POPULATION DYNAMICS AND DENNING ECOLOGY OF BLACK BEARS IN SHENANDOAH NATIONAL PARK, VIRGINIA

by

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Thesis submitted to the Faculty of the

Virginia Polytechnic Institute and State University

in partial fulfillment of the requirements for the degree

of

MASTER OF SCIENCE

in

Fisheries and Wildlife Sciences

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December, 1985
Blacksburg, Virginia

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(ABSTRACT)

During 1982-85, population dynamics and denning ecology of black bears (Ursus americanus) were investigated in Shenandoah National Park, Virginia. Foot snares and culvert traps were used to capture 115 bears a total of 149 times. Radio transmitter collars were fitted to 47 bears. The age structure of the bears captured was indicative of an exploited population. The minimum breeding age of females was 2 years, but 3 years was the modal age. Mean litter size determined by cub counts was 2.0 and females usually bred every second year. Annual mortality rates were estimated at 30% for cubs, 54% for yearlings, 39% for 2-year olds, and 21.5% for older bears. Radio collared adult males had an annual mortality rate of 41.5%, over 5-fold that of adult females (7.5%). Bear density was estimated at 1 bear/0.96-1.49 km^2. This high

density was explained in part by the difference in male and female mortality rates. The estimated rate of population increase indicated that the population was stable.

The most common den types were rock cavities (29 of 61) and above-ground tree cavities (19 of 61). Males did not den in tree cavities. Den sites were not selected for forest type, aspect, or elevation, but ground slope was greater at den sites ($P < 0.001$) than at random points. Among- and within-year differences in dates of den entry, den emergence, and parturition were unrelated to weather and hard mast production.

ACKNOWLEDGEMENTS

I would like to thank the members of my graduate committee, Drs. M. R. Vaughan, chairman, G. H. Cross, R. L. Kirkpatrick, and P. F. Scanlon for their advice and support throughout this study. I also thank Drs. D. F. Stauffer for help with computer analysis and population estimation and K. H. Pollock. for advice on population estimation techniques. I thank Nathan Garner, my fellow "bear-guy," for his friendship, assistance, and muscles throughout this study, and technicians Dave Horning, Jim Stuart, and Alison Teetor.

I thank the National Park Service, Virginia Commission of Game and Inland Fisheries, and Virginia Cooperative Wildlife Research Unit for financial support. Appreciation for a variety of help in the field goes to all the rangers and employees of Shenandoah National Park, especially Mike Hill, Pat Quinn, John Chew, Rob Yates, Clint Runyon, Dick Batman, and Dave Haskel. Thanks also goes to Jerry Blank for his help with trapping. I appreciate the cooperation of the Massanutten Hunting Club, especially Arnold Dean, in saving the reproductive organs from bears they killed.

I thank my family for their support throughout my schooling.

TABLE OF CONTENTS

GENERAL INTRODUCTION

Increases in black bear-human interactions in Shenandoah National Park, an increase in bear damage on farms adjacent to the Park, and an increase in the hunter harvest of bears, mostly around the Park, prompted the National Park Service and the Virginia Commission of Game and Inland Fisheries to fund research on the black bear population in Shenandoah National Park. In 1982, Virginia Cooperative Wildlife Research Unit personnel initiated an investigation of the population dynamics, density, denning ecology, seasonal food habits, and home range size of black bears in the Park. This thesis reports part of the results of that study. The results are reported in 3 papers. The first reports the population dynamics and estimates on the size of the bear population. The second paper describes the denning habits of bears in the Park. The third paper discusses efforts to introduce abandoned cubs to foster mothers in the wild.

POPULATION DYNAMICS OF BLACK BEARS IN SHENANDOAH NATIONAL PARK, VIRGINIA

When Shenandoah National Park (SNP) was established in 1936, the black bear population was low and sightings were rare. Since then, the population has increased dramatically in response to habitat improvement and protection from hunting within the Park. As bear numbers increased there was a concomitant rise in bear-human interactions within the Park and an increase in bear damage on farmland adjacent to the Park. In 1976, the Park implemented a bear management plan with objectives of (1) restoring and maintaining the natural integrity, distribution, and behavior of the bear population (sic), (2) minimizing nuisance bear conflicts, and (3) providing the opportunity for visitors to see bears. Elements of the program included controlling unnatural food sources in the Park, removal of problem bears, public education, and research. By 1981 the plan was judged successful and the objectives fulfilled. Since then, the number of backcountry bear incidents (i.e. bears robbing food from campers) and property damage complaints from private landowners near the Park have increased (Haskell 1982).

During the 1981 bear hunting season 432 black bears were legally harvested in Virginia. This represented an 86% increase over the 1980 harvest of 232 bears. The mean annual bear harvest from 1981 to 1984 was 399 bears, 77% greater than the mean annual harvest of 225 bears during the 8 previous years. In addition, about 47% of the state harvest consistently occurs in the 8 counties surrounding SNP (Virginia Commission of Game and Inland Fisheries 1984).

The apparent contribution of SNP to the Virginia bear population underscores the significance of the Park as a reservoir for black bear reproduction. The current SNP bear management plan calls for the maintenance of a healthy, viable bear population at levels which result in a minimum of bear-human conflicts. Thus, it is particularly relevant to Park managers and the Virginia Commission of Game and Inland Fisheries (VCGIF) to understand the dynamics of the SNP black bear population. In 1982, Virginia Cooperative Wildlife Research Unit personnel initiated a study to estimate density and determine the population dynamics of black bears in the Park. This paper reports the results of that study.

N. P. Garner, J. Stuart, A. Teetor, J. R. Rohlman, J. Blank, and a long list of SNP employees assisted with field work. D. F. Stauffer and K. H. Pollock advised on population estimation procedures.

STUDY AREA

The 777 km^2 Shenandoah National Park (SNP) is a narrow, irregular shaped strip of rugged terrain that runs in a southwest-northeast direction along the Blue Ridge mountains between Front Royal and Waynesboro in north central Virginia (38° 00' N, 79° 00' W)(Fig. 1). Its entire length is bisected by the 203 km Skyline Drive. The Park is divided into 3 districts, each containing numerous campgrounds, picnic areas, scenic overlooks, and foot trails, including a section of the Appalachian Trail.

This study was restricted to the 298 km^2 central district of the Park and included about 28 km^2 of VCGIF wildlife management land that was similar to and nearly surrounded by Park land (Fig. 2). Hunting is illegal on Park land but permitted on the VCGIF land. The study area

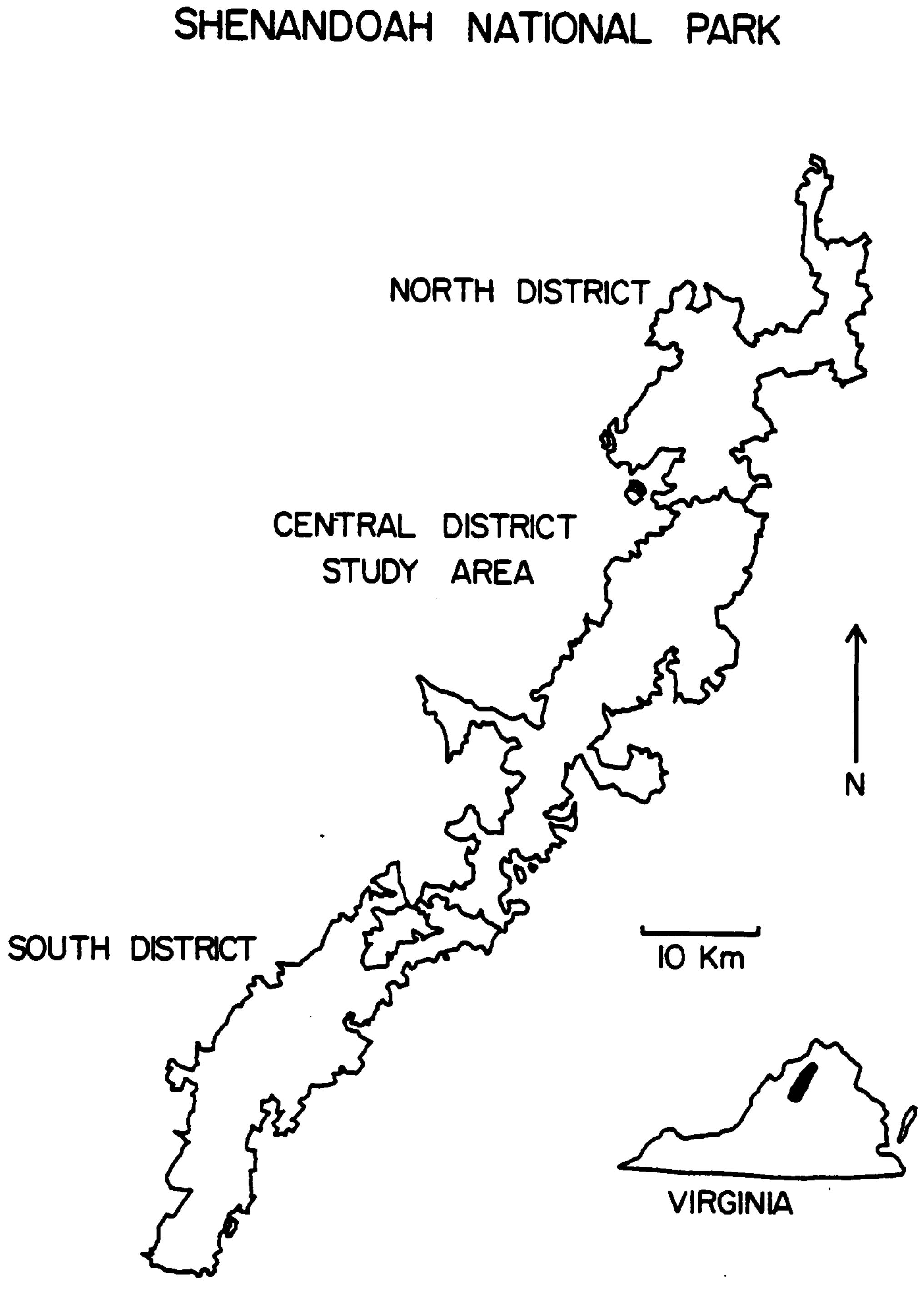

Fig. 1. Shenandoah National Park study area.

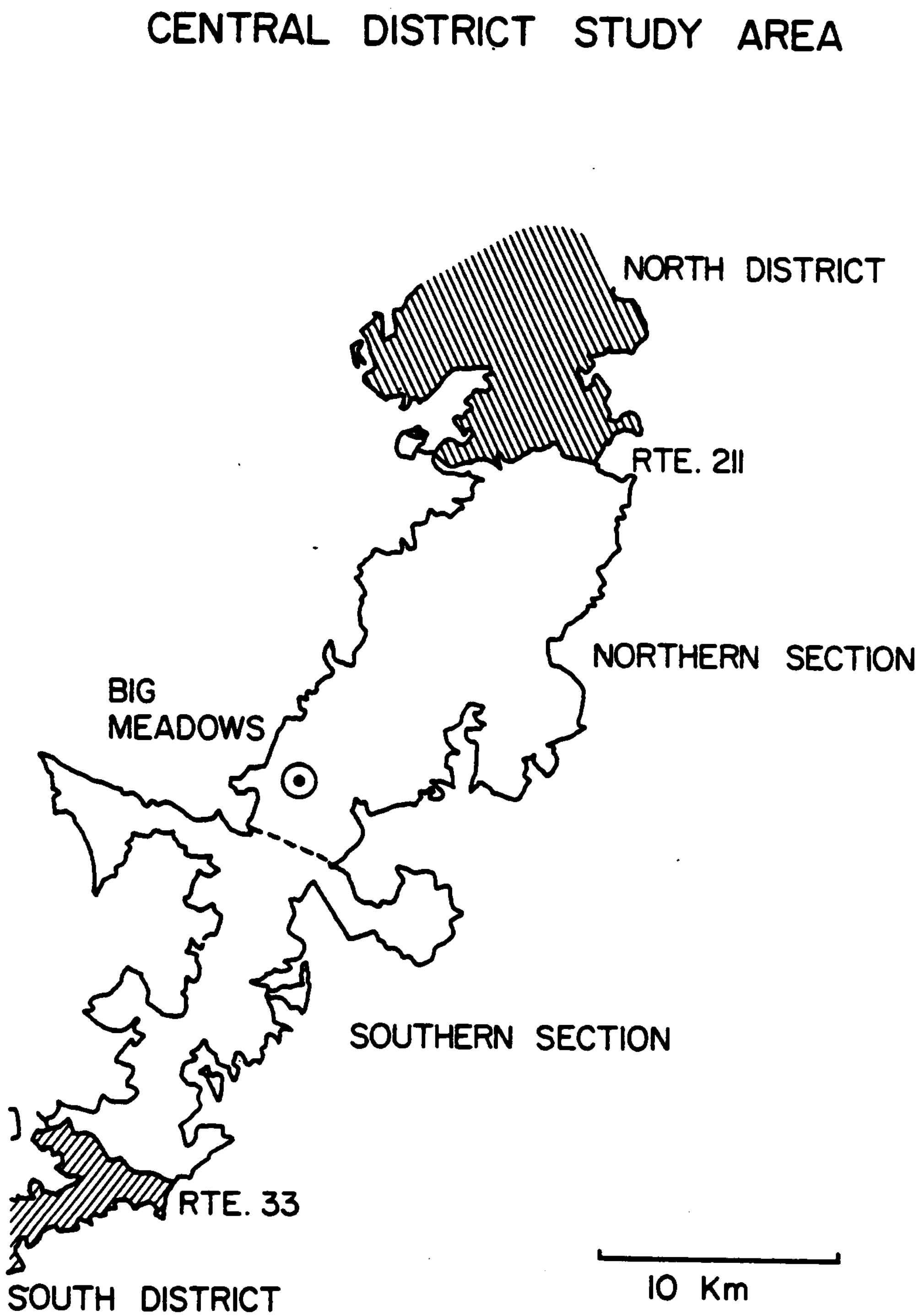

Fig. 2. Northern and southern trapping sections of the study area, Shenandoah National Park, Virginia, 1982-85.

ranges from 3.2 km to 21.0 km wide and is 40 km long. Elevations range from 274 m to 1234 m.

Major geologic types include the Catoctin and Swift Run volcanic formations, the Old Rag granitic formation, and the Pedlar sedimentary formation (Gathright 1976). Mixed hardwood forests, including chestnut oak (Quercus prinus), red oak (Q. rubra) and tulip poplar (Liriodendron tulipifera) dominate the area.

Precipitation in the high elevations of the Park averages 15-20% greater and the temperature about 10 C cooler than in the surrounding lowlands (Heatwole 1978). Mean January and July temperatures on top of the Blue Ridge are -2.6 C and 19.1 C, respectively. Average annual precipitation is 129.5 cm of rain plus 122 cm of snow.

METHODS

I divided the study area into 2 sections for trapping (Fig. 2). Trapping was concentrated in the 176 km^2 northern section from mid-April to mid-July, 1982, and in the 150 km^2 southern section during the same time period in 1983. I also trapped in the northern section during May-July, 1983 and October-November 1982 and 1983. I used Aldrich foot snares and to a lesser extent culvert traps.

Bears with estimated body weight over 254 kg were immobilized with freeze dried Ketaset (ketamine hydrochloride), redissolved at 200 mg/ml in Rompun (100 mg xylazine/ml) for a total concentration of 200 mg ketamine hydrochloride + 100 mg xylazine/ml. Dosage rate of the 2:1 mixture was 6-11 mg of the combined drugs/kg of body weight. Smaller bears were immobilized with the same drug ratios but in 100 mg/ml solutions. Each bear was tagged with 2 individually numbered ear tags (Allflex Tag Co., Culver City, California) and tattooed inside the lip with the same number. I recorded physical measurements and extracted a premolar for age determination (Willey 1974). Since I desired information on reproductive rates, I fitted radio transmitter collars (Telonics, Mesa, Arizona) to almost all adult females that I captured but only a small percentage of the captured males. I located bears from fixed-wing aircraft and by triangulation from the ground. Bear movements and home ranges were analyzed with program Telem (Koeln 1980) and the results compiled by Garner and Vaughan (unpubl. manuscript).

I used program Capture (Otis et al. 1978), a capture-recapture model designed to estimate the size of closed populations, to estimate bear numbers within each 2-3 month trapping period. I also analyzed the capture data from the northern section with program JOLLY (Hacker 1979), which simulates the Jolly-Seber method of population estimation (Seber 1973). For JOLLY analysis, I treated each 2-3 month trapping period as an individual trapping interval and ignored recaptures within an interval.

To determine litter size, I immobilized radio-instrumented females in their dens and tagged, weighed, and recorded the sex of each cub. if immobilization in the den was impractical, as in the case of tree dens, I attempted to observe the family group immediately after den emergence. Reproductive organs were collected from hunter- and road-killed females and examined for corpora lutea and placental scars.

I used survival of radio-marked bears to calculate maximum and minimum survival rates (Trent and Rongstad 1974). Maximum survival estimates considered as mortalities only those bears that were confirmed dead. Minimum survival estimates included as mortalities those bears confirmed dead plus those whose signals were lost due to unknown causes.

Statistical Analysis Systems (SAS Institute Inc. 1982) was used to analyze capture frequencies by age class and sex. I tested for differences in capture probabilities between sexes and age classes with the *z*-test for comparing binomial proportions. Differences in age between sexes were determined with the Wilcoxon rank sum test. I used the Spearman Correlation Coefficient to test for relationships between age and litter size.

RESULTS

Sex and Age Structure

During April 1982-November 1983 I captured 115 bears a total of 149 times (Table 1). Of these 149 captures, 114 (76.5%) were captured with snares. The overall sex ratio of first-time captures was 2.03M:1F. For adults (≥3 years), the ratio (1.3M:1F, N = 64), was not different from 1:1 (P = 0.32), but for subadults (1-2 years), the ratio favored males (3.8M:1F, N = 48, P = 0.001). Sex ratios of snared bears vs. those captured in culvert traps were not different for adults (30M:23F vs 6M:5F, P = 0.897) or subadults (30M:9F vs. 8M:1F, P = 0.424). Only

Table 1. Bear captures in the Central District of Shenandoah National Park, Virginia, 1982-83.

		Times Captured			
Sex	Ageclass	1	2	3	Total
Males	Adult[1]	36	11	4	51
	Subadult[2]	38	12	4	54
	Cub[3]	3	0	0	3
Female	Adult	28	2	0	30
	Subadult	10	1	0	11
	cub	0	0	0	0
Total		115	26	8	149

[1] ≥3 Years

[2] 1-2 Years

[3] <1 Year

3 cubs, all males, were captured in traps. Males dominated the sex ratio of recaptures in both adult and subadult age classes (15M:2F and 16M:1F, respectively). The sex ratio of cubs in dens was not different than 1:1 (0.85M:1F, N = 24, P = 0.68).

Adult males were recaptured more often than adult females (P = 0.016), but the same was not true for subadults (P = 0.159). I found no differences in recapture frequencies among age classes for males or females (P > 0.25).

Ages of captured bears ranged from 9 months to 14 years ($\bar{x}$ = 3.5, SE = 0.27, N = 112)(Fig. 3). Females were older than males ($\bar{x}$ = 5.1, SE = 0.61, N = 36 and $\bar{x}$ = 3.2, SE = 0.36, N = 76, respectively, P = 0.003).

Reproduction

Reproductive organs from 8 females were examined for corpora lutea and placental scars. Two 1-year olds had not ovulated, three 2-year olds each had 2 corpora lutea, two 3-year olds each had 2 corpora lutea, and an 8-year old had 3 corpora lutea (Table 2). Thus, the mean litter size determined by corpora lutea counts, excluding the 2

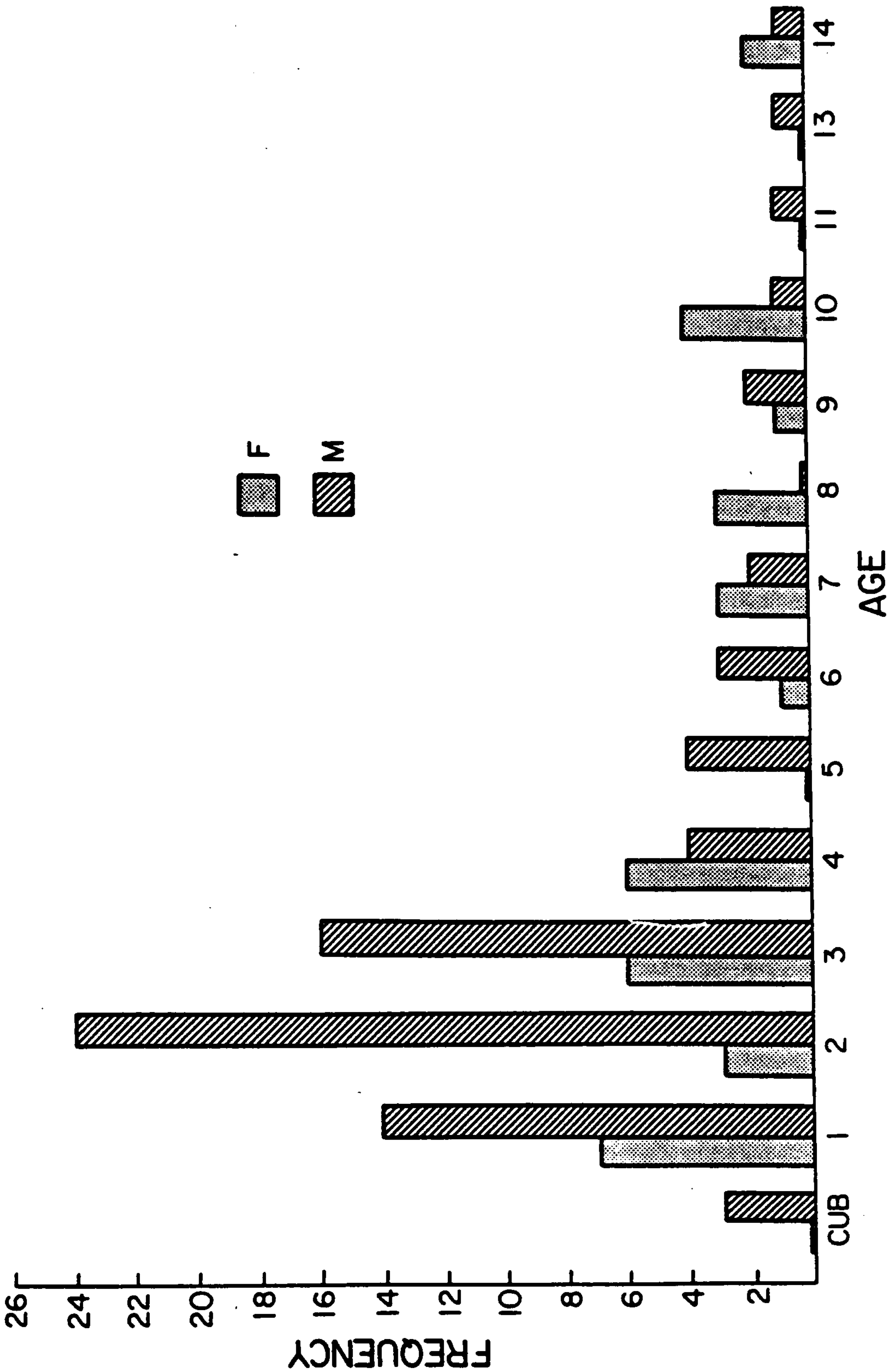

Fig. 3. Age frequencies of black bears captured in Shenandoah National Park, Virginia, 1982-85.

Table 2. Litter size of black bears in Shenandoah National Park, Virginia, 1982-85.

	Mean Litter Size Determined by			
	Corpora lutea		Cub observations	
Age	$\bar{x}$	N	$\bar{x}$	N
3	2.0	3	-	-
4	2.0	2	1.7	3
5	-	-	2.0	5
6	-	-	2.3	3
7	-	-	2.7	3
8	-	-	2.0	3
9	3.0	1	1.0	1
11	-	-	2.0	1
14	-	-	1.0	1
15	-	-	2.0	1
Total	2.17	6	2.0	21

1-year olds, was 2.17. No evidence of placental scars was found in any of the tracts.

Mean litter size, determined by observation in the den or immediately after den emergence, was 2.0 (N = 21, range = 1 to 3)(Table 2). Six litters contained only 1 cub, 9 litters contained 2 cubs, and 6 litters contained 3 cubs. Litter size was not related to the age of the mother (P = 0.232, N = 24).

The youngest observed age of breeding in SNP was 2 years. In addition to the evidence from reproductive tracts, one 3-year old female was captured in October with 2 cubs of the year. Six other females had cubs at 4 years of age, indicating that they had bred at 3. One 5-year old solitary female did not give birth when she was 6 and 7 years old. Generally, females gave birth every second year (N = 16) unless they lost their entire litters during the summer, in which case they gave birth in consecutive years (N = 7).

Cub Mortality

Fourteen family groups were successfully monitored for more than one year. Four of the 14 (28.6%) lost their entire litters and 2 (14.3%) lost 1 of 3 cubs. In three cases females abandoned their cubs in the den after researchers disturbed them. As a result, 7 cubs were introduced to other mother bears before den emergence. Two cases of entire litter loss and both cases of partial litter loss occurred to females that had accepted orphaned cubs I had introduced to them. All of the losses occurred by mid-September. If the above 4 cases are ignored because of the possibility that the cub introductions reduced chances of litter survival, 3 (30%) of 10 litters failed to survive their first summer. Litter sizes of the failed litters were 1, 3, and an unknown number of cubs. The litters with 1 and an unknown number of cubs were first litters for the females, but the female with 3 cubs had successfully raised cubs earlier.

In addition to mortalities after den emergence, 2 cubs were found dead after their mothers had left the den site with the rest of the litter. Both cubs weighed over 5.0 kg, indicating that they had not died at birth. In both cases, the dens were located in above-ground tree cavities and the cubs were part of a first litter.

Adult Mortality

Forty-seven of 115 (40.9%) captured bears were fitted with radio collars. Twenty-one (19.1%), including 13 instrumented bears, were reported killed (Table 3). One adult female died in her den sometime after immobilization. I attributed her death to my work and did not include her in the mortality calculations. Known mortalities from tagged bears therefore indicate a mortality rate of 18.4% over 3 years, or 6.1% annual mortality.

Four of the 47 collared bears (3 males, 1 female) were captured as subadults. Two of the 4 were monitored after they became adults but the signals of 2 were lost while they were still subadults. Twenty-eight radio collared bears survived until the end of the study or until their collars fell off, 12 (10 males, 2 females) were killed, 3 (2 males, 1 female) disappeared, and 1 male was removed as a result of property damage complaints.

I monitored a total of 21,409 radio-days for the 44 adult bears (43 captured as adults plus 2 subadults that

Table 3. Causes of bear mortality in SNP, Virginia. 1982-1985.

Cause of Death	Radio collared Bears[1]	Tagged but not Collared	Total
Hunter Kill	5	9	14
Illegal Kill	5	0	5
Damage Complaint Kill	1	1	2
Total	11	10	21

[1] Used to calculate reported mortality rates.

attained adulthood less 1 research related mortality). The overall maximum and minimum annual survival rates were 81% and 76%, respectively. Maximum and minimum annual survival rates of males, calculated from 7139 (33.3%) radio-days, were 60% and 57%, respectively. Female annual survival rates were 90% and 95%, calculated from 14,270 (66.7%) radio-days.

Population Density

Program Capture did not reject the null hypothesis of population closure for any of the 2-3 month trapping periods. The model selection procedure of the program indicated that either the null or the Jackknife estimators were appropriate for the data. Population estimates with the program-selected estimators ranged from 30 to 196 for the northern section of the study area and 145 for the southern section (Table 4). The population estimate with program JOLLY for the northern section was 172 bears.

Table 4. Black bear population estimates (95% CI) in the Central District of Shenandoah National Park, Virginia, 1982-83.

Trapping Period	Program Capture Models[2] M(O)	M(H)	M(B)	M(T)	(BH)	Number of Individuals Captured
<u>Northern</u> <u>Section</u> (176 km^2)						
Apr-Jul 1982	196[1] (20--372)	194[1] (127--262)	65 (9--121)	38 (37--39)	65 (9--121)	38
Oct-Nov 1982	30[1] (7--53)	23 (14--32)	18 (4--32)	30 (8--52)	18 (4--32)	14
May-Jul 1983	123[1] (-31--278)	84 (46--122)	- -	124 (-32--281)	- -	22
Oct-Nov 1983	154[1] (-43--376)	99 (57--140)	49(-19--118)	153 (-36--343)	49 (-19--118)	26
<u>Southern</u> <u>Section</u> (154 km^2)						
Apr-Jul 1983	75 (29--121)	145[1] (92--198)	- -	72 (30--114)	- -	35

[1] Models selected by program Capture

[2] M(O) assumes equal capture probabilities.

M(H) allows heterogenous capture probabilities among individuals.

M(B) allows capture probabilities to vary due to behavioral changes among trapping periods.

M(T) allows capture probabilities to change with time.

M(BH) is a combination of M(B) and M(H).

DISCUSSION

Population Structure

Cub sex ratios usually do not differ from 1:1 (Jonkel and Cowan 1971, Alt 1982a, Wathen 1983). However, black bear studies in Montana (Jonkel and Cowan 1971), Alberta (Kemp 1972), Virginia (Raybourne 1976), Minnesota (Rogers 1976), Washington (Lindzey and Meslow 1977), Idaho (Beecham 1980), Pennsylvania (Alt 1982a), and the southern Appalachians (Carlock et al. 1983) all reported capturing more males. Males tend to have larger home ranges and travel more extensively than females and therefore are more likely to encounter a trap (Gilbert et al. 1978, Bunnell and Tait 1980). In SNP, males predominated among subadults but not adults. Trapping bias favoring young males and a more rapid depletion of males as a result of their greater vulnerability to hunting may in part explain this difference in capture frequency between ageclasses (Rogers 1976, Gilbert et al. 1978, Bunnell and Tait 1981).

The mean age of SNP bears (3.5 years) was lower than those reported for Yosemite National Park, California (Graber 1982) and the Great Smoky Mountains National Park (GSMNP), Tennessee (Carlock et al. 1983). The percentage of adults captured in SNP (54%) was lower than reported for sections of Idaho (71%, Beecham 1980) and Arizona (70.9%, LeCount 1982) that received little hunting pressure. Age composition of SNP bears was more similar to those reported in more heavily hunted sections of Idaho (53% adults, Beecham 1980), Maine (mean age = 3.4 years, Hugie 1982), Pennsylvania (mean age = 2.8 years, Lindzey et al. 1983), and North Carolina (mean age = 3.8, Carlock et al. 1983). Thus, the age ratio of bears in SNP is indicative of an exploited population.

Reproduction

Mean litter size (2.17 or 2.0) of females in SNP, based on corpora lutea counts and cub observations (Table 2), was smaller than those reported in Pennsylvania (2.9, Alt 1982a) and the GSMNP, Tennessee (2.6, Wathen 1983), larger than the mean litter size reported in Montana (1.7, Jonkel and Cowan 1971), but similar to most reported litter sizes that used the same methods to gather data (2.0, 2.2, Erickson and Nellor 1964, 1.9, Reynolds and Beecham 1980, 2.1, 2.2, Hugie 1982). Minimum breeding age has been reported as 2 years in Virginia (Raybourne 1976), Pennsylvania (Kordek and Lindzey 1980), Maine (Hugie

1982), and the southern Appalachians (Carlock et al. 1983). This low breeding age was common only in Pennsylvania and the southern Appalachians, where 38% and 65%, respectively, of 2 year old females had bred. The modal age of first breeding in SNP, 3 years, is commonly reported in the literature. All but 1 SNP female was known to have bred earlier than the minimum breeding age reported for Montana (6 years, Jonkel and Cowan 1971).

Except for the one female that never produced cubs during this study, all females bred at least every second year. In New York and Pennsylvania, black bears usually breed every second year and raise cubs in intervening years (Free and McCaffrey 1972, Alt 1982a). In comparison, many bears in Montana (Jonkel and Cowan 1971), Washington (Poelker and Hartwell 1973), Tennessee (Beeman 1975), Idaho (Beecham and Reynolds 1980), and Virginia (DuBrock 1980) breed every 3 or 4 years. As I found, bears that lose their cubs in spring or early summer often breed again that summer and produce cubs again the following year (Erickson and Nellor 1964, Rogers 1977, Alt 1982a, Carlock et al. 1983, LeCount 1983). I found no evidence of synchronous breeding in SNP, probably because of inconsistencies in minimum breeding age and breeding cycles (Free and McCaffrey 1972).

Mortality

Mortality estimates based only on radio-marked bears are more realistic than those including hunter returns of tagged bears because of unreliable information about illegal kills and dependence on hunter cooperation for tag returns (Table 3). The midpoint of the maximum and minimum calculated annual survival rates, 78.5%, is probably the most realistic estimate of adult survival (Mytton and Keith 1981). The complement, 21.5%, is the annual adult mortality rate. These are similar to mortality rates reported in Pennsylvania (22%, Alt 1982b), Michigan (19%, Erickson et al. 1964) and the GSMNP (22%, Beeman 1975), but higher than those reported in Montana (13%, Jonkel and Cowan 1971), and Washington (15-18%, Poelker and Hartwell 1973). DuBrock (1980) calculated an overall mortality rate of 22% for SNP bears. Raybourne (1976) reported an average first year mortality of 24% for bears tagged and released in SNP. These high mortality rates are probably indicative of an exploited population.

The most remarkable aspect of the mortality calculations is the difference between adult male and female mortality rates. The midpoint of the adult male survival rate was 58.5% (41.5% mortality). Adult female survival, on the other hand, was 92.5% (7.5% mortality). Several authors have noted that adult males have higher mortality rates than adult females (Rogers 1976, Gilbert et al. 1978, Bunnell and Tait 1980) but none indicated that the difference was so great. I believe the long, narrow shape of the Park combined with larger home ranges and more extensive movements of males resulted in the higher mortality rate for males than females. Garner and Vaughan (unpubl. manuscript) located instrumented male and female bears outside Park boundaries 36.8% and 13.1% of the time, respectively. While outside the Park they are likely more vulnerable to hunting, poaching, and removal resulting from damage complaints. Females' home ranges were generally small enough that they fell within Park boundaries, so they were not exposed to as much risk as males.

Direct estimation of subadult mortality rates was not possible because of the small sample size of radio-equipped subadults and poor reliability of hunter tag returns. Over 3 years, only 3 of 51 (5.9%) tagged subadults were reportedly killed by hunters. I constructed a composite life table with the capture data to estimate subadult mortality rates (Caughley 1977:90). Age frequencies were smoothed in order to meet life table requirements. Capture frequencies of cubs and 1-year olds, 3 and 21, respectively, were not included in the regression because these frequencies were probably lower than the actual proportion of cubs and yearlings in the population. For the life table, the frequency of 1-year olds was extrapolated from the smoothed age distribution curve. Captures of cubs were possibly low because of their mothers' influence, decreased mobility due to size, and difficulty in snare capture because of their foot size. On the other hand, the capture frequency of 2-year olds, 27, was probably higher than their presence in the population would indicate because of their increased vulnerability to trapping. My life table, therefore, possibly contained higher than actual numbers of yearlings and 2-year olds, which would result in a high mortality estimate for the young age classes. The life table indicated that mortality rates, or in this case disappearance rates, of 1- and 2-year olds was 0.54 and

0.39, respectively. This is likely a conservative estimate.

Other reported subadult mortality rates are generally similar to or lower than adult mortality rates in exploited populations (Erickson et al. 1964, Jonkel and Cowan 1971, Lindzey and Meslow 1980, Fraser et al. 1982). Low hunter-induced mortality of subadults might be expected in Virginia because of game regulations that prohibit the taking of bears weighing less than 45 kg (100 lbs) live weight or 34 kg (75 lbs) dressed weight. Mean weights of female and male subadults captured throughout the year in SNP were 30.3 kg (N = 13, SE = 2.7) and 47.3 kg (N = 40, SE = 3.5), respectively. Hunters are probably less likely to shoot at bears in those weight ranges. Those that do might be reluctant to report kills, fearing possible penalties.

In 2 cases, cub mortality estimates were based on observation of females in their den for 2 consecutive winters. This assumes that cubs separating from their mothers before denning in the fall do not survive. In these 2 cases, the assumption was probably true because the females had cubs again the following spring, but such an assumption is not always valid. I captured and tagged a female and her 2 male cubs in October, 1982. She denned alone that winter but at least one of her offspring survived the winter and was captured in June, 1983, in good physical condition. This apparently was a rare case, however, and probably only the relatively larger male cubs successfully separate from their mother in their first year. Most of our reported cub mortalities were from observations made in September or October and then verified during the winter. I believe that most cubs that separated from their mother before September probably did not survive.

I attribute the deaths of 2 cubs to the inexperience of first time mothers. They were found in dens after the mothers had left the area with their other cubs. Alt (1982a) reported a higher rate of cub mortality in litters produced by young mothers. He attributed it to inexperience or inability of younger mothers to nourish cubs.

Wathen (1983) reported a first year mortality rate of 37.5% for cubs in the Great Smoky Mountain National Park. He found that the cub mortality rate differed between years and attributed the difference to changes in the yield of mast crops. Rogers (1976) also believed that mortality among cubs and yearlings was nutrition-related because lightweight individuals were more likely to die. He attributed more than 90% of cub and yearling mortality to natural causes. Both authors indicated that the yield of the previous fall's mast crop determines the physical condition of the female when she enters the den. Rogers (1976, 1983) explained that the mother's physical condition affects her milk production and thus the survival of cubs.

Alt (1982a) observed cub mortality in 28% of Pennsylvania bear litters, mostly in first litters produced by females. He found that litters of 1 and 2 cubs had higher mortality rates than larger litters, in contrast to Rogers (1976), who found that mortality was higher in larger litters.

Population Size

Generating reliable population estimates for large carnivores like bears is difficult because they range over large, inaccessible areas, their populations are sparse, and they are difficult to capture (Johnson and Pelton 1980). Although the most desirable experimental designs for the application of capture-recapture population estimators such as programs Capture and JOLLY were not practical for this study, I believe that they are presently the most appropriate methods for analyzing our data.

General assumptions for the different models available with program Capture include (1) the population is closed, (2) animals do not lose their marks during the experiment, and (3) marks are correctly noted and recorded (Otis et al. 1978). Alt et al. (1985) concluded that the assumption of no tag loss was being violated in Pennsylvania, and that tag loss should be accounted for in Pennsylvania black bear population analyses. In our study, captured bears were always checked for lip tattoos whether they had ear tags or not. Although 1 ear tag was sometimes missing, every bear with a tattoo had at least 1 ear tag, and every bear with a tag still had a visible lip tattoo. Therefore I believe that the multiple marking techniques ensured minimal loss of marks and I encountered no problems with mark identification and recording. I assume that immigration or emigration was minimal during the 2-3 month trapping periods and had little or no effect on population estimates for each period. Program Capture estimators were designed to relax the assumption of equal catchability. The various models allow capture probabilities to vary as a result of time (M_T), behavioral response to trapping (M_B), individual animal heterogeneity (M_H), or a combination of behavioral response and heterogeneity (M_{BH}).

The Jolly-Seber method of population estimation, assumes (1) equal catchability of animals, (2) equal probability of survival between capture periods, (3) equal probability for captured animals to be returned to the population, (4) marks are permanent, and (5) samples are instantaneous (Seber 1973:196). My experiment violated assumptions of equal catchability and equal probability of survival between capture periods for reasons explained previously.

Trapping efforts in the northern section of the study area were divided into 4 periods over 2 years. Otis et al. (1978:78) indicated that experiments in which only 10 or 20 animals are captured do not provide enough information for reliable population estimation with program Capture. Since the October-November, 1982 trapping period resulted in only 14 individuals captured, population estimates with program Capture probably were unreliable for this period (Table 4). The estimates for

May-July and October-November, 1983 had lower 95% confidence level limits of -31 and -43, respectively. This indicates that capture probabilities were too low and the experiments failed (Otis et al. 1978:26). The April-July, 1982 trapping period resulted in the largest sample and probably yielded the most reliable population estimate for the northern section. Program Capture indicated that either the null or the Jackknife estimators were appropriate (Table 4). Otis et al. (1978:64) recommended the Jackknife estimator in such cases because it is robust to heterogeneity and will tend to do well even if a competing model is true. Therefore, I believe the estimate of 194 (95% CI = 127-262) is the most reliable. This results in a density of 1 bear/0.91 km^2 (95% CI= 1 bear/0.67-1.38 km^2) for the northern section of the study area.

The Jolly-Seber estimate over the 4 trapping periods in the northern section (172 bears) resulted in a density of 1 bear/1.02 km^2. This model assumes equal catchability between individuals, an invalid assumption for our data. Pollock (1982) explained that the Jolly-Seber estimate is expected to be lower than the Jackknife estimate if heterogeneity of capture probabilities is present in the population. It still falls well within the 95% confidence interval of the Jackknife estimate.

Trapping efforts and sample size in the southern section of the study area during April-July, 1983 were similar to those in the April-July, 1982 period in the northern section. The data best fit the Jackknife estimator of program Capture, which gave a population estimate of 145 (95% CI = 92-198) or 1 bear/1.03 km^2 (95% CI = 1 bear/0.76-1.63 km^2). Thus the mean overall density estimate for the study area is 1 bear/0.96 km^2 (95% CI = 1 bear/0.70-1.49 km^2). This is actually an estimate of the number of bears with home ranges overlapping the trapped area, rather than the number of bears within Park boundaries. Several collared bears spent most of their time outside of the study area. A more realistic estimate of bear numbers within the study area probably lies between the mean estimate and the lower 95% confidence level limit (219-339 bears or 1 bear/0.96-1.49 km^2).

This SNP estimate is higher than most black bear density estimates reported in the literature (Table 5). I attribute this high density to a combination of factors. First, the shape of the Park contributes to a much higher mortality rate for males than females. In effect, the

Table 5. Black bear densities reported in North America.

Density (km^2/bear)	Location	Reporter
0.96-1.49	SNP, Virginia	This Study
2.1	Council Area, Idaho	Beecham 1980
2.3	Lowell Area, Idaho	Beecham 1980
8.8	Michigan	Erickson et al. 1964
2.0	Arizona	LeCount 1980
3.89	Wisconsin	Kohn 1982
2.1-4.4	Montana	Jonkel and Cowan 1971
1.3	Central Idaho	Beecham 1983
2.6	Alberta	Kemp 1972
1.6	Alberta (1974-75)	Young and Ruff 1982
3.0	Arizona	LeCount 1982
0.67-0.89	Washington	Lindzey and Meslow 1977
0.32	Alaska	McIlroy 1972
4.55	Spectacle Pond, Maine	Hugie 1982
8.67	Staceyville, Maine	Hugie 1982
1.7-11.8	Great Smoky Mountain National Park, Tennessee	Carlock et al. 1983

male segment of the population was exploited but the female segment was relatively unexploited. This resulted in a low proportion of adult males in the population. Jonkel and Cowan (1971), Rogers (1976, 1983), and Bunnell and Tait (1981) suggested that adult male bears direct aggression toward subadult males, resulting in the eviction of the subadults or their voluntary evacuation from the area. If it can be assumed that adult males would normally regulate population numbers in this manner, a low proportion of adult males would result in a lower dispersal rate of subadults, a higher rate of ingress of subadults from other areas, and possibly higher survivability of cubs and subadults. Kemp (1976) and Young and Ruff (1982) described a situation in Alberta where adult males were removed from a stationary population, followed by a more than doubling of bear numbers. Kemp (1976) explained this increase as a result of the population being released from the regulating action of adult males.

I found no direct evidence of population regulation by adult males in this study. No evidence was found to indicate that litter loss of females was due to adult male cannibalism (Garner and Vaughan unpubl. manuscript). If the adult male segment of the population is unnaturally low I would not expect to find such evidence. I did find evidence that males have a higher mortality rate than females and that the adult population is composed of more females than males. The sex ratio of captured bears over 5 years old was 14F:11M. Given the higher vulnerability of males to trapping (Bunnell and Tait 1980) they probably made up an even smaller portion of the population.

I incorporated the estimated reproduction and mortality rates in a computer program designed to model the SNP bear population. A similar program designed to model bird populations was described by Grier (1979). The program calculates population growth rates by solving the equation $\sum l_x e^{-rx} m_x = 1$ for r, the instantaneous rate of increase. Iterations can be used to make the totals equal 1. The program described by Grier assumed a constant mortality rate for individuals over 1 year of age and that the birds died before reaching their physiological limits. The program I used was modified to allow different mortality rates in cubs, 1-year olds, 2-year olds, and adults, and the ability to set a maximum age at which bears reproduce. I used 4 as the age that most females first have cubs and 18 as the end of reproductive life.

Females were assumed to produce an average of 1 female offspring per litter. Since 30% of the litters failed in my study and females always had cubs again the following year, 65% of the females in the population were assumed to produce cubs in any year. Cub, yearling, and 2-year old annual mortality rates were 30%, 54%, and 39%, respectively, assuming that differential mortality did not occur between sexes of these age classes. I realize that my subadult mortality rates are based on life table analysis and possibly inaccurate. Nelson and Peek (1982) and Eberhardt (1985) found that subadult mortality rates do not have as great an effect on population increase as adult rates. I believe that my estimate of the adult female mortality rate, 7.5%, is based on enough data to be accurate. These estimates resulted in a rate of population increase (λ) of 1.00 for the SNP bear population, indicating that bear numbers are stable.

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DENNING ECOLOGY OF BLACK BEARS IN SHENANDOAH NATIONAL PARK, VIRGINIA

Telemetry studies have been used to obtain data on bear denning ecology since 1972 (Craighead and Craighead 1972). Researchers have described variations in black bear denning chronology or den selection in Michigan (Erickson et al. 1964), Montana (Jonkel and Cowan 1971), Washington (Lindzey and Meslow 1976), Pennsylvania (Alt et al. 1977), Alberta (Tietje and Ruff 1980), North Carolina (Hamilton and Marchinton 1980), the southern Appalachians (Pelton et al. 1980, Johnson and Pelton 1980, Eiler 1981, Wathen 1983), California (Graber 1982), Maine (Hugie 1982), Idaho (Beecham et al. 1983), Arizona (LeCount 1983), and New York (O'Pezio 1983).

During 1982-1985, I studied black bear denning ecology in Shenandoah National Park (SNP), which likely supports the highest density of black bears in Virginia (Raybourne 1976, DuBrock 1980). The SNP bear management plan calls for maintenance of a visitor use policy that will cause minimal disruption to the natural behavioral patterns of the bear population. My study was designed to provide information on den type use, den site selection, and seasonal behavior of SNP black bears so that Park managers can incorporate it in the implementation of the bear management plan. This paper summarizes the results of that study.

N. P. Garner, J. Stuart, A. Teetor, P. Quinn, M. Hill, J. Blank, and R. Batman assisted with field work. D. F. Stauffer advised on data analysis.

STUDY AREA

The 777 km^2 Shenandoah National Park is a narrow, irregular strip of rugged terrain that runs in a southwest-northeast direction along the Blue Ridge mountains, between Front Royal and Waynesboro in north central Virginia. Its entire length is bisected by the 203 km Skyline Drive. The Park is divided into 3 districts, each containing numerous campgrounds, picnic areas, scenic overlooks, and foot trails, including a section of the Appalachian Trail.

I restricted the study to the 298 km^2 central district of the Park (Figs. 1, 2). The study area ranges from 3.2 km to 21.0 km wide and is 40 km long. Elevations range from 274 m to 1234 m.

Major geologic types include the Catoctin and Swift Run volcanic formations, the Old Rag granitic formation, and the Pedlar sedimentary formation (Gathright 1976). Mixed hardwood forests, including chestnut oak (*Quercus prinus*), red oak (*Q. rubra*) and tulip poplar (*Liriodendron tulipifera*) dominate the area.

Precipitation in the high elevations of the Park averages 15-20% greater and the temperature about 10 C cooler than in the surrounding lowlands (Heatwole 1978). Mean January and July temperatures are -2.6 C and 19.1 C, respectively, on top of the Blue Ridge. Average annual precipitation is 129.5 cm of rain plus 122 cm of snow.

METHODS

Bears were trapped in Aldrich foot snares and culvert traps. Bears with estimated body weight over 254 kg were immobilized with freeze dried Ketaset (ketamine hydrochloride), redissolved at 200 mg/ml in Rompun (100 mg xylazine/ml) for a total concentration of 200 mg ketamine hydrochloride + 100 mg xylazine/ml. Dosage rate of the 2:1 mixture was 6-11 mg of the combined drugs/kg of body weight. Smaller bears were immobilized with the same drug ratios but in 100 mg/ml solutions. Selected individuals were fitted with radio transmitter collars (Telonics, Mesa, Arizona). Radio locations were obtained from fixed-wing aircraft and by triangulation from the ground. I attempted to get locations on each bear at least twice per week.

Dens were located by monitoring activity patterns and locations of instrumented bears. When locations repeatedly occurred at the same place and the activity pattern was low, the area was visited more closely to determine if the bear was denned. If the den was located in a place where disturbing the bear seemed likely, such as a brush thicket, the visit was postponed until later in the winter. Den entrance dates were calculated by averaging the last date that a bear was located away from a den site with the first date that the bear was located at the den site and inactive. If the two dates were more than 14 days apart the data were not used for calculations.

Presence of cubs was determined by listening at the den entrance for suckling or crying sounds (Alt 1978). Listening periods lasted at least 15 minutes and were attempted every 3-6 days from January-March. Parturition dates were calculated by averaging the last date that cubs were not heard with the first date that cubs were heard in the den. Den emergence dates were calculated by averaging the last location date at the den with the first location away from the den site. Wilcoxon rank-sum tests were used to determine differences in dates of den entry, parturition, and emergence among years, sexes, and in reproductive status.

I checked for den reuse by visiting all known dens from previous years during January or February each year. Weather data were collected at Big Meadows weather station, in the center of the study area, by Park personnel. Hard mast production data were collected with acorn traps throughout the Park by SNP personnel.

Dens were categorized as above ground tree dens or ground level dens. Den measurements, including entrance width, height, and shape, height of the chamber at the bed, length and width of the bed chamber, entrance aspect, and for tree dens, distance from the ground to the entrance, distance from the bed to the entrance, tree species and dbh were taken during the summer. Information recorded at each den site included aspect, elevation, ground slope, and forest type. Garner and Vaughan (unpubl. manuscript) described the forest types and their abundance in the study area. I tested the utilization of forest types for denning vs. abundance (Neu et al. 1974). I determined aspect abundance (Marcum and Loftsgaarden 1980) and compared it to aspects observed at den sites (Neu et al. 1974). Mean elevation and ground slope at den sites were compared with measurements recorded from stratified random transect points. The chi-square goodness-of-fit and Student's *t*-test were used to detect differences.

RESULTS

Den Site and Den Characteristics

I located and measured 61 dens. Fifty-six were occupied by instrumented bears and 5 were used by unmarked bears (Table 6).

Den chamber floor area of ground dens used by males ($\bar{x}$ = 2.68 m^2, SE = 1.25, N = 7) was not different (P = 0.99) from ground dens used by females ($\bar{x}$ = 2.69 m^2, SE = 0.05, N = 14), but the chamber floor area of tree dens used by females ($\bar{x}$ = 0.45 m^2, SE = 0.05, N = 14) was smaller ($P < 0.01$) than in ground dens used by females (Table 7). No males denned in trees. Ground den entrances were not

Table 6. Den types of black bears in Shenandoah National Park, Va., 1982-85.

Den type	Male		Female		Unknown		Total	
	N	%[1]	N	%	N	%	N	%
Rock cavity	7	11.5	21	34.4	1	1.6	29	47.5
Above ground tree cavity	0	0	17	27.9	2	3.3	19	31.1
Ground level tree cavity	0	0	2	3.3	1	1.6	3	4.9
Brushpile	1	1.6	0	0	0	0	1	1.6
Hollow log	0	0	1	1.6	0	0	1	1.6
Dead snag	0	0	2	3.3	0	0	2	3.3
Upturned root system	1	1.6	0	0	0	0	1	1.6
Open bed	1	1.6	2	3.3	1	1.6	4	6.6
Excavation	0	0	1	1.6	0	0	1	1.6
Total	10	16.4	46	75.4	5	8.2	61	100.0

[1] Indicates the percentage in that category based on a total of 61 dens.

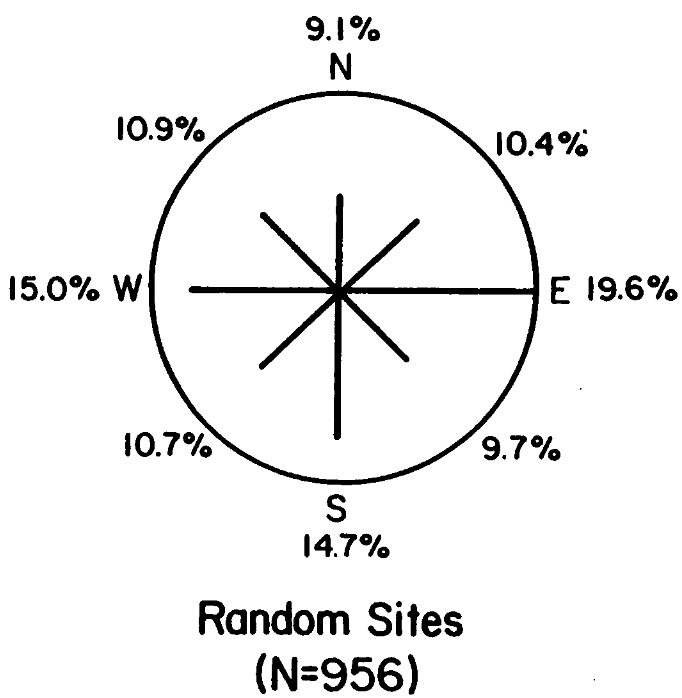
Table 7. Black bear den measurements in Shenandoah National Park, Virginia, 1982-85.

	Entrance length (cm)			Entrance width (cm)			Size of Chamber floor (m^2)			Distance from entr.- bed (m)			Ceiling ht at bed (cm)		
	$\bar{x}$	SE	N	$\bar{x}$	SE	N	$\bar{x}$	SE	N	$\bar{x}$	SE	N	$\bar{x}$	SE	N
Ground Dens															
Males	52.3	10.8	7	39.9	4.8	7	2.7	1.2	7	1.2	0.1	7	69	8.1	8
Females	57.3	6.9	25	70.7	12.3	25	2.7	0.1	14	1.6	0.2	24	65	4.6	23
Tree Dens															
Females	64.5	8.2	17	33.4	2.1	17	0.5	0.1	14	2.9	0.4	19	194	73	3

taller than tree den entrances ($\bar{x}$ = 54.6 cm, SE = 5.6, N = 34 and $\bar{x}$ = 63.6 cm, SE = 7.6, N = 18, respectively, P = 0.344), but they were wider ($\bar{x}$ = 63.4 cm, SE = 9.3, N = 34) than those in tree dens ($\bar{x}$ = 34.4 cm, SE = 2.0, N = 19) (P = 0.005).

I located 21 tree dens in northern red oak (61.9%), chestnut oak (28.6%), and tulip poplar (9.5%). Two additional tree dens were in dead snags which were broken off 4-6 m above the ground. The mean height of tree den entrances was 9.2 m (N = 19, range = 3.5 m - 23.8 m). The mean distance from the bottom of the den cavity to the entrance was 3.1 m (N = 19, range = 0.5 m - 7.0 m). Mean dbh was 94.6 cm (N = 17, range = 68.6 cm - 149.9 cm). The direction that den entrances faced was not different from random (x^2 = 4.97, df = 7, P > 0.10)(Fig. 4).

Mean elevation at den sites ($\bar{x}$ = 785.0 m, N = 61, SE = 18.7, range = 323.0 to 1073.0 m) was not different from random points ($\bar{x}$ = 761.6 m, N = 329, SE = 10.4, P > 0.10). I found no elevational differences between dens used by males vs. females or between tree vs. ground dens. (P > 0.10). Ground slope at den sites ($\bar{x}$ = 50.7%, N = 59, SE = 3.2%) was greater (P < 0.001) than ground slope at random points ($\bar{x}$ = 34.0%, N = 210, SE = 1.7%). In



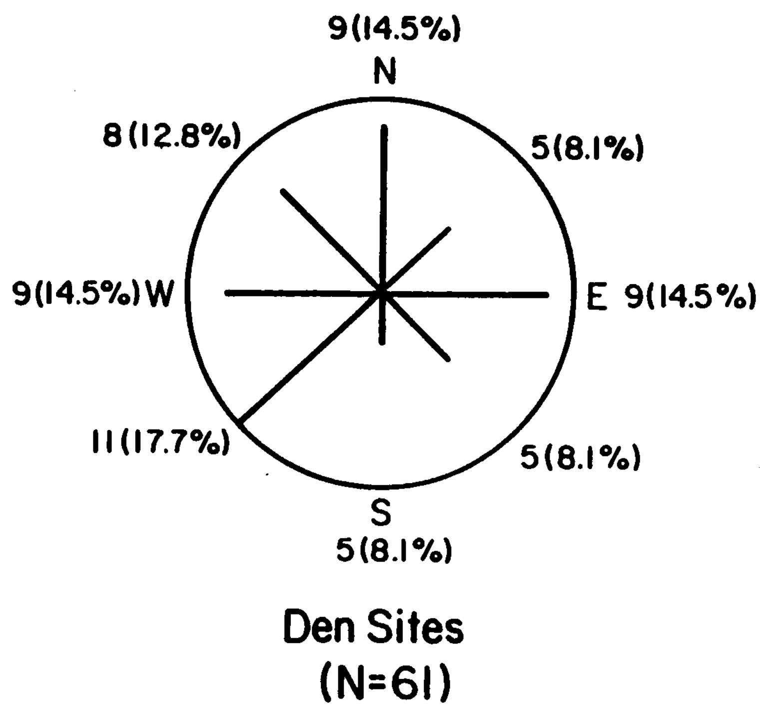


Fig. 4. Aspects at random points and at densites in Shenandoah National Park, Virginia, 1982-85.

addition, ground slope was greater ($P = 0.007$) at ground dens ($\bar{x} = 56.1\%$, $N = 39$, $SE = 4.3\%$) than at tree dens ($\bar{x} = 40.1\%$, $N = 20$, $SE = 3.4\%$). Aspects at den sites were not different ($P = 0.317$) from aspect abundance ($\chi^2 = 8.18$, $df = 7$)(Fig. 5).

Forest types were recorded at 53 den sites (Table 8). Hemlock, locust/cherry, and pine forest types were combined with rock and open areas for the chi-squared analysis because of low expected values. Overall, den occurrence in forest types was proportional to availability ($\chi^2 = 5.10$, $df = 4$, $P = 0.277$). However, dens occurred in the poplar forest type less than expected at the $\alpha = 0.10$ level but not the $\alpha = 0.05$ level.

Denning and Parturition Chronology

I recorded 4 cases in which bears did not den or hibernate for the winter. Two cases involved subadult males that were active throughout the winter. The other 2 cases were females accompanied by yearlings. In all 4 cases, the bears were never located in the same place for more than 2 weeks at a time.

Females entered dens earlier than males in 1983 ($P = 0.001$) and 1984 ($P = 0.064$)(Table 9). Den entry was not

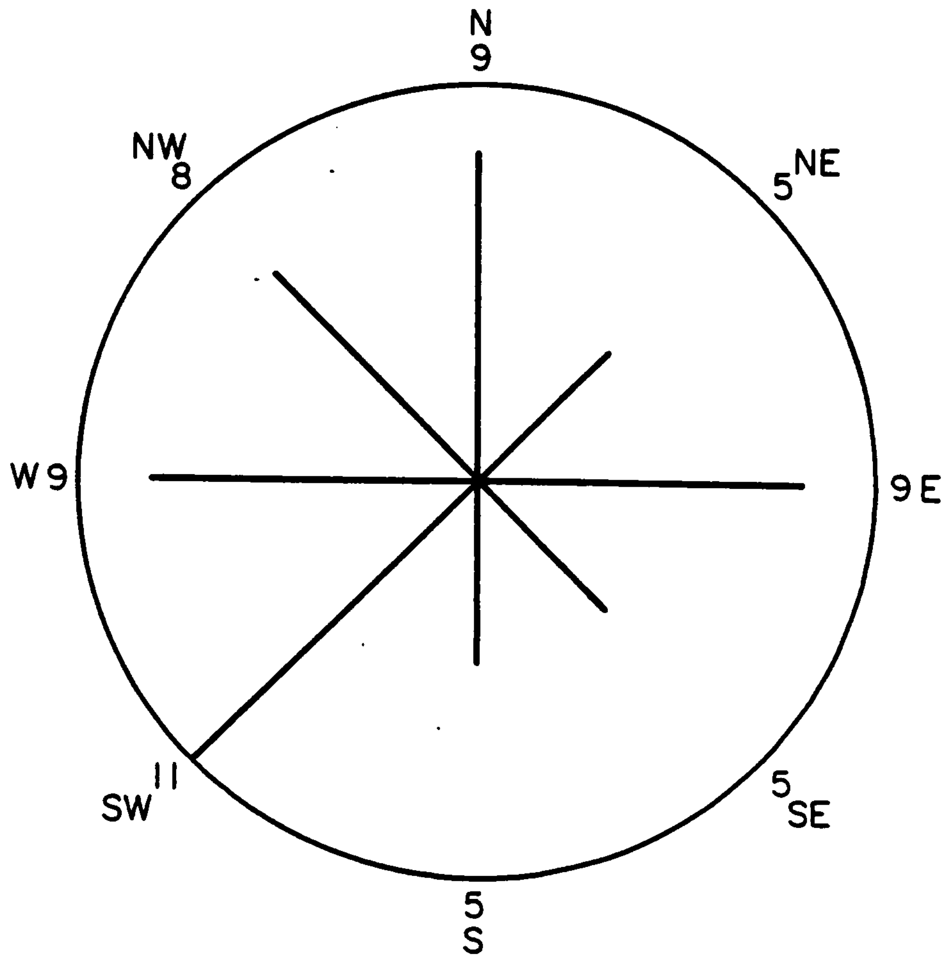


Fig. 5. Aspects of den entrances in Shenandoah National Park, Virginia, 1982-85

Table 8. Forest types used for denning by Black Bears in Shenandoah National Park, Virginia, 1982-1985.

	Amount of Use		Percent
Forest Type	N	%	Occurrance
Chestnut oak/Red oak	26	49.1	38.33
Red oak/White oak	9	17.0	16.46
Poplar	6	11.3	22.30
Red oak/Ash/Basswood	6	11.3	13.93
Pine	1	1.9	3.18
Locust/cherry	1	1.9	3.08
Hemlock	2	3.8	2.21
Rock	2	3.8	0.25
Open areas	0	0	0.26
Total	53	100.0	100.0

Table 9. Den entry, parturition, and emergence dates of black bears in Shenandoah National Park, Virginia, 1982-1985.

Class[1]		1982-83			1983-84			1984-85		
		N	$\bar{x}$	Range	N	$\bar{x}$	Range	N	$\bar{x}$	Range
Solitary Females	Entry	2	25 Nov	16 Nov-4 Dec	2	5 Dec	3-7 Dec	0	.	.
	Emerg.	2	25 Mar	15 Mar-4 Apr	2	12 Apr	11-14 Apr	0	.	.
	Period (days)	2	119	118-120	2	129	129	0	.	.
Females with cubs	Entry	5	22 Nov	7 Nov-6 Dec	15	10 Dec	15 Nov-3 Jan	6	22 Dec	6 Dec-3 Jan
	Part.	4	20 Jan	9-30 Jan	11	5 Feb	23 Jan-2 Mar	4	2 Feb	27 Jan-17 Feb
	Emerg.	5	15 Apr	29 Mar-30 Apr	13	21 Apr	13-29 Apr	4	19 Apr	13-28 Apr
	Period (days)	5	144	113-162	12	152	125-153	4	118	111-131
Females with Yearl.	Entry	1	8 Dec	.	3	13 Dec	3-26 Dec	0	.	.
	Emerg.	1	24 Mar	.	3	11 Apr	10-14 Apr	0	.	.
	Period (days)	0	.	.	3	120	110-129	0	.	.
Males	Entry	3	29 Nov	17 Nov-6 Dec	6	4 Jan	23 Dec-16 Jan	2	6 Jan	5-8 Jan
	Emerg.	5	28 Mar	17 Mar-25 Apr	3	13 Apr	11-15 Apr	1	25 Mar	.
	Period (days)	3	123	110-140	3	106	100-115	1	76	.

[1] Class at the end of the winter, i.e. a female with cubs emerged from her den with cubs.

different between reproductive classes of females within any year. Pregnant females dominated the sample of monitored bears each year. They entered dens later in 1984 than 1983 (P = 0.039) and later in 1983 than in 1982 (P = 0.011). Males also entered dens later in 1983 than in 1982 (P = 0.028), but no other between year differences were significant.

Dates of parturition ranged from 9 January to 2 March (Table 9). Mean dates of parturition were later in 1983-84 than in 1982-83 (P = 0.022). Dates of parturition were not affected by the age of the mother (P > 0.10) nor were they correlated with dates of den entry (r = 0.303, P = 0.194, N = 20).

Male den emergence earlier than that of females with cubs in 1983 (P = 0.094) and 1984 (P = 0.079). Females with cubs emerged later in 1984 than they did in 1983 (P = 0.008).

The average length of the denning period was 128 days. Females that gave birth denned longer in 1982-83 and 1983-84 than they did in 1984-85 (P = 0.086 and P = 0.013, respectively). In addition, females that gave birth denned longer than males in 1983-84 (P = 0.010) and possibly in 1982-83 (P = 0.101).

Only 2 cases of den reuse were observed in SNP, both with the same solitary female. This bear, a 5-year old in 1982, occupied at least 3 different dens during each winter she was monitored. During the winter of 1983-84 she was located for about 2 weeks in a rock cavity that she had used the previous winter. In March, 1985, she was observed in a different rock cavity that she had occupied for most of 1983-84.

DISCUSSION

Den Selection and Availability

All den types used in SNP have been reported in other areas. The most common types, rock cavities and tree cavities have been reported in Pennsylvania (Alt pers. comm.), Montana (Jonkel and Cowan 1971), Idaho (Beecham et al. 1983), and Tennessee (Wathen 1983).

Males in SNP did not den in trees but both sexes denned frequently in rock cavities (Table 6). Females did not show a preference for either den type. Most females (63.6%) monitored more than one winter used both den types. The use of tree dens may have been unique to females because of their small size relative to males (x

= 61.9 kg vs. x = 100.8 kg). Wathen (1983) reported a switch in the pattern of den use one year, from mostly tree dens to mostly ground dens. He speculated that an exceptionally good mast year resulted in heavier and larger females that could not use small tree dens. This would tend to support the hypothesis that body size may be a factor restricting the use of tree dens. Carlock et al. (1983) stated that females have a greater selection of dens from which to choose because they den earlier than males or subadults. Each year in SNP, tree dens were available that were not used, so availability was probably not a factor in den type selection.

Behavioral differences between males and females may also influence den type selection. During the summer and fall months, females were frequently observed foraging or loafing in trees but males were not. Local bear hunters indicated that, when pursued by dogs, females were much more prone to climbing trees than males.

Pelton et al. (1980) believed that the availability of tree dens could have been a factor limiting population growth and size in a Tennessee black bear population. Den availability is probably not a factor in SNP due to the wide variability in den types used and an abundance of potential dens. In several cases, bears that were disturbed during the winter went directly to another den, possibly indicating previous knowledge of the den. These moves occurred both from rock cavities to tree cavities and from tree cavities to rock cavities.

Low occurrence of den reuse is consistent with studies in Pennsylvania (Alt pers. comm.), Tennessee (Johnson 1981, Wathen 1983), Idaho (Beecham et al. 1983), and Arizona (LeCount 1983), where den availability was believed to be high, and Alberta, where most bears excavated dens (Tietje and Ruff 1980). In contrast, Lindsey and Meslow (1976) in Washington and Eiler (1981) in Tennessee reported frequent den reuse where den site availability was reduced by logging.

Neither elevation nor aspect appeared to be an important factor in den site selection in SNP. However, ground slope at den sites was steeper than at random points. Johnson and Pelton (1980) believed that ground dens were located on steeper slopes than tree dens because they were more vulnerable to disturbance than tree dens, and disturbance was less likely to occur on the steeper slopes. During my study, disturbance by humans did not appear to be an important factor in den site selection, at least for females. Six females, 3 of which successfully raised cubs, occupied ground dens within 30 m of heavily used foot trails. Only 1 of the 6, a barren female denned less than 10 m from a prominent overlook on the trail, left the den probably as a result of human disturbance. All of these dens were in areas where similar den types were plentiful farther away from the trail.

Although I have no quantitative data to show it, den abundance may be higher on steeper slopes. Effects of wind and water erosion would be more likely to create rock cavities on steep slopes than on gentle slopes. Tree dens also may be more abundant on steep slopes in SNP. Wathen (1983) reported that suitable den trees in the Great Smoky Mountains National Park were more abundant on steep slopes where they were less accessible to pre-Park logging.

Chronology

The 4 cases in which bears did not enter dens are similar to cases reported by other authors. Alt et al. (1977) in Pennsylvania, reported that females with yearlings were the only bears that sometimes did not enter dens. Hamilton and Marchinton (1980) in North Carolina and Smith (1983) in Arkansas presented evidence that some subadult males did not den. Hamilton and Marchinton (1980) concluded that fat reserves are sometimes not adequate on young bears to allow them to hibernate all winter.

In SNP, I found among- and within-year differences in den entry dates (Table 9). The stimuli that induce a bear to enter its den are unclear. Jonkel and Cowan (1971) reported that bears in Montana responded to heavy snowfall as a stimulus for den entry. Lindzey and Meslow (1976) concluded that bears in Washington, where weather is milder than in Montana, were stimulated to den by the cumulative effects of low temperatures and above average precipitation, but good physical condition was an ultimate prerequisite for denning. Johnson and Pelton (1980) reported that den entry was influenced by food availability and weather. They reported that den entry dates were associated with low pressure systems. Earlier den entry dates were reported in years of poor mast availability and mild weather than in years of good mast availability and harsh weather. However, Eiler (1981) found no relationship between food availability and den entry. In contrast to Johnson and Pelton (1980), Wathen

(1983) reported that weather was a poor predictor of den entrance or emergence dates, and that bears denned earlier in a good mast year than in a poor one. All of these authors worked in the same general area of the southern Appalachians.

Average den entry dates for all bears in SNP were later in 1983 than in 1982 but the difference was statistically significant only for pregnant females and males (Table 9). Lack of statistical significance for solitary females and females with yearlings was in part due to low sample sizes. In 1984, females with cubs denned later than in the 2 previous years. All bears denned earliest in the first year of the study, when hard mast production was lowest (Tables 9, 10, Fig. 6). During the second year of the study, the mast crop was excellent but bears denned later. Temperatures averaged 2°-3° cooler and about 25 cm more rain fell from September through December. In the third year of the study, the white oak group again failed to produce mast but the red oak group did well. Fall temperatures were slightly warmer than in the 2 previous years and precipitation was similar to the first year, but bears generally denned even

Table 10. Weather and acorn production[1] in Shenandoah National Park, Virginia, 1982-1984.

	1982	1983	1984
Mean max. daily temp.[2] (°C)	12.6	11.1	13.1
Mean min. daily temp. (°C)	2.6	0.9	3.4
Total rain (cm)	34.5	64.6	35.2
Total snow (cm)	34.3	27.8	8.9
Red oak group[3] production (gr/trap)	15	48	51
White oak group[4] prod. (gr/trap)	<1	45	<1
Average hard mast prod. (gr/trap)	8	46.5	26

[1] Data obtained from SNP records.

[2] Weather data reported from 1 September - 31 December only.

[3] Includes red oak, scarlet oak, and black oak.

[4] Includes white oak and chestnut oak.

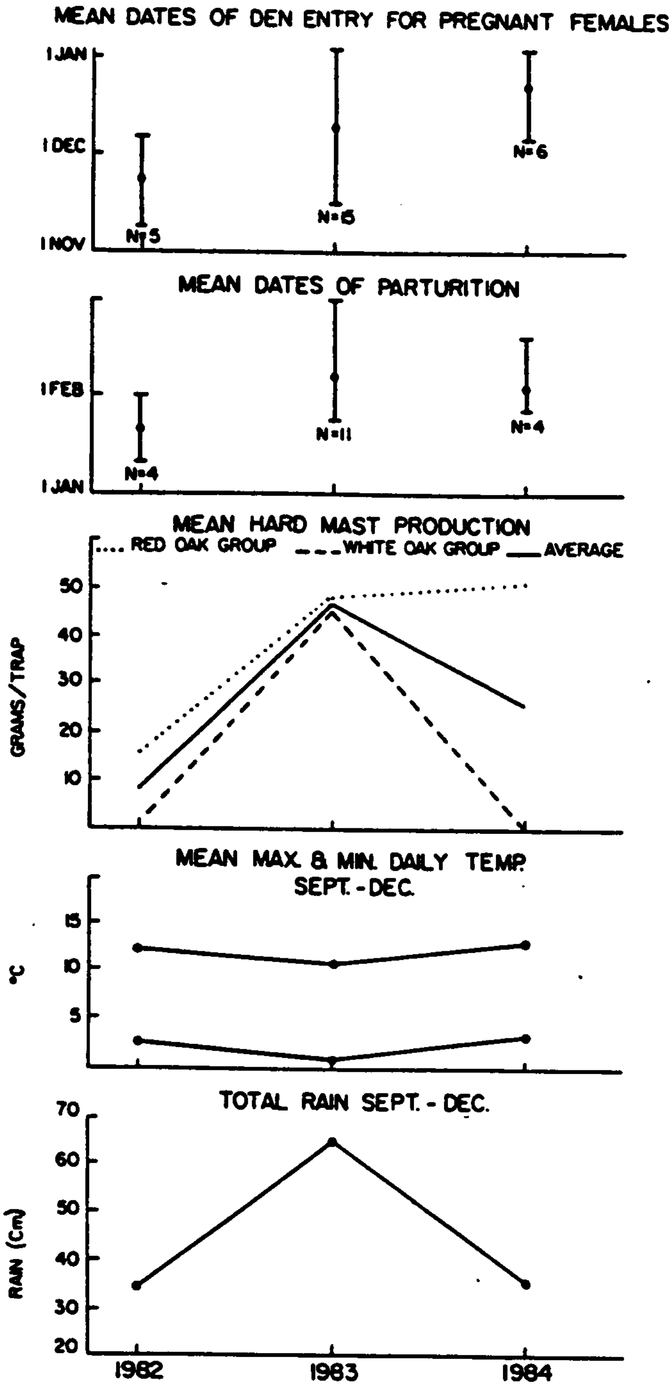


Fig. 6. Den entry and parturition dates, hard mast production, mean temperatures, and rainfall in the Central district of Shenandoah National Park, Virginia, 1982-85.

later. Timing of den entry seems to have been influenced by something other than fall weather and mast production.

Black bears exhibit delayed implantation. After mating occurs, the fertilized egg divides to form a blastocyst and remains unattached in the female's uterus until late fall or early winter. Then it attaches to the uterine wall and begins further development (Pelton and Burghardt 1976). Timing of den entry and parturition were not closely related in this study ($r = 0.303$). Parturition dates of bears in SNP were generally later and showed more variability than those reported by Alt (1983) in northeastern Pennsylvania. Alt (1980) reported that the diversity of Pennsylvania forests and food of human origin provided an abundant and dependable food source for bears on an annual basis. He attributed accelerated growth rates, early age breeding ($\bar{x}$ = 2.5 years) and large litter size ($\bar{x}$ = 2.9 cubs) of Pennsylvania bears to this abundant food supply. Food availability or habitat quality has been reported as an important factor influencing reproduction in other bear studies (Jonkel and Cowan 1971:49, Rogers 1976, Beecham 1980, Beeman and Pelton 1980). I believe that the high variability in parturition dates in SNP may be related to variability in food abundance. The greatest difference in timing of parturition occurred between years that were most different in mast production; 1982-83 and 1983-84 (Tables 9, 10, Fig. 6). When average mast production dropped again in the third year, parturition dates did not change much. It is unclear if food availability may have influenced timing of blastocyst implantation in the uterus, in turn influencing the date of parturition, or if food availability combined with other factors to influence timing of den entry, which, although not correlated in this study, may influence timing of parturition. More research is necessary to determine the relationships among and the factors that influence timing of den entry, blastocyst implantation, and parturition.

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SURVIVAL OF BLACK BEAR CUBS INTRODUCED TO FOSTER MOTHERS AND LITTER SUCCESS IN SHENANDOAH NATIONAL PARK, VIRGINIA

Introductions of orphaned or abandoned bear cubs (*Ursus* sp.) to foster mothers have been attempted in New York (Clarke et al. 1980), Maine (Hugie 1982), Minnesota, Idaho, and Pennsylvania (Alt and Beecham 1984). Successful adoptions were reported in most cases. Jonkel et al. (1980) and Alt and Beecham (1984) suggested that fostering cubs may be a viable management alternative for threatened or endangered bear species.

I conducted a radio-telemetry study on black bears in Shenandoah National Park (SNP), Virginia during 1982-1985. While attempting to immobilize females in their dens, I encountered several cases of females abandoning their cubs. In each case, I introduced the abandoned cubs to foster mothers. This paper reports the results of those introductions.

METHODS

I monitored radio-collared females after den visits or other activities that might disturb them in their dens. If they left the den area, monitoring was increased to a 24-hour basis. I chose monitoring points so they would not interfere with the mother bear if she tried to return to the den. Cubs were considered abandoned if the female made no attempt to return to the den site within 24 hours. Abandoned cubs were transported in a 0.30 m x 0.45 m milk crate lined with cloth bedding. Some cubs were marked with numbered metal (National Band and Tag Co., Newport, Kentucky 41072) or plastic (Allflex Tag Co., Culver City, California) ear tags. Potential foster mothers were chosen on the basis of age, cub-raising experience, and den type. Older bears and experienced mothers were chosen over young bears or females with their first litters. Only females that had cubs of their own were considered for introductions. I preferred tree dens with above-ground entrances for introduction because the occupant could not see the researcher approach, therefore den abandonment was less likely. When possible, I introduced cubs on the same day that they were picked up.

If they were kept overnight, I fed them a mixture of warm cow milk and raw eggs from a baby bottle, ad libitum.

I approached dens from a direction where I was not likely to be seen by the mother bear. Introduced cubs were dropped into the den entrance or, in the case of tree dens, on top of the mother bear. Introductions were considered successful if the mother was observed licking the cub after the introduction or if the cubs were observed with the mother bear after den emergence. I attempted to observe the family groups throughout the summer to determine if cub losses occurred. Dens of foster mothers were visited the winter following the introductions to confirm the number of yearlings with the mothers.

RESULTS

I introduced 7 cubs (6 females, 1 male) to 8 foster mothers. Two of the selected foster mothers had not successfully raised cubs previously. Only 1 (12.5%) introduced cub was known to be rejected. In that case, upon approaching a tree den of a first-time mother, I observed her running out of a ground bed that she had constructed near the tree, leaving her single natural cub at the bed. I placed the cub to be introduced with the mother's natural cub and left the area. Radio signals indicated that the mother returned to the den within 4 hours and left again. In the next 20 hours the mother moved farther from the den site and showed no signs of returning. I returned to the den site and found only the introduced cub. I later confirmed that the mother had taken her natural cub with her after she returned. The twice-abandoned cub was fed and successfully introduced to another foster mother in a tree den.

One introduced cub was never confirmed as accepted or rejected. The foster mother lost her radio collar in her tree den and was not observed after den emergence. There were no dead cubs or ear tags in the den after she left and I have no reason to suspect that the cub was not accepted. I successfully introduced 5 other abandoned cubs to foster mothers (3 tree dens, 2 ground dens). Four were observed with their family groups after den emergence. One family group was not observed after den emergence to confirm acceptance, but the mother was observed licking the introduced cub immediately after the introduction.

Three of the foster mothers that accepted cubs had 2 cubs of their own. Sightings of the family groups in August indicated that 2 (66.6%) had lost 1 of the 3 cubs in their litter. Den checks the following winter confirmed that only 1 had successfully raised the extra cub through the summer and denned with a larger litter than she produced. Two foster mothers with an unknown number of their own cubs lost their entire litter during the summer. The fate of the other 2 introduced cubs was never determined because their foster mothers lost their radio collars.

I monitored 10 natural family groups in addition to the family groups that contained introduced cubs. Three (30%) of the 10 litters did not survive their first summer. Size of the litters that failed were 1, 3, and an unknown number of cubs. The litters of 1 and an unknown number of cubs were first litters for the females, but the female that lost 3 cubs had successfully raised cubs before.

In addition to post-den emergence fatalities, 2 cubs were found dead in dens after their mothers had left the den area with the rest of their litter. In both cases the dens were in above-ground tree cavities and the cubs were part of a first litter.

DISCUSSION

Alt and Beecham (1984), using similar methods of cub introduction, reported a high rate of successful adoptions and at least 9 of 21 (42.9%) cubs survived >9 months after placement. My adoption rate was high (≥85.7%) but the verifiable survival rate of introduced cubs was low (20.0%). I could not determine the cause of mortality in any case. Since all but 1 of the mothers that accepted cubs had raised cubs before the introductions, I believe that inexperience was probably not a factor in most of the failures. Rogers (1976) documented lower cub survival in large litters in Minnesota. Both Rogers (1976) and Wathen (1983) related cub survival to nutritional condition of the mother. Alt and Beecham (1984) suggested that depletion of fat reserves of nursing mothers is an important consideration for cub introductions, especially in areas of poor quality habitat, characterized by low reproductive rates and slow growth rates.

Since the survival rate of introduced cubs was much lower than that observed in natural litters, I assume that most of the mortalities were probably related to the nutritional condition of the mothers. Partial litter loss did not occur in any of the natural family groups but single cubs were lost twice from family groups with introduced cubs. If a mother was not nutritionally capable of supplying enough milk for the extra cub, 1 cub rather than the entire litter might be weakened so that it was more vulnerable to disease or predation. An introduced cub may decrease the chances of survival for the entire litter. Two (33.3%) of the foster mothers lost their entire litters. However, this is not different than the rate of litter loss of natural family groups.

I attribute the deaths of the 2 cubs found in tree dens to inexperience of first-time mothers. Alt (1982) reported a higher rate of cub mortality in litters produced by young mothers. He attributed it to inexperience or inability of younger mothers to nourish cubs.

In conclusion, I do not recommend introduction of cubs to foster mothers in marginal or poor quality habitat. The low success rate does not justify the possibility of reducing survival of the mother's natural cubs. Other techniques of reintroducing cubs into the wild described by Alt and Beecham (1984) and Jonkel et al. (1980) such as feeding them through the summer and then releasing them or introducing them to females with cubs after den emergence, might be more successful.

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