, which will exceed the recorded mortality. The record of the observed female mortality over the course of the present study (Table 1) thus supports the notion of a continuing decline.

Some calculations (Knight and Eberhardt 1985) suggest that roughly half of the actual mortalities may have been recorded in the 1959–70 period. During the course of the present study, 13 adult bears died with active radios. Five (38%) of these mortalities were located without use of the radio transmitter. Table 1 lists 31 mortalities in 11 years, or 2.82 recorded mortalities/year. If we assume an actual average population of 50 adult females and an annual mortality rate of 10% (based on a weighted average of estimated annual survival of all adult females as reported by Knight and Eberhardt [1985, Table 6]), then the fraction recorded is 2.82/5 = 0.56. If the recent populations average 40 adult females, then we have 70% reported (2.82/4). Undoubtedly the fraction recorded will vary substantially with cause of death and age of bear, and chance has a major influence on year-to-year fluctuations. Nonetheless, a useful guideline would appear to be that a record of an average loss of one or two adult females per year might suggest that the population could stabilize. The observed losses of four or more adult females per year (Table 1) clearly cannot be sustained. The difficulties in reducing losses can be appreciated from the diversity of causes of death recorded in Table 1.

We emphasize that the course of events described here is a projection and not a prediction. Forecasting future abundance requires assessment of any actions taken to reduce interactions between man and grizzlies, along with the prospects of increased human activities in occupied habitats. Possibly a decreasing population would eventually be stabilized through a "refuge" effect due to the sizable protected area that is occupied by grizzlies. The uncertainty here lies in the very large areas used annually by individual bears, as demonstrated by radiotelemetry data, combined with the fact that the occupied area contains various corridors and enclaves of existing and increasing prospects of man-bear interactions. Inherent regulatory ("density-dependent") mechanisms within the population might also be expected to influence trends. We believe that dispersal of subadult bears is a key feature in this process, again leading to the need to evaluate the "refuge" issue. Our telemetry data suggest that the dispersal process largely amounts to extensive, random wanderings over long time intervals. Unfortunately, the areas unoccupied by other bears that also have good food supplies often turn out to be occupied by humans.

Acknowledgments.—This research was supported by the Natl. Park Serv., U.S. Fish and Wildl. Serv., U.S. For. Serv., Wyo. Game and Fish Dep., Mont. Dep. of Fish, Wildl., and Parks, and Idaho Dep. of Fish and Game. Participation of the junior author was supported by U.S. Dep. of Energy Contract DE-ACO6-76RLO-1830.

LITERATURE CITED

COLE, G. F. 1974. Management involving grizzly bears and humans in Yellowstone National Park, 1970–73. BioScience 24:335–338.

———. 1976. Management involving grizzly and black bears in Yellowstone National Park 1970–75. Natl. Resour. Rep. 9, Natl. Park Serv. 26pp.

CRAIGHEAD, J. J., F. C. CRAIGHEAD, JR., AND J. SUMNER. 1976. Reproductive cycles and rates in the grizzly bear, *Ursus arctos horribilis*, of the Yellowstone ecosystem. Pages 337–356 *in* M. R. Pelton, J. W. Lentfer, and G. E. Folk, Jr., eds. Bears—their biology and management. Int. Union Conserv. Nat. Publ. New Ser. 40, Morges, Switzerland.

———, J. R. VARNEY, AND F. C. CRAIGHEAD, JR. 1974. A population analysis of the Yellowstone grizzly bears. Montana For. Conserv. Exp. Stn. Bull. 40, Univ. Montana, Missoula. 20pp.

KNIGHT, R. R., AND L. L. EBERHARDT. 1985. Population dynamics of Yellowstone grizzly bears. Ecology 66:In Press.

MCCULLOUGH, D. R. 1981. Population dynamics of the Yellowstone grizzly bear. Pages 173–196 *in* C. W. Fowler and T. D. Smith, eds. Dynamics of large mammal populations. John Wiley & Sons, New York, N.Y.

NATIONAL ACADEMY OF SCIENCES. 1974. Report of committee on the Yellowstone grizzlies. Natl. Acad. Sci., Washington, D.C. 61pp.

Received 17 April 1984.
Accepted 8 June 1984.