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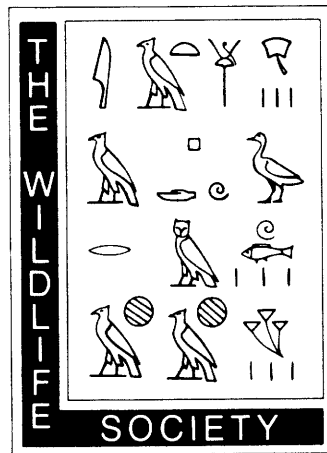
THE WILDLIFE SOCIETY

INTERRELATIONSHIP OF BLACK BEARS TO MOOSE AND FOREST SUCCESSION IN THE NORTHERN CONIFEROUS FOREST

by

CHARLES C. SCHWARTZ AND ALBERT W. FRANZMANN

FRONTISPIECE. Black bear cub in the spring. Up to 3 generations of bears were followed during the course of the study. (Photo by Charles C. Schwartz)

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Abstract: We compared characteristics of 2 black bear (*Ursus americanus*) populations living in middle-aged (1947 burn area) and recent (1969 burn area) burned forest stands on the Kenai Peninsula, Alaska, during 1982–87. Densities of bears on the 1947 (205 bears/1,000 km²) and 1969 (265 bears/1,000 km²) burn areas were similar. Sex ratios of the 2 populations were not different ($P = 0.478$), but there were significantly more ($P = 0.007$) females than males in both areas. Age structures of the population were different ($P = 0.003$). There were more yearlings in the 1969 burn area due to higher cub production and survival.

Female bears in the 1947 burn bred at a later age ($P = 0.03$) (5.8 yrs) than females in the 1969 burn (4.6 yrs). Females in the 1947 burn also had a longer interval between successful weaning of yearlings ($P = 0.03$) (2.4 yrs) than females in the 1969 burn (2.0 yrs). Weights of adult females and yearlings in the 1947 burn area were significantly less ($P < 0.001$) than those in the 1969 burn area.

Food habits and food abundance in the 2 areas were similar except that bears in the 1947 burn area consumed more lowbush cranberry (*Vaccinium vitis-idaea*) and bears in the 1969 burn area consumed approximately 4 times more moose calves (*Alces alces*) per individual. Most bears in both areas migrated each summer from their traditional use areas to old-growth forest where they consumed American devilsclub (*Oplopanax horridus*) fruit. Timing of migration and length of stay in American devilsclub stands were related to fruit abundance.

Estimates of survival using the Kaplan-Meier procedure were significantly lower ($P = 0.05$) for cubs in the 1947 burn (0.74) than in the 1969 burn (0.91) but higher for subadult females in the 1947 burn. Survival was not different for all other age and sex classes of bears. Human, primarily hunters, caused 85% of the deaths ($n = 35$) in the 1969 burn, but only 52% ($n = 31$) in the 1947 burn, where there also was significant mortality from black bears (13%) and brown bears (*U. arctos*) (10%).

Vigor of black bears was linked to moose abundance. The superior growth and reproduction of black bears in the 1969 burn was attributed to a greater consumption of moose calves. Our findings demonstrated a link between neonatal predation and demographics of bear populations.

CONTENTS

INTRODUCTION

The American black bear (*Ursus americanus*) lives in almost every forest biome in North America (Cowan 1972; Herrero 1972, 1978). In each of these biomes, fire, logging, and other forces create an array of seral stages, each with different welfare factors influencing bear abundance.

The Kenai Peninsula has a long history of wildfires with an increase in moose (*Alces alces*) numbers following each fire (Spencer and Chatelain 1953, Peterson 1955, Spencer and Hakala 1964, Viereck and Schandelmeier 1980, Bangs et al. 1985). Major wildfires on the Kenai lowlands in 1947 and 1969 produced large areas of early successional forest. Excellent habitat, light hunting pressure, a lack of wolves (*Canis lupus*), and a series of mild winters contributed to an increasing moose population in the 1947 burn that peaked by 1971. Subsequent deterioration of habitat (Oldemeyer et al. 1977) in conjunction with 3 severe winters in the early 1970's resulted in more than a 50% decline in the moose population by the mid-1970's. Concurrent with this decline, wolves, which had been extirpated from the Kenai Pen-

insula around 1913, again reoccupied much of their former range (Peterson et al. 1984). Wolves, antlerless moose hunts from 1970 to 1974, road kills, and poaching contributed to the moose decline.

The Alaska Department of Fish and Game (ADF&G) and the U.S. Fish and Wildlife Service, Kenai National Wildlife Refuge (KNWR) initiated a cooperative predator–prey study to investigate the impacts of wolf and bear predation on the Kenai moose population. Certain aspects of these studies dealt with moose calf mortality (Franzmann et al. 1980, Franzmann and Schwartz 1986) and wolf ecology (Peterson et al. 1984). The primary objective of the present investigation was to evaluate factors influencing demographics of black bears on the Kenai Peninsula and relate these to predation rates of moose. From 1978 to 1981 we concentrated our studies within the 1947 burn, which was in an advanced seral stage and declining as moose habitat (Oldemeyer et al. 1977). Black bear numbers and predation rates on moose calves were high.

In contrast, the 1969 burn was still in an early seral stage, providing excellent habitat for moose; moose numbers were

increasing and densities were more than twice those in the 1947 burn. Aerial over-flights suggested that black bear densities were low. From 1982 to 1987, we compared moose calf mortality rates (Franzmann and Schwartz 1986) and black bear demographics in this early successional stage of forest regeneration with those of the 1947 burn. Unless otherwise stated, comparisons made here between the 1969 and 1947 burn areas were during 1982-87. Data collected in the 1947 burn area during 1978-81 were tabulated and included because they enhanced the long-term data record for the 1947 burn population.

Acknowledgments.—Numerous individuals provided help at many levels in the Alaska Department of Fish and Game, and they are gratefully acknowledged. The U.S. Fish and Wildlife Service aided in early stages of project development and provided assistance throughout the study.

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DESCRIPTION OF THE REGION AND STUDY AREAS

The 23,310-km² Kenai Peninsula is located in south-central Alaska between 59° and 61° north latitude and 148° and 152° west longitude. It is bounded on the west by Cook Inlet, east by Prince William Sound, and south by the Gulf of Alaska (Fig. 1). It is connected to mainland Alaska by a narrow isthmus of land and ice only 17.7 km wide (Spencer and Hakala 1964, Peterson et al. 1984, Oldemeyer and Regelin 1987). The major physiographic land form occupying the eastern two-thirds of the peninsula is the rugged, heavily glaciated Kenai Mountain Range, which rises to 2,000 m. The western third is dominated by the Kenai lowland, a glaciated plain with a relief of 15–100 m that is dotted with numerous lakes (Spencer and Hakala 1964). Our study sites were located on this plain.

The climate of the plain has characteristics of both continental and maritime zones, although moderating influences of Cook Inlet diminish rapidly with increasing distance from the coast. Annual precipitation ranges from 40 to 50 cm (1944–
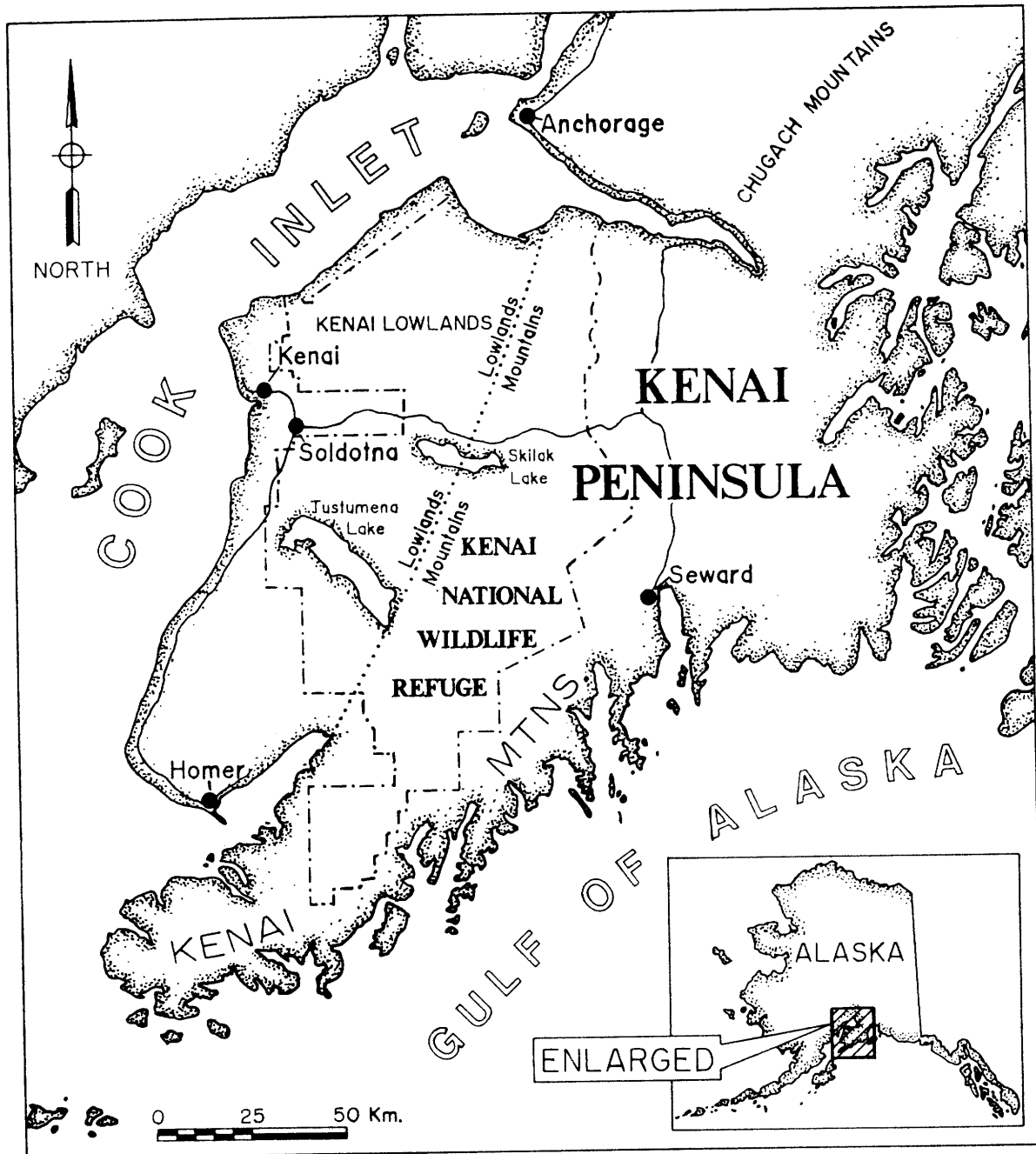
Fig. 1. The Kenai Peninsula, Alaska, showing major geographic land forms within the Kenai National Wildlife Refuge and human settlements.

77 mean of 48 cm) and is evenly distributed throughout the year (Sigman 1977). Snow cover lasts from November through April; snow depths range from 40 to 60 cm for short periods of time (Cushwa and Coady 1976). Winter thaws and rain are common, and bare ground may be exposed at any time. Annual snowfall ranges from 140 to 165 cm (Oldemeyer and Regelin 1987). The growing season averages 88 days (range 67–133), usually beginning about 11 June and ending 6 September (Spencer and Hakala 1964). Temperatures are more moderate than interior Alaska and range from −30 to 21 C (Sigman 1977); the mean annual temperature is 1 C (Sigman 1977).

The Kenai Peninsula lowlands support typical northern coniferous forest containing a mixture of white spruce (*Picea glauca*), black spruce (*Picea mariana*), black cottonwood (*Populus trichocarpa*), quaking aspen (*Populus tremuloides*), and paper birch (*Betula papyrifera*). On dry upland sites the mature forest vegetation is white spruce, paper birch, quaking aspen, or some combination of these species, whereas black spruce dominates poorly drained sites (Lutz 1956, Spencer and Hakala 1964). The deciduous tree species represent successional stages of revegetation after fire. The revegetation sequence following fire in the northern coniferous forests is related to fire intensity, preburn vegetation composition and age, climate, time of burn, parent material, and weather (Lutz 1956, Zasada 1971, Rowe and Scotter 1973, Viereck 1973, Zasada et al. 1979).

The understory associated with these successional stages of forest also follows a pattern of regeneration. Shortly after a fire, a lush herb layer is established; fireweed (*Epilobium angustifolium*) and bluejoint reedgrass (*Calamagrostis canadensis*) are most common. Depending on the severity of the fire, shrubs (*Salix, Ledum,* and *Vaccinium* spp.) reinvade from 6 to 25 years after a burn. As the overstory matures, many of these understory species are shaded out, leaving the more shade-tolerant plants like highbush cranberry (*Viburnum edule*) and northern twinflower (*Linnaea borealis*) and scattered areas of rusty menziesia (*Menziesia ferruginea*) and American devilsclub (*Oplopanax horridus*). Finally, when the white spruce forest matures, the dominant understory species are mosses and lichens (Oldemeyer and Regelin 1987).

The 1947 Burn Area

Our study area in the northern portion of the 1947 burn area was located near the Moose Research Center, a research facility of the ADF&G (Fig. 2). The study area was bounded on the north and west by mixed upland forest and on the east and south by the extensive Moose and Chickaloon river flats. These flats were primarily open bog–meadows interspersed with stands of black spruce. Ground water was on or near the surface.

The 1947 burn started on 3 June and burned unimpeded for 6 weeks until extinguished by late summer rains (Spencer and Hakala 1964). According to Bangs et al. (1985), the 1947 burn (125,000 ha) occurred during average summer weather conditions. Due to differences in topography, fuel loading, and fire intensity, numerous unburned islands of mature timber were left within the perimeter of the fire (Table 1). Bangs et al. (1985) estimated the center of the burn had more ($P < 0.01$) burned forest (80%) and less ($P < 0.01$) remnant forest (11%) than boundary areas (67 and 19%, respectively). Within our study area 42% was burned whereas 30% was in remnant forest (Smith 1984). Bangs et al. (1985) believed that this difference was due, in part, to the concentration of upland forest in the northern part of the burn where our study area was located. Within a 2.5-km² area sampled in the center of the study area, LeResche et al. (1974) identified 624 individual forest stands ranging in size from 0.02 to 18.4 ha; remnant mature forest composed 411 different stands (Table 1). The sample contained a mosaic of vegetation types interspersed with lakes and ponds. The large number of stands and their irregular shapes resulted in 112 km of ecotone in the 2.5-km² area. The area sampled by LeResche et al. (1974) was typical of much of our 1947 burn area.

Approximately 5% of the mixed regrowth vegetation (Table 1) in the 1947 burn area was mechanically treated with LeTourneau tree crushers (1974–76) to improve moose habitat (Oldemeyer et al. 1978). This tree crushing had a negative impact on bears by eliminating this portion of regrowth forest as habitat (Schwartz and Franzmann 1983).

The moose population in the 1947 burn area peaked at 3.6 moose/km² in 1970–71 and declined to 1.3 moose/km² by 1981–82. A recent census conducted in 1986–87
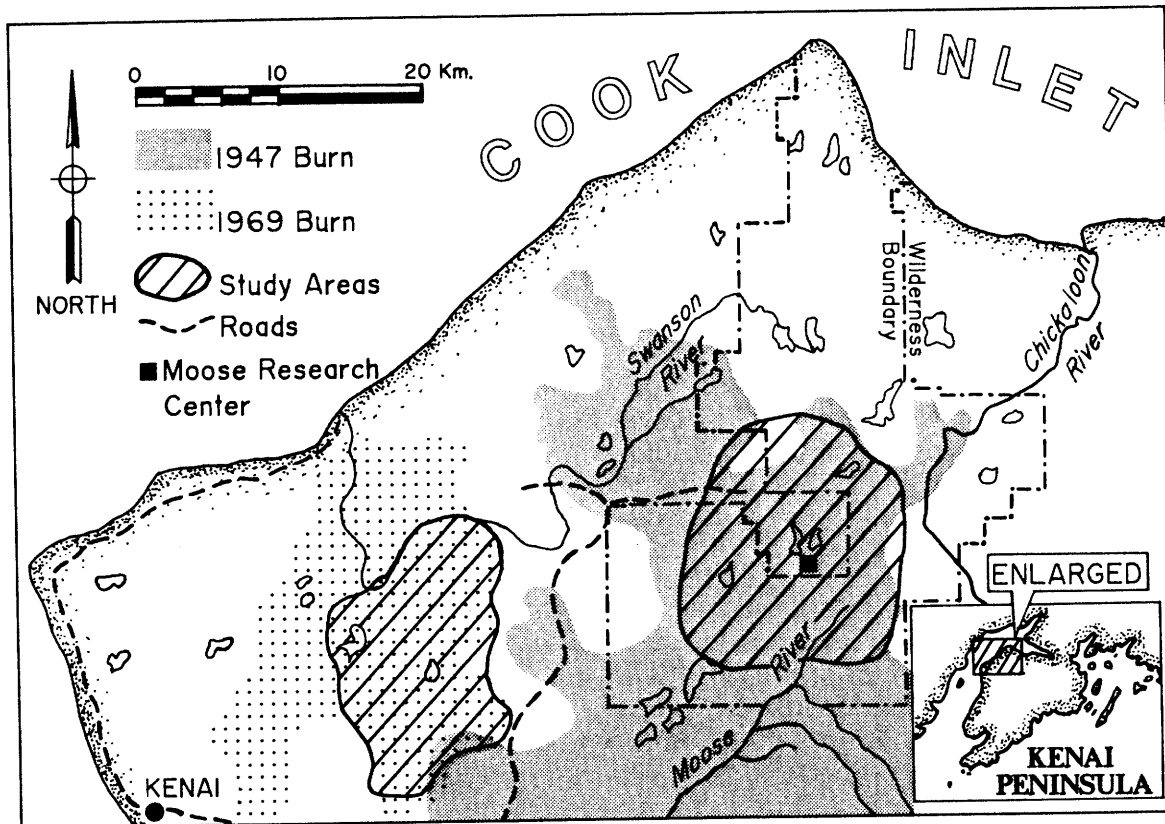
Fig. 2. Locations of perimeter boundaries of the 1947 and 1969 burn areas and our black bear study areas within them, northwestern Kenai Peninsula lowlands.

indicated that the population had further declined to 0.3 moose/km² (Appendix A).

Although we observed moose calving throughout the entire study area, a major moose calving area, the Moose and Chickaloon river flats, was located on the eastern edge of our study area; up to 15% of the moose population calved here in 1978 and 1979 (Franzmann et al. 1980). The proximity of our study area to this calving area was intentional because earlier objectives addressed possible bear movements to

Table 1. Vegetative composition (%) within the 1947 and 1969 burn areas on the Kenai Peninsula, Alaska.

	1947 burn				1969 burn		
	Bangs et al. (1985)			LeResche et al.	Bangs et al. (1985)		
Source	Center	Boundary	Smith (1984)	(1974)	Center	Boundary	Smith (1984)
Burned forest	80.8	67.0	42.1	48.0	71.1	71.9	66.9
Mixed regrowth			33.5	38.3			66.9
Spruce regrowth			3.5	9.7			
Crushed regrowth			5.1				
Unburned forest	11.0	19.0	30.2	46.5	6.6	9.7	7.9
Mixed mature			15.3	44.7[a]			3.8
Mature deciduous			12.8				2.6
Mature spruce			1.5	1.8			1.1
Alder			0.6				0.4
Bog and muskeg	3.0	5.9	13.7	5.4	17.1	9.2	14.0
Water	5.3	7.9	14.0		5.2	9.1	11.2

[a] LeResche et al. (1974) did not distinguish between mixed mature and mature deciduous forest, and they did not include water in their calculations.

calving areas (Schwartz et al. 1983). Additionally, a small group of cows used an area of rehabilitated habitat in the northwest portion of the study area, i.e., the Willow Lake crushed area (Schwartz and Franzmann 1983). About 22% of the cow moose producing calves in the 1947 burn twinned in 1977 and 1978 (Franzmann and Schwartz 1985).

The 1969 Burn Area

Our study area on the 1969 burn was located south of the Swanson River, west of the Swanson River road, east of Beaver Creek, and north of a line from Elephant Lake east to Sunken Island Lake (Fig. 2). Topography and upland vegetation were similar to those of the 1947 burn area, but vegetation was younger.

Unlike the 1947 fire that burned during average weather conditions, the 1969 fire followed two of the hottest and driest summers on record. The fire began on 3 August 1969 and burned for 3 weeks (Bangs et al. 1985). The fire burned over 35,000 ha and could not be suppressed until weather conditions facilitated containment. Because of the intensity of the 1969 burn, there were only slight differences between habitat configurations within the center and the boundary areas (Table 1) (Bangs et al. 1985). Smith (1984) reported the vegetation in the center of our study area was 67% burned forest, 8% remnant forest, 14% bog, and 11% water (Table 1).

Moose numbers in the 1969 burn area were estimated at 0.3 moose/km² in 1970–71, 3.3 moose/km² in 1981–82, and 3.7 moose/km² in 1986–87 (Appendix A). The moose population calved throughout the burn area. Seventy percent of the cows producing calves in the 1969 burn twinned, the highest reported anywhere in North America (Franzmann and Schwartz 1985).

Human Activity and Regulations

Human activity within the 2 burn areas was controlled by regulations of the KNWR and ADF&G. The Swanson River oilfield was in the northeast part of the 1969 burn

area, and access roads and well sites had been constructed there. Public access to both areas was via the Swanson River and Swan Lake roads. There were 2 wilderness canoe routes in the 1947 burn area. Human activity consisted of spring bear hunting and summer fishing and canoeing; fall activities were primarily hunting (grouse, bear, moose) and berry picking.

Black bear hunting regulations changed twice during our study. Bear season was open from 10 August to 30 June prior to 1980; after that, the season remained open all year. In addition, bear baiting was reinstituted in July 1982 after a 5-year closure. The bag limit of 3 bears remained unchanged; both the taking of cubs and the taking of females accompanied by cubs were prohibited. Although the ADF&G did not measure hunter effort for black bears, hunting increased as our studies progressed. This increase coincided with an almost doubling of the human population on the Kenai Peninsula (i.e., 24,611 in 1977, 43,612 in 1987). Beginning in 1985, black bear baiting was prohibited in designated wilderness areas within the KNWR and further restricted to an area west of the Swanson River and north of the Swan Lake roads. This restriction effectively concentrated bear baiting within the 1969 burn area. Starting in 1986, bear baiting was further restricted to 1 permit/2.54 km². Each permit holder was allowed to maintain 2 bait stations; however, no limit on the number of persons hunting over those baits was established.

METHODS
Capture, Immobilization, and Handling

We captured 167 individual black bears a total of 308 times. Bears (n = 308) were captured in snares (1.6%) and barrel traps (41.6%), darted from a helicopter (27.3%), or immobilized in their winter dens (29.5%). In the 1947 burn area in 1977 and 1978, we used Aldrich foot snares (Jonkel and Cowan 1971) following techniques described by Flowers (1977). Snares were set

Table 2. Trapping success at the 1947 burn area on the Kenai Peninsula, Alaska, from 1977 through 1985.

| Year | Date | Method | Trap-days | Bears captured | | | Sex and age of new bears | | | | Success (trap-days/bear) |
| | | | | Total | Different | | Male | | Female | | |
					Marked	New	Subad	Ad	Subad	Ad	
1977	22 Sep–9 Oct	Snare	474	3	0	3	0	0	1	2	159.0
1978	26 Apr–18 May	Snare	158	3	0	3	2	1	0	0	52.7
1979	1 Jun–29 Jun	Barrel	439	24	6	8	4	1	0	3	18.3
1979	25 Sep–17 Oct	Barrel	255	4	2	2	2	0	0	0	63.8
1980	2 Jun–14 Jul	Barrel	653	47	13	6	2 (1)[a]	2	(1)[a]	0	13.9
1980	22 Sep–3 Oct	Barrel	158	6	3	0	0	0	0	0	26.3
1981	1 Jun–1 Jul	Barrel	723	25	10	1	0	0	0	1[b]	28.9
1981	8 Sep–28 Sep	Barrel	280	17	7	1	1	0	0	0	16.5
1982	2 Jun–10 Jul	Barrel	674	15	7	4	(1)[a]	1	(1)[a]	1	44.9
1983	31 May–1 Jul	Barrel[c]	811	41	11	10	(1)[a]	7	0	1 (1)[d]	19.8
1984	31 May–25 Jul	Barrel[c]	1,118	32	7	7	0	5	(1)[a]	(1)[d]	34.9
1985	9 Jun–14 Jul	Barrel[c]	636	31	11	3	(2)[a]	0	(1)[a]	0	20.5

[a] Number in parentheses represents cub(s).
[b] Adult female known to be in study area prior to trapping.
[c] Barrel traps were modified by extending their length and by improving the trigger mechanism.
[d] Number in parenthesis represents adult female that was not a resident of the study area.

in cubby-type trap sites and baited with meat scraps or salmon carcasses; however, because of poor capture success (Table 2), we abandoned their use. From 1979 through 1985, bears were captured in barrel traps systematically located throughout the study area. These traps were constructed from 2 55-gallon drums welded together and fitted with a sliding steel door (Rogers 1987). Like Rogers (1987), we experienced problems with large bears tipping over the traps instead of entering them, and we caught few adult males (Table 2). In 1983 we modified these traps by extending them an additional half-barrel length and altering the trigger mechanism as suggested by Kohn (1982). We also fitted each trap with brackets that allowed us to stake the trap to the ground with steel fence posts and eliminate any tipping. Our improved catch rate of adult males reflected these modifications (Table 2). From 1979 to 1985 our overall catch success with barrel traps averaged 1 bear/22.0 trap-days. Catch rate in the spring (20.4 trap-days/ bear) was not different ($t = -1.00$, 2 df, $P = 0.37$) from fall (35.5 trap-days/bear) comparing years (1979–81) when both seasons were trapped.

In both study areas, we captured bears from a helicopter (Bell Jet Ranger) using drugs delivered from a Cap-Chur gun (Palmer Chemical and Equipment Co., Douglasville, Ga.). We also immobilized previously radioed bears (adult females) and their offspring in their dens during winter, using techniques described by Rogers (1977). When we immobilized these bears, we often did not remove adult females from the den chamber because it was very difficult to return them, especially if the den entrance and/or tunnel was small. In these cases we simply immobilized the adult female and her offspring, removing only the offspring for data collection and marking. No morphometric or blood data were collected from the female. Radio collars of females were replaced in the dens.

Bears were immobilized with phencyclidine hydrochloride (Sernylan, Bio-Ceutic Laboratories, Inc., St. Joseph, Mo.) and promazine hydrochloride (Sparine, Wyeth Laboratories Inc., Philadelphia, Pa.) ($n = 274$) following recommendations of Seal et al. (1970) or etorphine hydrochloride (M-99, Lemon Company, Sellersville, Pa.) and diprenorphine hydrochloride (M50-50, Lemon Company, Sellersville, Pa.) as the antagonist ($n = 24$) (Miller and Will 1974). Cubs <5 kg were not tranquilized ($n = 10$).

Ten bears (3.2%) died because of capture-related complications (Appendix B).

Mortality rates were not different between Sernylan and M-99 (χ^2 = 0.066, 1 df, P = 0.938), but they were different among capture methods (χ^2 = 11.67, 3 df, P = 0.009). Mortality occurred at a higher rate than expected with helicopter darting (n = 6) and at a lower rate than expected with barrel traps (n = 0). Two bears were killed as a direct result of the dart; the remaining four died of complications with the drug and/or overheating.

Captured bears (with the exceptions noted above) were examined for injuries, weighed, measured, and ear tagged. Blood samples were taken from bears older than cubs to determine nutritional status and seasonal changes in physiology (Franzmann and Schwartz 1988). Natural markings were recorded. A premolar was extracted for age determination. Teeth were decalcified and stained using the technique described by Cable (1958) and Goodwin and Ballard (1985). Age was determined by counting cementum annuli (Willey 1974, Rogers 1978). Each year a bear was captured, we extracted 1 premolar until only 1 remained; this tooth was left for age determination if and when the bear was harvested or found dead. Annuli were counted on all extracted teeth, and, when a discrepancy in age occurred, age was assigned based on the most readable tooth (good cross section, distinct annuli, and clearly stained) or combination of teeth. For our study, cubs were <1 year old, yearlings were ≥1 and <2 years old, subadults were ≥2 and <4 years old, and adults were ≥4 years old. We assumed that parturition occurred in the den sometime in late January or early February, and therefore we set birth dates at 1 February.

Radiotelemetry

All female (72) and resident male (62) bears were fitted with radio-transmitter collars (680 g; Telonics, Inc., Mesa, Ariz.). Subadult bears (77) were fitted with breakaway collars (390 g; Telonics, Inc.); these collars were replaced each year in the case of females or until the bear dispersed in the case of males. Subadult males were not fitted with collars unless they were born in the study area (i.e., collared in winter den while still with their mother) or captured within the study area for 2 subsequent years. Cubs were not collared unless we suspected they were with an unmarked female. Battery life for adult collars was 48 months; breakaway collars lasted 12–18 months.

Bear location data (5,258 locations) consisted of aerial fixes (92.5%), capture location (6.2%), location at death (1.2%), and ground observations (0.1%); but virtually all locations were obtained from aerial radio-tracking techniques (Mech 1974) using a Piper Super Cub (PA-18). Bears were radio tracked each year from 1978 to 1987, but effort was most intensive during 1978–85. In 1986, bears were tracked during the spring and fall to determine cub production and to obtain additional data for mortality studies. In 1987, adult females were located in the spring to verify cub production. During the study, some individuals were monitored up to 10 years, but the average length was 2.8 years (Appendix B). Duration of monitoring was influenced by years remaining in the study, transmitter failure, dispersal, and mortality.

Tracking flights occurred every 3–10 days, usually beginning in early spring prior to den emergence and continuing into early winter when all marked individuals had again entered their winter dens and weather was such that no more movements were expected. Tracking flights occurred throughout the day, the majority during midmorning (Fig. 3). Each time a bear was located by radio-fix, we circled the area in an attempt to sight the animal, identify the specific habitat type, determine activity, pinpoint the location on a 1:63,360 scale map, and, during the moose calving season, locate kills. We attempted to see each bear to verify habitat type and activity but were successful only for 56.9% of the 4,863 aerial locations from 1978–1987. Sightability varied with season and habitat and was poorest when the bears were in American devilsclub stands or still in their dens (Fig. 4). The number of bears
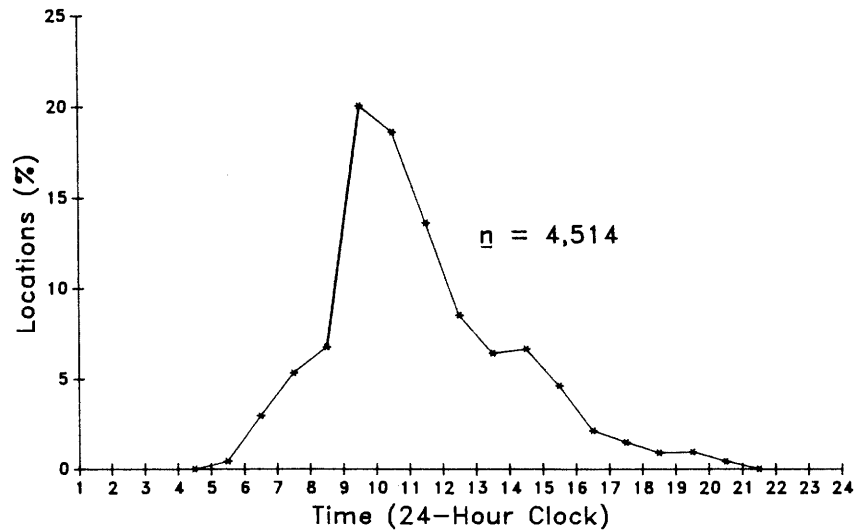
Fig. 3. Temporal distribution of bear locations (n = 4,514) as determined from radio-tracking flights, 1978–87.

radio tracked each year varied along with the number of locations (Table 3, Appendix B).

Numerous lakes and ponds in the study area made it easy to accurately plot aerial locations on the map. This accuracy was confirmed by our ability to locate bears during the winter based on den locations marked on maps the previous fall. Although we did not measure plotting error, we believe it was small.

We used location data to determine areas occupied by bears (minimum convex polygon, Mohr 1947), summer migration

distances and feeding areas, survival rates (Pollock et al. 1989), and production and survival of cubs. We did not radio collar cubs of radio-collared females. Our estimates of cub production were based solely on observations of family groups after den emergence in the spring when we made a special effort to get complete counts of cubs with each marked female.

Most bears we studied used 2 distinct areas during the nondenning period. We referred to these as "traditional use areas" and "summer feeding areas." Traditional use areas were occupied by bears during
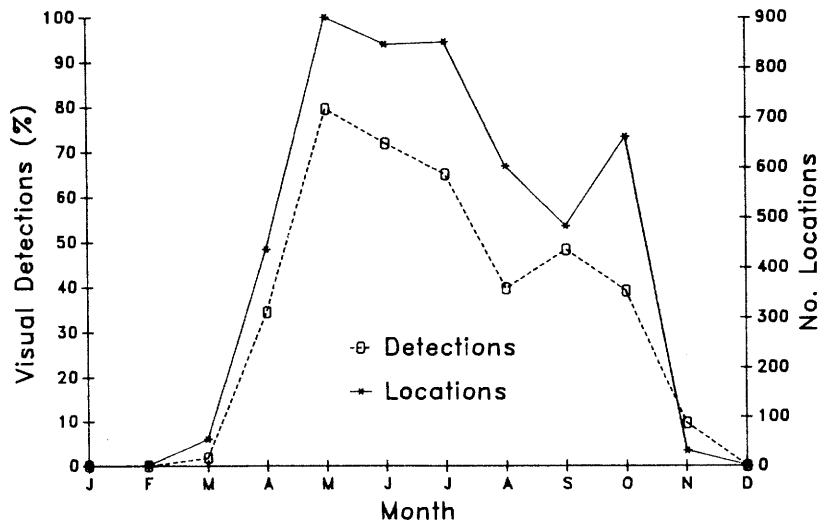
Fig. 4. Percentage of visual observations of bears by month made from 4,863 total radiolocations from aircraft between 1978 and 1987 on the Kenai Peninsula, Alaska.

Table 3. Number of telemetry locations (L) and number of adult and subadult black bears radio tracked in the 1947 burn and 1969 burn areas on the Kenai Peninsula, Alaska during 1978–87.

| Sex and year | 1947 burn | | | 1969 burn | | | |
| | L | No. bears | | L | No. bears | | No. bears |
		Ad	Subad		Ad	Subad	
Females							
1978	178	5	2				7
1979	376	11	2				13
1980	204	10	3				13
1981	184	9	4				13
1982	260	11	1	163	9	0	21
1983	398	13	6	438	13	8	40
1984	317	14	6	291	12	7	39
1985	226	16	7	232	11	11	45
1986	50	12	3	24	6	4	25
1987	8	8	0	4	3	1	12
Subtotal[a]	2,201	109	34	1,152	54	31	228
Males							
1978	172	9	0				9
1979	141	5	0				5
1980	140	7	3				10
1981	111	8	4				12
1982	138	8	1	87	3	4	16
1983	162	8	3	186	8	4	23
1984	74	7	1	129	3	10	21
1985	64	5	3	94	4	12	24
1986	13	2	3	6	1	2	8
Subtotal[a]	1,015	59	18	502	19	32	128
Total[a]	3,216	168	52	1,654	73	63	365

[a] Subtotals and the total for numbers of bears represent bear years. The number of different adult and subadult females radio tracked was 17 and 21, and 15 and 19 for the 1947 and 1969 burn areas, respectively. The number of different adult and subadult males radio tracked was 16 and 13, and 9 and 24 for the 1947 and 1969 burn areas, respectively.

the majority of the year and contained a den site. Each year most bears migrated from their traditional use areas to forest types containing an abundance of food in summer and fall, their summer feeding areas.

Migration timing was compared between the 2 areas with t tests. In order to control overall experimental-wise error for this data set at $P = 0.05$, the Bonferroni t was used in each test (Neter et al. 1983: 158–159). This effectively changed the P value by α/k, where k was the number of comparisons; in this case the level of significance was 0.017 (0.05 ÷ 3).

Age Structure, Sex Ratio, Density, and Reproduction

We used 2 methods to estimate bear densities within the 2 areas: (1) extrapo-

lation estimates required the collaring of all resident individuals (Rogers 1987) and summing bears or fractions of bear areas occupied within the central core (23.3 km²) of each study area (Hugie 1982, Schwartz et al. 1983) and (2) mark–recapture (Miller et al. 1987).

During 1978–85, we attempted to capture and mark all resident animals within the 2 study areas. Trapping success (Table 2), sightings of unmarked bears, and distribution of radio-collared females indicated that following spring tagging in 1979 and 1983, we had virtually all resident bears collared in the 1947 and 1969 burn study areas, respectively. During 1982–85, 64 and 99 different bears were residents of the 1947 and 1969 burn areas, respectively. Information on approximate date of recruitment or loss was complete for most bears (Appendix B). Sex ratio of cubs

of known sex born in the study area was 33 males : 35 females. Cubs not handled (n = 25) were assigned randomly a 50:50 male : female sex ratio; assumptions for older bears were listed in Appendix C.

Estimates of density using the extrapolation technique were made with the proportion of each bear's traditional use area that overlapped the center of each study area; polygons were constructed using all locations except those during migration and in summer feeding areas. Estimates represented seasonal density; bears dying or dispersing were not counted.

Estimates using the mark–capture technique of Miller et al. (1987) were made in 1985. Limited funding allowed us to only survey the 1947 burn area for 2 days and the 1969 burn area for 3 days.

May was chosen as the month to determine population sex and age structure. This was a period before family breakup and yearling dispersal, and during this period all resident bears were foraging within their traditional use areas.

Sex and age compositions were compared between the 2 areas using a hierarchical log-linear model with backward elimination (Norusis 1986a,b). Differences were determined using the likelihood-ratio chi-square (G^2) statistic. Differences between median age of male and female bears were determined with a median test (Zar 1974:114–115).

Reproductive parameters including age at first litter production, reproductive interval, and litter size were compared using a chi-square test (Zar 1974). Growth as reflected by body weight was analyzed for yearling male and female bears separately using t tests. There was no difference in weights of bears in the 1947 burn during 1978–81 versus 1982–86 (t = 1.34, df = 21, P = 0.194); therefore data were combined and compared to the 1969 burn for years 1982–86. Because we made multiple comparison t tests (k = 4), we used the Bonferroni t statistic. Adult male and female body weights were analyzed separately because males weighed more than females. Because bears weighed more as they aged, we used log$_e$ (age) as a covariate.

Comparisons of weight data collected in the 1947 burn during 1978–81 versus 1982–86 were not different for male (t = 0.113, P = 0.911) or female (t = 1.283, P = 0.206) bears; therefore data were combined and compared to the 1969 burn for years 1982–86 using Bonferroni t tests. To control overall experimental-wise error at P = 0.05, statistical significance was accepted at P = 0.0125 (0.05 ÷ 4).

Food Habits

Details of bear food habits and lowbush cranberry production studies were available in an unpublished M.S. thesis (Smith 1984). In general, food habits were determined by examining fresh scats collected in both study areas. Scats were collected from 1979 to 1983 and 1982 to 1983 in the 1947 and 1969 burn areas, respectively. Scats were frozen until analyzed. Frozen scats were then thawed, mixed with water, and washed through 3 (4, 0.7, and 0.4 mm) U.S.A. Standard Testing Sieves (Hubbard Scientific Co., North Brook, Ill.). Washed contents were transferred to a white enamel pan and examined under a lighted viewing lens (Electri X, Model V117, New Haven, Conn.). Volume of each food item was estimated as trace–5%, 6–25%, 26–50%, 51–75%, or 76–100%. Mean volume was calculated using the midpoint of categorical data. Grasses and sedges were identified by epidermal characteristics, using the microhistological technique (Croker 1959, Davis 1959). Food habits were quantified seasonally: (1) spring = den emergence–30 June, (2) summer = 1 July–15 August, and (3) fall = 16 August–den entrance.

An index of diet diversity (H) for each season was calculated (Shannon 1948) as suggested by Zar (1974:35–38). Diversity indices between study areas within each season were compared (Zar 1974:115–117) with a multiple comparison Bonferroni t statistic (P = 0.05/3 = 0.017). We proportionalized Shannon's index of diversity into J (Pielou 1966) as suggested by Zar (1974). J ranged between 1 and zero; 1 represented the maximum possible diversity.

Production (kg/ha) of lowbush cranberry fruit was measured by picking berries in 40 or 80 1-m² plots/stand using a 2-stage sampling design (Smith 1984). Plots were located in 3 seral stands (i.e., 1969 and 1947 burns and old growth) as well as in different forest types based on overstory composition and other site characteristics. Berries were harvested between 30 August and 22 September in 1982 and 1983. To preserve them for analysis, harvested berries were frozen. Dry matter was determined from samples dried at 60 C for 48 hours. Relative abundance of American devilsclub and lowbush cranberry fruit was visually estimated during field operations and classified as scarce, common, or abundant. Comparisons between the 2 study areas of the frequency of occurrence and volume of moose calf detected in fecal samples and the effects of berry abundance on cub production were made using chi-square tests (Zar 1974).

Survival Estimation

To examine survival rates of bears, we developed a model that divided the year into 2 periods: (1) the active period started 1 May and continued through 31 October and (2) the inactive period, or denning season, encompassed 1 November to 31 April. Dates of den emergence in the spring ($\bar{x}$ = 19 Apr, range 3 Apr–9 May) and entrance in the fall ($\bar{x}$ = 18 Oct, range 21 Sep–11 Nov) (Schwartz et al. 1987a) overlapped this active period, and no mortalities were recorded before 1 May or after 31 October. Data were imputed into the model in monthly time steps thus accounting for newly collared animals, those lost to censuring, and death.

Survival and cause-specific mortality were calculated for cubs, yearlings, and subadult and adult females and males using the Kaplan-Meier procedure (Pollock et al. 1989). Survival functions for different age, sex, and/or study areas were compared with the log-rank and an approximate chi-square test statistic with one degree of freedom; we used the most conservative chi-square presented by Pollock et al. (1989). A Z statistic was used to compare annual survival rates (Pollock et al. 1989).

The Kaplan-Meier procedure was simple, flexible, and allowed staggered entry of newly tagged animals. It allowed for animals being lost (or censored) due to radio failure, radio loss, or emigration of the animal from the study area. The assumptions required for the procedure were as follows:

1. Animals of a particular sex and age class were sampled randomly.
2. Survival times were independent for different animals.
3. Capturing the animal or having it carry a radio tag did not influence its future survival.
4. The censoring mechanism was random.
5. A definition of a time origin was crucial.
6. Newly tagged animals had the same survivial function as previously tagged animals.

We met assumption 1 because we tagged virtually every resident animal within both study areas. We violated assumption 2 because the fate of cubs was not independent of the death of their mother. Violating this assumption did not cause bias, but it did result in a smaller variance associated with the survival estimates (Pollock et al. 1989). We do not think that our tagged animals were influenced by the radio collar or other marks. We encouraged hunters to treat radio-collared bears exactly the way they would treat an unmarked bear. And with only a few exceptions, most hunters did not realize that a bear was marked until after they killed it. The assumption that the censoring mechanism was random was important. During the course of the study (1982–86) 23 and 34 bears were censored (lost radio contact) in the 1947 and 1969 burn areas, respectively. Of these 57 censored bears, 20 (35.1%) were shot by hunters one to several years after their radios failed, 6 (10.5%) were captured and re-collared, and fates of 31 (54.4%) were undetermined. Therefore, the fate of almost half (45.6%) of all censored bears was sub-

sequently determined. Of the 31 bears whose fate was not determined, 15 were subadults fitted with breakaway collars (age 1–3) designed to fall off. Presumably many of these dispersed from the study area shortly after loosing their collars, or we would have recaptured them. Based on this evidence and our general observations, we had no reason to suspect nonrandom censoring of radioed animals. Regarding assumption 5, our time origin began in the spring after den emergence when the first group of animals was tagged. Because we witnessed no mortality during the denning period, survival curves from this origin were influenced by this seasonal effect; annual survival estimates were not affected. Assumption 6 required that newly tagged animals had the same survival function as previously tagged animals. Contingency table tests of this assumption for adult male ($\chi^2 = 0.664$, 1 df, $P = 0.415$) and female bears ($\chi^2 = 0.228$, 1 df, $P = 0.228$) indicated that the two were not different. All cubs, yearlings, and most subadults (age 2 and 3) were new each year precluding a test of this assumption.

Inputs to calculate cub survival were obtained by monitoring adult females with cubs from den emergence to den entrance. We treated cubs as if they were radio collared, because it was possible to visually count the number of cubs with each radioed female; a permanent loss of a cub was assumed to represent mortality. To be consistent with our model, estimates of survival for cubs did not include the time period from birth to the beginning of May. Den emergence occurred around 19 April (range, 3 Apr–9 May), and litters were first counted during this time period; we did not witness any cub losses prior to 16 May. Because litter size and reproductive interval were calculated with information from these cub counts, lack of information on possible cub loss in the den would not affect population modeling.

Harvest Statistics

Bear harvest statistics were obtained from the sealing program that began in 1973. Hunters harvesting black bears on the Kenai Peninsula (Alaska Game Management Units 7 and 15) were required to present the hide and skull to an authorized representative of the ADF&G within 30 days of harvest, at which time metal locking tags (seals) were affixed to the skull and hide. During this sealing process, date, location of kill, sex, and other statistics were collected and a tooth was taken for age determination.

POPULATION CHARACTERISTICS
Age Structure and Sex Ratio

Records, sightings of unmarked bears, and distribution of traditional use areas indicated that nearly all resident females were marked by 1979 and 1983 in the 1947 and 1969 areas, respectively. Prior to trap modification in 1983, resident males were more difficult to trap in the 1947 area, and it also was more difficult to keep functional radio transmitters on them. Consequently, our estimates of the number of resident males in both areas were probably minimal.

Sex ratios (Tables 4, 5; Fig. 5) between the 1947 and 1969 areas (1982–85) were not different ($G^2 = 0.478$, 1 df, $P = 0.490$), but both areas contained significantly more females than males ($G^2 = 7.25$, 1 df, $P = 0.007$). In the 1947 burn area, the sex ratio was near parity in cubs, but it tended to favor females in the yearling to 10-year-old age classes; after that it tended to favor males. The overall sex ratio in the 1947 burn was 1.5 females/male. In the 1969 burn area, the sex ratio was roughly equal until age 3; after that, there were more females than males. The overall sex ratio in the 1969 burn area was 1.2 females/male. There were 1.5 and 1.8 adult females/adult male in the 1947 and 1969 areas, respectively. The proportion of adult males and females was not different between areas ($G^2 = 0.711$, 1 df, $P = 0.399$). Likewise, there were 0.53 and 0.50 female cubs/adult female in the 1947 and 1969 burn areas.

Age structure was significantly different

Table 4. Sex and age of resident black bears in the 1947 burn area on the Kenai Peninsula, Alaska, each May during 1979–85.

Age (yrs)	1979		1980		1981		1982		1983		1984		1985		1982–85		
	M	F	M	F	M	F	M	F	M	F	M	F	M	F	M	F	Total
0	4	3	3	3	0	0	2	6	3	3	5	6	5	5	15	20	35
1	3	3	3	3	3	3	0	0	2	6	2	2	3	5	7	13	20
2	2	0	3	2	2	1	1	1	0	0	1	5	0	2	2	8	10
3	0	2	2	1	1	0	3	1	3	2	0	0	1	3	7	6	13
4	1	3	0	3	1	1	0	1	1	1	4	2	0	0	5	4	9
5	0	2	1	3	0	3	1	0	0	1	0	1	3	2	4	4	8
6	2	0	0	2	1	2	0	2	1	0	0	0	0	1	1	3	4
7	0	0	2	0	0	2	0	3	0	2	1	0	0	0	1	5	6
8	1	0	0	0	2	0	0	2	0	2	0	2	1	0	1	6	7
9	0	0	1	0	0	0	2	0	0	2	0	2	0	2	2	6	8
10	0	1	1	0	1	0	0	0	2	0	0	2	0	2	2	4	6
11	2	0	0	1	1	0	1	0	0	0	2	0	0	2	3	2	5
12	0	0	2	0	0	1	1	0	1	0	0	0	0	0	2	0	2
13	0	0	0	0	2	0	0	1	2	0	1	0	0	0	3	1	4
14	0	0	0	0	0	0	1	0	0	1	1	0	0	0	2	1	3
15	0	0	0	0	0	0	0	0	0	0	0	1	0	0	0	1	1
16	0	0	0	0	0	0	0	0	0	0	0	0	0	1	0	1	1
All	15	14	18	18	14	13	12	17	15	20	17	23	13	25	57	85	142

($G^2 = 15.87$, 1 df, $P = 0.003$) between the 2 areas (Fig. 5), mainly in the yearling age class. On the average during the period from 1982 to 1985 in the 1947 burn area, 25% of the population was cubs, 14% yearlings, and 16% subadults; adult males and females composed 18% and 27% (Table 6). During those same years in the 1969 burn area, 25% of the population was cubs, 23% yearlings, and 16% subadult; adult males and females composed 13% and 24%, respectively (Table 6).

Median age of male bears was significantly different ($\chi^2 = 35.5$, 1 df, $P = 0.000$) in the 1947 (4 yrs) and 1969 (1 yr) burn areas. Similarly, median age of female bears was significantly different ($\chi^2 = 6.95$, 1 df, $P = 0.008$) in the 1947 (4 yrs) and 1969 (1 yr) burn areas.

The oldest bears that we observed in our

Table 5. Sex and age of resident black bears in the 1969 burn area on the Kenai Peninsula, Alaska, each May from 1982 to 1985.

Age (yrs)	1982		1983		1984		1985		All years		
	M	F	M	F	M	F	M	F	M	F	Total
0	5	8	8	5	7	5	7	6	27	24	51
1	4	4	5	8	8	5	7	5	24	22	46
2	4	0	0	0	2	5	4	5	10	10	20
3	0	3	2	3	0	0	1	3	3	9	12
4	0	0	1	2	1	2	0	0	2	4	6
5	1	2	0	0	1	2	1	2	3	6	9
6	0	2	1	2	0	0	0	2	1	6	7
7	2	0	0	2	1	2	0	0	3	4	7
8	0	0	2	0	0	2	1	1	3	3	6
9	0	2	0	0	2	0	0	2	2	4	6
10	1	0	0	2	0	0	2	0	3	2	5
11	2	2	1	0	0	2	0	0	3	4	7
12	0	3	2	2	1	0	0	2	3	7	10
13	0	0	0	2	2	1	0	0	2	3	5
14	0	0	0	0	0	2	2	1	2	3	5
15	0	0	0	0	0	0	0	2	0	2	2
All	19	26	22	28	25	28	25	31	91	113	204
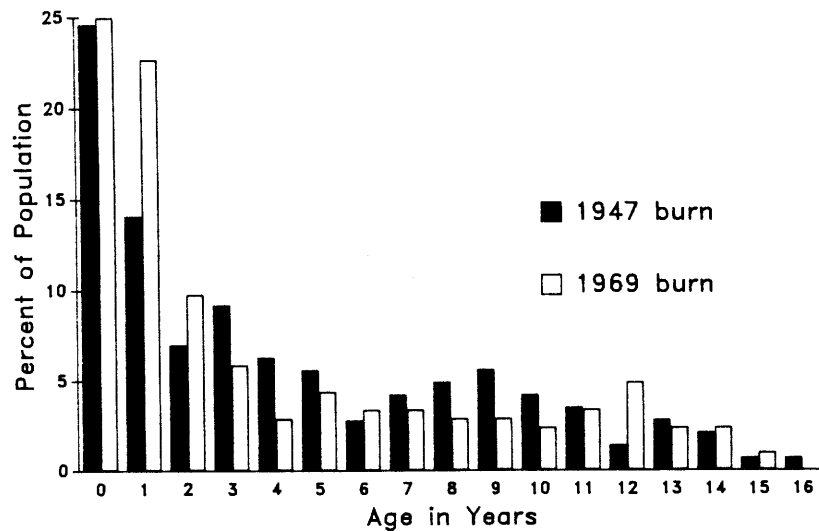
Fig. 5. Mean percent frequency of occurrence by age class for black bears captured in the 1947 and 1969 burn areas on the Kenai Peninsula, Alaska, 1982–85. Sex ratio was 1.5 and 1.2 females:male in the 1947 and 1969 burn areas, respectively.

study were 16 years of age; one was a male and one a female. The oldest bears harvested on the Kenai Peninsula between 1973 and 1980 ($n = 853$), when bears were aged, were a 21-year-old male and a 16-year-old female. According to Bunnell and Tait (1981), the oldest free-ranging black bears reported were 27 (Poelker and Hartwell 1973) and 32 years old (Sauer 1975); both were females.

Composition of the bear populations in the 1947 and 1969 burn areas was similar to that reported by Rogers (1987) for a population in Minnesota (Table 6), except that the 1947 burn area population had a higher percentage of adult males and the

Minnesota population had more subadults. The percentage of cubs was similar to that of the Minnesota population but higher than that reported in Montana (Jonkel and Cowan 1971) and Alberta (Young and Ruff 1982). The percentages of cubs in the populations from Montana and Alberta were obtained from capture records that tend to be negatively biased against cubs captured. Beecham (1983) demonstrated that the proportion of subadults (age <4 yrs) was higher in a heavily hunted population in Council, Idaho, than in a very lightly hunted population in Lowell, Idaho (Beecham 1980) (Table 6). Likewise, Young and Ruff (1982) reported a marked in-

Table 6. Comparison of sex and age composition and density of 2 black bear populations from the Kenai Peninsula, Alaska,[a] with other studies in North America.

Area	Source	Age (yrs)						Density (bears/1,000 km²)	
		0	1	2–3	0–3	Male >3	Female >3	Estimate	SE
1947 burn (1982–85)		25	14	16	55	18	27	189	18
1969 burn (1982–85)		25	23	16	63	13	24	211	12
Minnesota	(Rogers 1987)	23	16	24	64	12	24	159–243	
Idaho, Council	(Beecham 1983)	19	14	37	70	13	17	769	
Idaho, Lowell	(Beecham 1980)	8[b]	6[b]	15[b]	29	35	36	435	
Montana	(Jonkel and Cowan 1971)	12	17	30	59			482	
Alberta	(Young and Ruff 1982)								
Before male removal		12	13	21	46			370	
After male removal		9	9	49	67			625	

[a] Areas studied on the Kenai were in forest burned by fire in 1947 and 1969.
[b] Personal communication, J. J. Beecham, Idaho Fish and Game, Boise.

Table 7. Density (bears/1,000 km²) estimates for black bears in the 1947 and 1969 areas on the Kenai Peninsula, Alaska, from 1979 to 1985 and 1983 to 1985, respectively.

| | 1947 burn area | | | | 1969 burn area | | | |
| | All bears | | Bears >1 | | All bears | | Bears >1 | |
Year	x̄	SE	x̄	SE	x̄	SE	x̄	SE
1979	246	49	115	19				
1980	255	29	118	9				
1981	133	18	115	15				
1982	155	46	91	18				
1983	193	40	104	22	192	50	102	19
1984	237	34	116	17	202	33	105	19
1985	172	24	119	18	239	41	108	17
1985[a]			152				204	
95% CI[a]			132–239				130–226	
Mean of years								
79–85	199	18						
82–85	189	18			211	12		

[a] Estimate obtained by mark–recapture technique of Miller et al. 1987; range is the lower and upper 95% confidence interval for a binomial distribution. Estimate includes bears ≥ 1 year of age.

crease in the proportion of subadults in their Cold Lake, Alberta, study area following the removal of adult males. The higher proportion of yearlings in the 1969 area over that of the 1947 area reflected higher recruitment of yearlings as a result of better cub survival; this will be addressed in a later section.

Density of Resident Population

Bear density (Table 7) calculated by the extrapolation method was similar for the 1947 and 1969 burn areas in all years of study. Density in the 1947 burn area was similar in 1979 and 1980, but it dropped 48% in 1981. This dramatic decline was caused by a complete failure of cub production in 1981 as well as high yearling mortality because of starvation; the density of bears >1 year of age did not change (Table 7). Bear numbers in the 1947 burn area gradually recovered from 1981 through 1984 reaching 1979–80 densities. The population declined again in 1985 due to high cub mortality (4 cubs from 2 radio-collared females died); the density of bears >1 year of age did not change. Density of bears >1 year in the 1969 burn area was relatively stable during the 3 years of our investigations (Table 7), whereas cub and yearling numbers increased slightly.

We believe that our extrapolation esti-

mates of density were accurate. Because we only used the central portion of the study areas to estimate bear density where we had virtually all bears marked, unmarked bears using peripheral portions of the study area did not influence our estimates. Underestimating the size of the traditional use area would have resulted in an overestimate for a bear with a traditional use area that overlapped a large portion of the central study area, but would have resulted in an underestimation for a bear where this central portion of the study area occurred on the edge of the traditional use area. Because we used the same criteria in both study areas and radio located bears on the same days in both areas, any biases in the technique were consistent between study areas. Hugie (1982) used a similar technique, comparing it to several mark–recapture models (Petersen, Schnabel, Bailey's triple catch) described by Caughley (1977); Hugie (1982:37) subjectively concluded "that the extrapolation estimates were the most accurate of all the estimates made, particularly for calculating densities." We did not attempt to calculate density using mark–recapture techniques with our catch data because of violations in the assumptions for each model.

Our estimate of bear density, obtained in 1985 with the mark–recapture census

using the technique of Miller at al. (1987), allowed for population closure and overcame many potential assumption violations concerning mark–recapture models. These density estimates (bears/1,000 km²) for bears ≥1 year old were 152 (95% CI = 132–239) and 204 (95% CI = 130–226) for the 1947 and 1969 areas (Table 7). If we assume that cubs represented 26% and 23% of the 1947 and 1969 area populations in 1985 (Tables 4, 5), the total population would have been 205 (152 ÷ 0.74) and 265 (204 ÷ 0.77) bears/1,000 km², respectively. This mark–recapture estimate was higher than the extrapolation estimate in 1985 (Table 7).

Several factors may have been responsible for the disparity in density estimates between the extrapolation technique and mark–recapture. The extrapolation technique may have underestimated the population because not all of the individuals using the study area were collared; this was particularly the case for subadult male bears. Also, extrapolation estimates only included bears that remained in the study ares(s) the entire year. Mark–recapture may have overestimated the population because it did not differentiate between "resident" and "transient" bears; all bears sighted were included in the estimate.

Our estimates of density from both study areas were within the range reported for black bears through much of the North American (0.1–0.4 bears/km²) range (Table 6), but lower than that reported in Washington and Idaho (Kolenosky and Strathearn 1987:446).

BREEDING SEASON

Based on observations of females in estrus (swollen vulva at time of handling), breeding pairs (actual mating observed), and associations of adult bears (radio-collared adults with either marked or unmarked adult bears), the mating season extended from mid-May through early July (Fig. 6). This generally agreed with observations from other areas (Knudsen 1961, Rausch 1961, Stickley 1961, Wimsatt 1963, Erickson and Petrides 1964, Jonkel and

Cowan 1971, Poelker and Hartwell 1973, Beeman and Pelton 1980, Reynolds and Beecham 1980, Rogers 1987).

REPRODUCTIVE SUCCESS

Reproductive success was studied during 1978–87 in the 1947 burn area and during 1982–87 in the 1969 burn area (Tables 8–10). Reproductive success during the period of simultaneous study (1982–87) is compared below. All available information from each individual female was presented in Appendixes D and E. Biases in individual female data sets tended to reduce apparent differences in reproductive success between the 2 areas. It was assumed that females >4 years old that died or were lost from radio contact before they produced their first offspring would have produced cubs the year after their death or loss (see footnote d in Table 8). This provided us with a minimum estimate for age at which females produced their first litter, because some of these females may not have produced cubs that following year.

Age at First Breeding

Females produced their first litters at a significantly earlier mean age in the 1969 burn area (4.6 yrs, range 4–5 yrs, $n = 7$) than in the 1947 burn area (5.8 yrs, range 5–7, $n = 10$) (Table 8) ($\chi^2 = 8.74$, 3 df, $P = 0.03$).

Reproductive Interval

We defined reproductive interval as years between surviving litters. We did not count litters that were lost prior to weaning because this could have resulted in a reproductive interval of 1 year, which would have been incorrect. We observed 10 reproductive intervals between litters of cubs in the 1947 burn: 8 were 2 years in length and 2 were 3 years (Table 9). Of 14 intervals observed in the 1969 burn area, 13 were 2 years in length and 1 was 3 years. The proportion of females producing litters at 2- or 3-year intervals was not dif-
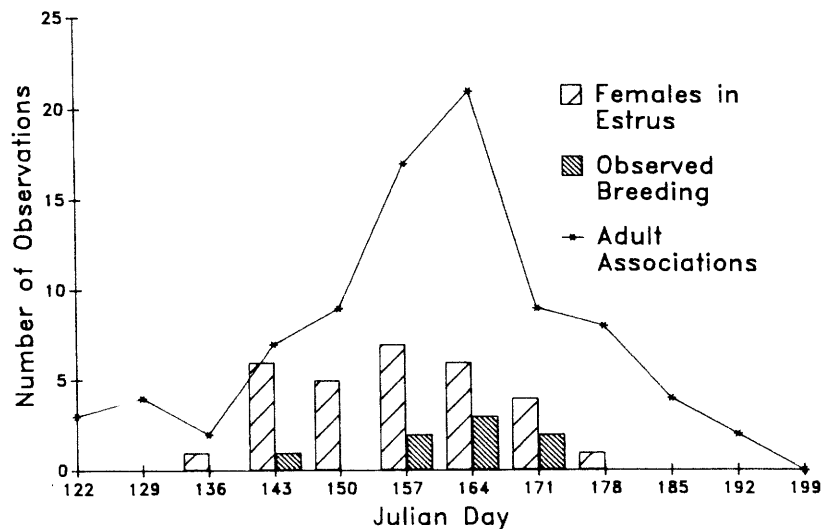
Fig. 6.   Observations of females in estrus, mating, and adult associations over time on the Kenai Peninsula, Alaska, 1978–85.

ferent ($\chi^2 = 0.881$, 1 df, $P = 0.348$) between the 2 areas. The 3-year intervals suggested that some females required more time to rebuild body reserves before another litter was produced.

We also calculated a reproductive interval between successful weaning of yearling litters (Table 9). In the 1947 burn area we observed 11 intervals; 7 were 2 years in length, and 4 were 3 years in length. In the 1969 burn area we observed 11 intervals; all were 2 years in length. The mean interval was 2.4 and 2.0 years for the 1947 and 1969 burn areas, respectively. The

proportion of females producing yearlings at 2- and 3-year intervals was significantly different ($\chi^2 = 5.0$, 1 df, $P = 0.03$) between the 2 areas. The greater proportion of females producing yearling litters at 2-year intervals, but not cubs in the 1969 burn, was caused by higher cub mortality in the 1947 burn; this is discussed later.

Litter Size

Postemergence litters averaged 2.2 cubs (range 1–3, $n = 30$) in the 1947 burn and 2.3 cubs (range 1–3, $n = 27$) in the 1969

Table 8.   Percent of female black bears that produced cubs by a given age in the 1969 burn area (1982–87) and 1947 burn area (1978–87 and 1982–87) on the Kenai Peninsula, Alaska, and the percent of first litters by age class.[a]

| | 1969 burn area[b] | | | 1947 burn area[c] | | | | | |
| | 1982–87 | | | 1978–87 | | | 1982–87 | | |
Age (yrs)	n	No. with cubs present	No. having first litters	n	No. with cubs present	No. having first litters	n	No. with cubs present	No. having first litters
3	6	0	0	16	0	0	8	0	0
4	5[d]	3	3	15[d]	6	6	6	0	0
5	4	4	4	11[d]	5	5	9[d]	4	4
6	5	5	0	12[d,e]	5	4	8[d,e]	4	4
7	1	1	0	9	8	2	8	7	2
8	18	16	0	21	19	0	18	16	0

[a] Females with yearling were not included in the sample.

[b] Mean age of first litter was 4.6.

[c] Mean age of first litter was 5.1 for 1978–87 and 5.8 for 1982–87.

[d] One adult female in the 1969 burn area at age 4 years and 6 adult (5 in yrs 1982–87) (≥ 4 yrs) female bears in the 1947 burn area died before they produced their first litter: 3 at 4 (2 at age 4 in yrs 1982–87), 2 at 5, and 1 at 6 years of age. The earliest they could have possibly produced a litter was the following year. We included these individuals in our calculations for earliest age at first breeding because to exclude them would bias our estimate toward an earlier age. The estimate of age at first breeding should be considered the lowest as we do not know if these females would have bred and produced a litter the year after their death as we have assumed.

[e] Five of the 7 females (3 of 4 in 1982–87) that did not produce cubs at age 6 had previously produced cubs at age 4; 2 females at age 6 had never produced cubs.

Table 9. Number of 2- and 3-year intervals between litters born (cubs) to or successfully weaned (yearlings) by black bear females at the 1947 (1978–87 and 1982–87) and 1969 burn areas (1982–87) on the Kenai Peninsula, Alaska.

| Age class and interval (yrs) | 1947 burn area | | 1969 burn area |
| | 1978–87[a] | 1982–87[a] | 1982–87 |
	No. with litters	No. with litters	No. with litters
Cubs			
2	14	8	13
3	5	2	1
$\bar{x}$ interval	2.26	2.20	2.07
Yearlings			
2	10	7	11
3	6	5	0
$\bar{x}$ interval	2.38	2.36	2.00

[a] Excluded is an interval of 1 year (B24); this female lost her entire litter prior to mating, and the next successful weaning was not observed.

burn area (Table 10); the proportion of females producing litters of 1, 2, or 3 cubs was not different ($\chi^2 = 0.859$, 2 df, $P = 0.65$) between areas; the median age (9 yrs) of adult females also was the same. Unlike results of Rogers (1987) in Minnesota and Elowe (1987) and Elowe and Dodge (1989) in Massachusetts, there was no difference in the number of cubs produced in first versus subsequent litters.

Although the number of cubs produced in first and subsequent litters did not differ (Table 10), survival did. Yearling litter size

in the 1947 burn averaged 1.7 and 1.9 for first and subsequent litters, respectively. We followed 4 first-litter females in the 1947 burn long enough to document cub losses. Of 10 cubs produced, 5 died; all 4 females lost part of all of their litters. During the same period, we followed 25 females (54 cubs) that produced subsequent litters and documented 4 cub deaths (7%) from 2 litters. Similarly, yearling litters in the 1969 burn area averaged 2.0 and 2.3 for first and subsequent litters, respectively (Table 10). We followed 3 females with first litters in the 1969 burn long enough to document cub losses. Of 7 cubs produced, 2 died; 1 of 3 females lost her entire litter. During the same period, we followed 24 females (56 cubs) that produced subsequent litters and documented 2 cub deaths from 1 litter. Elowe (1987) in Massachusetts documented greater litter loss for females with first litters (57%) than for females that had already raised a litter (7%).

Postemergence litters for all females averaged 1.9 yearlings (range 1–3, $n = 17$) in the 1947 burn and 2.2 yearlings (range 1–3, $n = 24$) in the 1969 burn area (Table 10); the proportion of females producing litters of 1, 2, or 3 yearlings was not different ($\chi^2 = 2.65$, 2 df, $P = 0.265$) between areas.

Table 10. Number of litters with 1, 2, or 3 cubs and yearlings for black bears at the 1947 (1978–87 and 1982–87) and the 1969 burn areas on the Kenai Peninsula, Alaska.

| No./litter | 1947 burn area | | | | 1969 burn area | |
| | 1978–87 | | 1982–87 | | 1982–87 | |
	First litters	Subsequent litters	First litters	Subsequent litters	First litters	Subsequent litters
Cubs						
1	2	5	1	4	0	3
2	7	21	2	13	2	10
3	2	9	2	8	1	11
Mean[a]	2.0	2.1	2.2	2.2	2.3	2.3
Yearlings						
1	2	4	1	4	1	4
2	7	11	2	7	3	6
3	0	3	0	3	1	9
Mean[b]	1.8	1.9	1.7	1.9	2.0	2.3

[a] Mean of all cub litters (first and subsequent combined) for the 1947 burn area was 2.1 and 2.2 for years 1978–87 and 1982–87, respectively. The mean for the 1969 burn was 2.3.

[b] Mean of all yearling litters (first and subsequent combined) for the 1947 burn area was 1.9 for years 1978–87 and 1982–87. The mean for the 1969 burn was 2.2.

Table 11. Body weight (kg) of adult (age >3 yrs) and yearling black bears from the 1969 (1982–85) and 1947 (1979–85) burn areas, on the Kenai Peninsula, Alaska.

Age (months) and study area	Male weight			Female weight		
	n	$\bar{x}$	SE	n	$\bar{x}$	SE
Adults (May–Jul)						
1947 burn	43	95.5ᵃCᵇ	4.0	50	55.9B	1.0
1969 burn	10	116.4ᶜC	12.7	20	61.7A	2.3
Yearlings (Nov–Apr)						
1947 burn	9	19.5AB	1.1	14	15.9A	0.7
1969 burn	15	26.4C	1.6	12	21.5B	1.4

[a] Two bears weighed in excess of 136 kg, which was the capacity of our scale; their weight was estimated.

[b] Any 2 means within an age class and season with different letters are significantly ($P = 0.5 \div 3 = 0.0125$, Bonferroni t) different.

[c] Six bears weighed in excess of 136 kg, which was the capacity of our scale; their weight was estimated.

GROWTH AND BODY WEIGHT

As reported by others (Jonkel and Cowan 1971, Rogers 1976, Bunnell and Tait 1981), age at first reproduction, reproductive interval, and litter size all appear to be dominated by nutritional condition. In Massachusetts, Elowe and Dodge (1989) observed that 26 of 28 adult females with access to high fat and carbohydrate mast diets produced cubs whereas 10 females with low carbohydrate fall diets failed to produce cubs. In northern Minnesota, Rogers (1976, 1987) noted that none of 16 female black bears weighing <67 kg on 1 October produced cubs, whereas 28 of 30 females weighing >80 kg produced cubs. He also observed that black bears that had consumed garbage had a larger mean litter size (3.4 vs. 2.5), an earlier age of first litter production (4.4 vs. 6.3 yrs), and a shorter interval between litters (2.0 vs. 2.3 yrs) than those existing on natural foods. Bunnell and Tait (1981) found that age of first reproduction correlates with the age at which females reach adult weight. Our observations support their findings.

Both sexes of bears grew slower on the 1947 burn area than on the 1969 burn area. Winter weights of yearlings of both sexes were significantly (Bonferroni $t = 6.07$, $P < 0.001$, $n = 50$) less in the 1947 burn area than in the 1969 burn area (Table 11) (Please recall that for an overall experimental-wise error of $P = 0.05$, the P value for Bonferroni t must be <0.0125 to be significant). Yearling males from both areas were significantly heavier (Bonferroni $t = 4.47$, $P < 0.001$, $n = 50$) than yearling females. Winter weights were indicative of growth in cubs during their first year. Similarly, spring weights of adult females from the 1947 burn area (55.9 kg) were less (Bonferroni $t = 5.06$, $P < 0.001$, $n = 70$) than those from the 1969 burn area (61.7 kg); weights of females from both areas were significantly less than those of males (1947 burn, Bonferroni $t = 11.07$, $P < 0.001$; 1969 burn, Bonferroni $t = 14.14$, $P < 0.001$) (Table 11). Adult males from the 1947 burn area tended to weigh less ($\bar{x} = 95.5$) than those from the 1969 burn area ($\bar{x} = 116.4$), but these 2 weights were not significantly different (Bonferroni $t = 1.77$, $P = 0.0415$, $n = 53$).

PHYSICAL CHARACTERISTICS OF BEARS

Physical condition of captured bears as indicated by blood parameters (Franzmann and Schwartz 1988) fluctuated seasonally. Blood profiles demonstrated that bears were in better condition in fall and winter than in spring and early summer. Average percent packed cell volume (PCV) was less in summer (41.5) than fall (45.7) and winter (48.9) when combined over both sexes. Using discriminant analysis, Franzmann and Schwartz (1988) found that the best parameters to determine good versus poor physical condition of female black bears were hemoglobin (Hb), alpha 1 globulin (A1G), and calcium (Ca); for males, the best parameters were globulin

(G), PCV, and albumin : globulin (A:G) ratio. We compared these blood parameters for adult male and female bears in the 1947 and 1969 burn areas during the spring (May and Jun) to see if blood constituents of bears in the 1969 burn area differed from those in the 1947 burn area, using a Hotellings-T^2 test (Winer 1971:305–308). The 3 blood constituents for females (T^2 = 0.05, P = 0.778) and males (T^2 = 0.22, P = 0.302) did not differ between the 2 areas. Franzmann and Schwartz (1988) used these parameters to evaluate and compare the condition of bears during the fall versus spring when large differences in body condition were apparent. They did not determine if the same parameters detected differences between populations during the same season when differences were less pronounced. Because of the large variation associated with measurements taken among individuals we were unable to detect differences between the 2 burns.

SURVIVAL

Excluding cubs, 139 different bears were monitored in the 1947 and 1969 burn areas. From 1978 to 1986 we observed 72 bears in the 1947 burn area, and from 1982 to 1986 we observed 67 bears in the 1969 burn area; we studied 51 and 43 of these bears for a period of from 1 to several years (Appendix B) in the 1947 and 1969 burn areas.

Survival data were derived from a sample equivalent to 240 and 181 bear years in the 1947 and 1969 burn areas, respectively (Table 12). During that period, 66 bears died: 31 in the 1947 burn and 35 in the 1969 burn (Table 13). Thirty-nine were killed by hunters, 4 were wounded by hunters and died later, 1 was snared, 2 starved, 7 were killed by other bears, and 13 died of undetermined causes. Survival estimates were derived for cubs, yearlings, and subadult and adult males and females. We combined data from 1978 to 1981 with data 1982 to 1986 in the 1947 burn area because comparisons indicated survivor functions were not different for yearlings (χ^2 = 0.10, 1 df, P = 0.752), subadult fe-

males (χ^2 = 0.57, 1 df, P = 0.450), subadult males (χ^2 = 0.14, 1 df, P = 0.708), adult females (χ^2 = 0.02, 1 df, P = 0.888), and adult males (χ^2 = 2.18, 1 df, P = 0.140); we did not combine data for cubs because years 1978–81 were significantly different than years 1982–86 (χ^2 = 5.8, 1 df, P = 0.016).

Annual Survival and Cause-specific Mortality

Annual cub survival in the 1947 burn area during 1982–86 (0.74) was significantly (Z = −1.96, P = 0.047) lower than that in the 1969 burn area (0.91) (Table 12). Cub survival in the 1947 burn area from 1978 to 1981 was 1.0.

From 1982 to 1986 we observed 18 litters (36 cubs) in the 1947 burn area and documented 9 deaths (Table 13). Because we did not have radio collars on 8 of these cubs, causes of death were speculative except for the 1 radio-collared cub that was killed and eaten by a brown bear. This cub was 1 of 3 siblings orphaned when a radio-collared female (B1) was killed by a hunter on 27 July 1985. Of the 6 remaining unmarked cubs, 2 probably were eaten by a black bear. Female B51, an adult with 2 cubs, was killed and eaten by a 10-year-old male black bear (B25) in the spring of 1983. We suspect her 2 cubs also were eaten by B25, although no remains were found. Cause of death of the other 4 cubs was unknown.

In the 1969 burn area, we followed 43 cubs from 17 litters and observed only 4 deaths. Although we did not confirm specific causes of death, a contributing factor in 2 of the deaths was the loss of the mother (C58) to a hunter in September 1985.

We did not quantify early mortality of cubs prior to den emergence in the spring; however, we knew some died during this period. On 3 occasions, females known to have cubs in the den (based on cub vocalizations) were not accompanied by cubs after emergence in spring. Dens of these females did not contain cub remains, and causes and timing of cub losses were unknown.

Table 12. Annual survival (1 May–30 Apr) of radio-collared bears in the 1947 and 1969 burn areas on the Kenai Peninsula, Alaska.[a]

	1947 burn					1969 burn				
	No. of	No. of	Annual survival		% cen-	No. of	No. of	Annual survival		% cen-
Age	bears[b]	deaths	Survival	95% CI	sored	bears[b]	deaths	Survival	95% CI	sored
Cubs										
(May–Jan)[c]	39 (20)[d]	9 (0)	0.74 (1.0)	0.60–0.88	1.7 (0)	43	4	0.91	0.82–0.99	0.0
Yearlings	29	5	0.81	0.64–0.97	17.2	34	7	0.73	0.54–0.91	38.2
2- and 3-yr olds										
Male	16	3	0.70	0.45–0.95	37.5	14	7	0.38	0.00–0.79	35.7
Female	25	1	0.93	0.79–1.00	12.0	20	6	0.66	0.43–0.89	20.0
>4 yrs										
Male	50	5	0.90	0.81–0.99	22.0	21	4	0.77	0.56–0.98	23.8
Female	85	8	0.89	0.82–0.96	14.3	49	7	0.85	0.74–0.95	12.2
Total	244	30				181	35			

[a] The 1947 burn data span 1978–86; 1969 burn data span 1982–86.
[b] Bear numbers represent all individuals monitored in all years. Bears monitored >1 year therefore were counted more than once.
[c] Cub survival estimates began after den emergence; therefore, early survival from February to April was not measured.
[d] Survival rates for cubs were different in the 1947 burn in years 1978–81 and 1982–86; data are presented separately with the number in parentheses being the 1978–81 data.

Annual survival rates for yearlings were not significantly different in the 1947 (0.81) and 1969 (0.73) burn areas (Table 12, $Z = 0.72$, $P = 0.47$). Yearling survival was similar to cub survival in the 1947 burn area ($Z = 0.67$, $P = 0.50$); although yearling survival was much lower than cub survival in the 1969 burn area, the two were not different ($Z = 1.85$, $P = 0.06$).

During 1978–86 we radio-tracked 29

Table 13. Cause specific mortality for black bears in the 1947 burn area (1978–86) and the 1969 burn (1982–86) on the Kenai Peninsula, Alaska.

	Man-caused			Natural				
Areas and age class	Hunting	Other	Total	Starvation	Predation	Total	Unknown	Total
1947 burn								
Cub	0	0	0	0	5[a]	5	4	9
Yearling	1	0	1	2	1[b]	3	1[c]	5
Subadult male	2	1[d]	3	0	0	0	0	3
Subadult female	1	0	1	0	0	0	0	1
Adult male	3	1[d]	4	0	0	0	1[c]	5
Adult female	6	1[d]	7	0	1[b]	1	0	8
Subtotal no. (%)	13 (42)	3 (10)	16 (52)	2 (6)	7 (23)	9 (29)	6 (19)	31
1969 burn								
Cub	0	0	0	0	0	0	4	4
Yearling	7	0	7	0	0	0	0	7
Subadult male	7	0	7	0	0	0	0	7
Subadult female	4	1[e]	5	0	0	0	1[f]	6
Adult male	4	0	4	0	0	0	0	4
Adult female	4	1[d]	5	0	0	0	2[f]	7
Subtotal no. (%)	26 (74)	2 (6)	28 (80)	0 (0)	0 (0)	0 (0)	7 (20)	35
Total no. (%)	39 (59)	5 (8)	44 (67)	2 (3)	7 (11)	9 (14)	13 (20)	66

[a] Three were killed by brown bears and 2 by black bears.
[b] Black bear predation.
[c] Natural causes.
[d] Crippling loss.
[e] Snared.
[f] Suspected man-caused death.

yearlings and observed 5 deaths in the 1947 burn area. One yearling was eaten by a black bear (predation), 2 starved (different litters), 1 died from unknown natural causes, and 1 was shot by a hunter (Table 13). The 2 yearlings that starved to death, died in the spring following a year with a poor fall berry crop and a winter with little snowfall and heavy rain (Schwartz et al. 1982). Weights of these 2 yearlings (9.6 ± SE 0.5 kg) were significantly lighter than mean body weights of yearling bears caught in other years (22.9 ± SE 1.5 kg, $n = 5$). We radio-tracked 34 yearlings in the 1969 burn area from 1982 to 1986 and observed 7 deaths; all were hunter caused.

Annual survival rates for subadult males (Table 12) were the lowest for any age class examined (0.70 and 0.38 for 1947 and 1969 burn areas). Although the estimate of survival in the 1947 burn was almost 2 times higher than that of the 1969 burn, the two were not significantly different ($Z = 1.30$, $P = 0.19$). Confidence intervals about both estimates were large (Table 12) because of a small sample size in combination with censoring; 11 of 30 individuals (37%) were censored during the study. Censoring was caused by shed radios or dispersal from the area and subsequent lost radio contact.

During the period 1978–86, we radio tracked 16 subadult males in the 1947 burn area and observed 3 deaths (Table 13). Two bears were shot by hunters, and the third was a presumed wounding loss (Schwartz et al. 1983). During 1982–86 we radio tracked 14 bears in the 1969 burn area and observed 5 deaths; all were hunter caused (Table 13).

Survival of subadult females was significantly greater ($Z = 1.98$, $P = 0.50$) in the 1947 burn area (0.93) than in the 1969 burn area (0.66). During 1978–86 we radio tracked 25 bears in the 1947 burn; 1 was shot by a hunter. During 1982–86, we observed 20 bears in the 1969 burn area and documented 6 deaths: 4 from hunters, 1 from a wolf snare inadvertently left after the trapping season, and 1 from unknown causes.

Survival of adult females in the 1947 burn area (0.89) was similar to that of subadult females. In the 1969 burn area, adult female survival (0.85) was second only to cub survival (0.91) (Table 12). Survival rates of adult females in the 1947 burn area were not different from those of the 1969 burn areas ($Z = 0.74$, $P = 0.46$). During 1978–86 we radio tracked 84 female bears in the 1947 burn area and observed only 8 deaths: 6 from hunters, 1 (B15) probable wounding loss, and 1 (B51) black bear predation. We observed 49 female bears during 1982–86 in the 1969 burn area and documented 7 mortalities: 4 from hunters, 1 (C58) probable wounding loss, and 2 of unknown causes (both bears were found in advanced states of decay and died during the fall when most hunting occurred).

Survival rates of adult males in the 1947 burn during 1978–86 (0.90) were not different ($Z = 1.11$, $P = 0.27$) from the 1969 burn area (0.77) (Table 12). Similarly, the survival rate of adult males was not different from adult females in the 1947 burn ($Z = 0.08$, $P = 0.94$) and 1969 burn ($Z = 0.65$, $P = 0.52$) areas. During 1978–86 we radio tracked 50 male bears in the 1947 burn area and documented 5 deaths: 3 from hunters, 1 (B11) probable crippling loss, and 1 (B8) probable natural death (Schwartz and Franzmann 1980, Schwartz et al. 1983). During 1982–86 we radio tracked 23 adult male bears in the 1969 burn area and observed 6 deaths; all 6 were due to hunting.

Hunting was the primary source of mortality for all age classes, except cubs (Table 13). In the 1969 burn area, all deaths were attributed to humans with the possible exception of 2 adult females and 1 subadult female. In the 1947 burn area, hunting and human-caused mortality accounted for 52% of all mortality (including cubs) and 88% of the mortality in subadult and adult bears (Table 13).

We also estimated survival rates for all bears each year of the study (Table 14). Annual survival in the 1947 burn area was high during 1978–83, declined in 1984 and 1985, and then increased again in 1986. Cub mortality and hunter harvest of adult and juvenile bears in 1984 and 1985 con-

Table 14. Survival for black bears in the 1947 burn area (1978–86) and the 1969 burn (1982–86) on the Kenai Peninsula, Alaska. Estimates include all bears.

Year	1947 burn				1969 burn			
	No. at risk	No. of deaths	Survival estimate	95% CI	No. at risk	No. of deaths	Survival estimate	95% CI
1978	16	1	0.93	0.80–1.00				
1979	25	0	1.00	1.00–1.00				
1980	31	4	0.85	0.72–0.99				
1981	27	3	0.86	0.71–0.99				
1982	30	1	0.97	0.89–1.00	25	3	0.87	0.73–1.00
1983	37	3	0.90	0.80–1.00	45	3	0.92	0.83–1.00
1984	35	8	0.76	0.62–0.90	46	4	0.90	0.80–1.00
1985	39	10	0.72	0.58–0.86	51	23	0.51	0.36–0.66
1986	33	0	1.00	1.00–1.00	14	2	0.86	0.64–1.00

tributed to the lower survival rates in those years. Survival in the 1969 burn was high in all years (1982–84 and 1986) except 1985. Cub mortality and high harvest by hunters of subadult and adult bears contributed to the poor survival rate in 1985.

Cannibalism has been reported in black bears elsewhere (LeCount 1982, 1987; *see* Rogers 1987:table 12) in North America. In this study we witnessed 2 cases (yearling male, adult female) and suspected a third case (2 cubs).

Predation of black bears by other carnivores is uncommon (LeCount 1987, Rogers 1987), but mortality in black bears due to brown bear attacks has been reported (Hornocker 1962, Jonkel and Cowan 1971, Murie 1981). During our studies we documented 1 case of predation and suspected 2 others; all 3 cubs were orphaned, which likely precipitated the event. We also observed 2 interspecific encounters between black bears and brown bears. In both cases, the black bear fled the area when it detected the presence of the brown bear (Schwarz et al. 1983).

Survival rates in cubs vary considerably throughout North America (Bunnell and Tait 1985). For example, LeCount (1987) witnessed 48% cub mortality in a heavily exploited population (24% of animals were shot annually) in northern Arizona and 52% cub mortality in a stable old-aged population in central Arizona that was lightly exploited (1.8% adult mortality annually) (LeCount 1982:865). Elowe (1987) documented 41% mortality in Massachusetts,

and Jonkel and Cowan (1971:30, 42) estimated survival rates in Montana at 95% when research and hunting mortalities were excluded and 86% when all deaths were included. Kemp (1972:30) estimated black bear cub survival rates in an unexploited population in Alberta, based on a trap–retrap program, to be 73%, and Erickson and Petrides (1964:66) estimated maximum annual survival rates of tagged cubs in Michigan at 74%.

Cub survival can be limited by habitat quality (Rogers 1987:53), social regulation (Lecount 1982, 1987), and experience of the mother (Elowe 1987, Elowe and Dodge 1989). We did not find a significant relationship between fall food abundance and cub survival. The sex ratio and proportion of adult males was not different between areas, and cannibalism was suspected in only 2 cases of cub mortality. Experience of the female in rearing young likely influenced cub survival.

Hunting and other human activities represented the greatest cause of mortality in many bear populations (except cubs) throughout North America. Manville (1983) estimated that 10–18% of a marked bear population was known or suspected of being shot annually from 1977 to 1980 on a study area in the lower peninsula of Michigan. Similarly, Kolenosky (1986) estimated that hunters annually removed an average of 18% of available males and 10% of available females during spring hunts and 5% of available males and 2% of available females during fall hunts from an On-
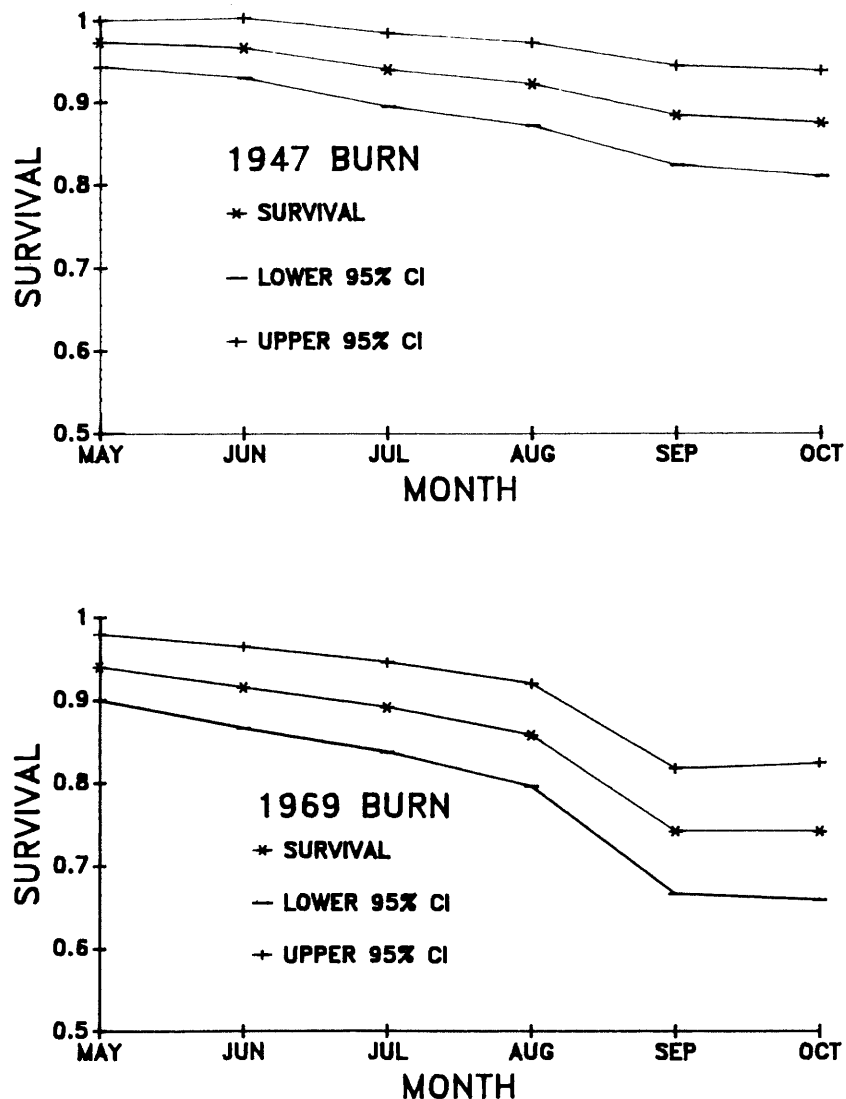
Fig. 7. The Kaplan-Meier survival function (modified for staggered entry of animals) for black bears (age > cub) in the 1947 and 1969 burn areas, Kenai Peninsula, Alaska, 1982–86.

tario study area. LeCount (1982) documented a heavy exploitation rate (24% annually) in his northern Arizona study area but only a 1.8% human-related mortality rate in adults in an unexploited old-aged population in central Arizona. Of the 126 marked bears older than cubs (Table 12) in the 1947 burn area during 1982–86, we documented 12 deaths (9.5%) attributed to humans (Table 13), while in the 1969 burn there were 28 (20.3%) human-caused deaths in 138 marked bears. Clearly the 1969 burn population was more heavily exploited than the 1947 popula-

tion. Except for cubs and subadult females, survival estimates were not different between study areas for other age and sex classes of bears, suggesting that hunting to a degree may represent a compensatory form of mortality.

Seasonal Survival Rates

We examined survival during 2 periods: the active and inactive. We observed no mortality in either study area during the inactive period (1 Nov–30 Apr); therefore, our estimate of survival for the denning
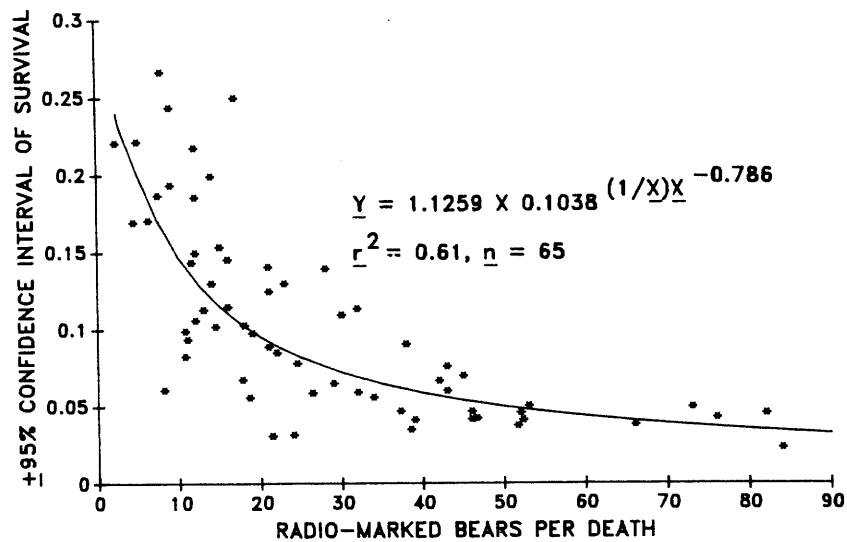
Fig. 8.   Relationship between 95% confidence intervals on survival rate of black bears and radio-collared bears per death from the Kenai Peninsula, Alaska.

season was 1.0. Because cub mortality was (1) different within the 1947 burn in early (1978–81) and later (1982–86) years of study, (2) different between the 1947 and 1969 burn areas during comparable years of study, and (3) influenced by annual variations in food abundance, we excluded cubs when we calculated seasonal survival curves for the 2 burn areas. Overall survival (i.e., at end of Oct) was greater (χ^2 = 5.77, 1 df, P = 0.016) in the 1947 burn (0.873) than the 1969 burn (0.741) (Fig. 7) during 1982–86. Lower survival in the 1969 burn was caused by the higher number of bears being shot.

Confidence Intervals

The 95% confidence intervals on survival rates varied with sample size and mortality rate (Table 12, Fig. 8). The 95% confidence intervals on survival rates for bears in the 1947 burn area generally were <0.17 and ranged from a high of 0.25 for subadult males to a low of 0.07 for adult females. Similarly, the 95% confidence intervals in the 1969 burn area generally were <0.23 but ranged from a high of 0.41 for subadult males to a low of 0.09 for cubs.

Our results indicated that a minimum of 19 bears/death/age class must be sam-

pled to obtain a 95% confidence interval no greater than ±10% on the survival estimates (Fig. 8), assuming no losses (death or censoring). Censoring resulted from premature radio failure, loss of breakaway collars on yearling and subadult bears, or dispersal from the area. Censoring varied (Table 12) among age classes and between sexes, with the greatest censoring occurring in juvenile males (35.7–37.5% of marked bears censored) and the lowest in adult females (12.2–14.3%). Given the survival rates we measured, it would require only 25–26 marked adult females in any year (19 ÷ 0.89 ÷ 0.857 = 25 for the 1947 burn; 19 ÷ 0.85 ÷ 0.875 = 26 for the 1969 burn) to obtain a 95% confidence interval of ±10% on the annual survival estimate. The denominators 0.89, 0.85, 0.857, and 0.875 were the yearly survival rates and proportion of noncensored animals (1 − censoring rate) for adult females in the 1947 and 1969 burn areas, respectively (Table 12). Given the poor survival and high censoring rates of juvenile males it would require marking between 43 and 78 individuals (19 ÷ 0.70 ÷ 0.625 = 43 for the 1947 burn area; 19 ÷ 0.38 ÷ 0.643 = 78 for the 1969 burn area) to obtain the same degree of precision. Sampling rates for other age classes fell between these estimates.

Table 15. Seasonal frequency of occurrence[a] (%) and mean volume (%) of food items eaten by black bears in the 1947 (1979–83) and 1969 (1982–83) burn areas and from old-growth summer feeding areas (SFA) on the Kenai Peninsula, Alaska.[b]

Food items	Spring				Summer						Fall					
	1947 (213)[c]		1969 (28)		1947 (89)		1969 (11)		SFA (24)		1947 (54)		1969 (17)		SFA (52)	
	Freq	Vol	Freq	Vol	Freq	Vol	Freq	Vol	Freq	Vol	Freq	Vol	Freq	Vol	Freq	Vol
Fruits and berries	23.6	11.0	16.4	10.8	23.1	23.8	34.3	51.5	45.4	51.3	59.2	57.2	58.9	68.5	69.7	73.9
Lowbush cranberry (Vaccinium vitis-ideae)	84.0	19.9	32.1	20.0	48.3	8.5	9.1	2.5	8.4	8.8	94.4	70.8	5.9	2.5	1.9	2.5
American devilsclub (Oplopanax horridus)	1.9	5.6	7.1	2.5	18.0	22.8	36.4	41.2	87.5	71.1	9.3	36.5	94.1	75.9	100.0	77.9
Claspleaf twistedstalk (Streptopus amplexifolius)	0.5	2.5	0.0	0.0	6.7	16.7	18.2	15.0	45.8	2.5	1.9	2.5	52.9	9.2	73.1	3.8
Cloudberry (Rubus chamaemorus)	0.0	0.0	0.0	0.0	3.3	6.7	0.0	0.0	4.2	2.5	9.3	2.5	0.0	0.0	11.5	2.5
Pacific red elder (Sambucus callicarpa)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	8.3	2.5	1.9	2.5	0.0	0.0	19.2	2.5
Current spp. (Ribes spp.)	0.0	0.0	0.0	0.0	1.1	15.0	0.0	0.0	12.5	2.5	0.0	0.0	5.9	2.5	3.8	8.8
Highbush cranberry (Viburnum edule)	0.0	0.0	0.0	0.0	0.0	0.0	9.1	2.5	8.3	8.8	3.7	2.5	17.6	2.5	1.9	37.5
Rosehips (Rosa spp.)	0.0	0.0	0.0	0.0	3.3	6.7	9.1	2.5	4.2	15.0	31.5	20.1	0.0	0.0	9.6	2.5
Red raspberry (Rubus idaeus)	0.0	0.0	0.0	0.0	2.2	8.8	9.1	15.0	4.2	2.5	9.3	14.5	11.8	8.8	13.5	4.3
Bunchberry dogwood (Cornus canadensis)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	5.9	37.5	0.0	0.0
Blueberry (Vaccinium spp.)	0.5	15.0	0.0	0.0	0.0	0.0	9.1	37.5	0.0	0.0	3.7	2.5	0.0	0.0	0.0	0.0
Crowberry (Empetrum nigrum)	0.0	0.0	0.0	0.0	0.0	0.0	9.1	37.5	0.0	0.0	1.9	2.5	0.0	0.0	0.0	0.0
Flowers	1.5	8.2	0.0	0.0	10.3	10.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Clover (Trifolium spp.)	3.3	12.9	0.0	0.0	34.8	6.8	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Lousewort (Pedicularis spp.)	2.3	19.0	0.0	0.0	2.2	32.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

Table 15. Continued.

Food items	Spring 1947 (213)c Freq	Vol	Spring 1969 (28) Freq	Vol	Summer 1947 (89) Freq	Vol	Summer 1969 (11) Freq	Vol	Summer SFA (24) Freq	Vol	Fall 1947 (54) Freq	Vol	Fall 1969 (17) Freq	Vol	Fall SFA (52) Freq	Vol
Green vegetation	34.7	47.6	49.3	49.4	28.9	51.5	25.7	34.9	15.5	39.9	20.4	33.7	14.3	16.4	12.0	19.5
Horsetail (*Equisetum* spp.)	60.6	39.1	92.9	67.6	39.3	52.5	54.5	55.0	29.2	45.4	7.4	20.6	35.3	28.3	11.5	2.5
Grass and sedge	43.2	27.4	21.4	30.4	19.1	9.6	9.1	2.5	4.2	2.5	9.3	12.0	0.0	0.0	17.3	3.9
Clover leaves, stems	13.6	37.0	0.0	0.0	42.7	68.1	0.0	0.0	0.0	0.0	5.6	50.8	0.0	0.0	0.0	0.0
White spruce cambium (*Picea glauca*)	0.9	37.5	0.0	0.0	0.0	0.0	9.1	37.5	0.0	0.0	0.0	0.0	0.0	0.0	3.8	26.2
Menziesia leaves	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	33.3	3.9	0.0	0.0	0.0	0.0
Claspleaf twistedstalk	2.8	12.5	0.0	0.0	1.1	15.0	9.1	2.5	25.0	2.5	1.9	2.5	11.8	2.5	7.7	2.5
Pedicularis leaves	2.8	6.7	3.6	2.5	1.1	37.5	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Black cottonwood leaves (*Populus trichocarpa*)	3.8	20.9	0.0	0.0	0.0	0.0	0.0	0.0	4.2	37.5	0.0	0.0	0.0	0.0	0.0	0.0
Vertebrates	22.9	29.3	20.9	37.4	13.2	9.7	14.3	8.9	11.3	6.6	14.4	6.6	10.7	12.3	5.1	3.9
Moose, calf (*Alces alces*)	31.0	21.9	28.6	23.8	16.9	17.5	0.0	0.0	0.0	0.0	11.1	4.6	0.0	0.0	0.0	0.0
Moose, adult	21.1	13.7	10.7	14.2	15.7	7.7	0.0	0.0	20.8	7.5	18.5	8.5	0.0	0.0	1.9	2.5
Snowshoe hare (*Lepus americanus*)	14.1	16.9	7.1	2.5	10.1	3.9	27.3	6.7	12.5	2.5	3.7	2.5	17.6	22.5	5.8	2.5
Birds (*Aves*)	11.7	13.7	3.6	37.5	4.5	5.6	18.2	20.0	8.3	2.5	7.4	2.5	17.6	2.5	0.0	0.0
Fish (*Orcorhyncus* spp.)	2.8	6.7	0.0	0.0	0.0	0.0	0.0	0.0	4.2	2.5	0.0	0.0	0.0	0.0	9.6	2.5
Black bear (*Ursus americanus*)	3.8	41.9	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
Invertebrates	17.3	3.5	13.4	2.4	24.5	4.2	25.7	4.3	27.8	2.2	5.9	2.4	16.0	2.4	13.1	2.6
Insects, ants, and bees	58.2	10.3	21.4	2.5	74.2	12.5	54.5	10.4	58.3	2.5	14.8	4.1	17.6	2.5	9.6	2.5
Insect larvae, maggots (*Diptera* spp.)	5.6	3.5	10.7	2.5	13.5	2.5	27.3	2.5	54.2	2.5	1.9	2.4	35.3	2.5	34.6	2.5

a Relative % frequency of occurrence of food group (i.e., fruit and berries, green vegetation, etc.) in the diet during a season. This % frequency for all 5 food groups sums to 1.0.
b Seasons: spring = den emergence to 30 June, summer = 1 July–15 August, and fall = 16 August to den entrance.
c Number of scats examined given in parentheses.

1947
SPRING

1969
SPRING

1947
SUMMER

1969
SUMMER
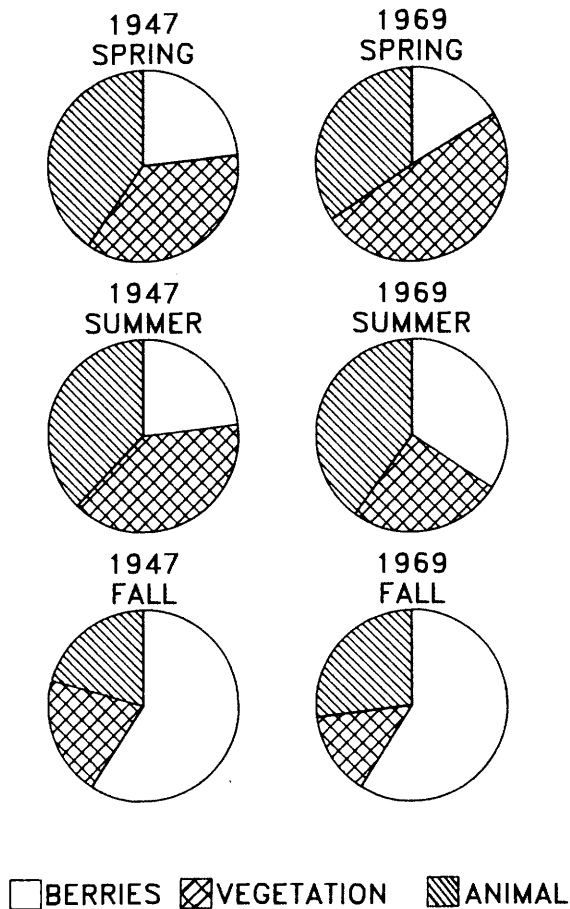
1947
FALL

1969
FALL

☐BERRIES ▨VEGETATION ▧ANIMAL

Fig. 9. Frequency of occurrence of seasonal food groups eaten by black bears in the 1947 (1978–83) and 1969 (1982–83) burn areas. Seasons were spring (1 May–30 Jun), summer (1 Jul–15 Aug), and fall (16 Aug–30 Oct).

FEEDING ECOLOGY

Food habits of black bears were evaluated from scat analysis in the 1947 area during 1979–83 and during 1982–83 in the 1969 area (Table 15, Fig. 9) (Smith 1984). Consumption of the major food groups (i.e., berries, flowers, vegetation, and animal matter) varied between the 3 seasons (Fig. 9); the most noticeable change occurred in the fruit and berry component of the diet.

Spring Foods

The index of diversity of foods eaten in the spring by bears in the 1947 burn (J = 0.69) was significantly greater (t = 4.54, df 553, P = 0.001) than in the 1969 burn (J = 0.60). The higher index of diversity in the 1947 burn was likely caused by more

foods being available in the 1947 burn coupled with a higher sampling rate of scats in the 1947 burn. The increased sampling rate increased the probability that rare or infrequently consumed foods were identified in fecal remains. The greater diversity of foods is discussed below.

In spring, bears in both areas ate primarily green vegetation (i.e., 5 different species of *Equisetum*) that was common throughout both areas in all forest types (Table 15); of secondary importance were grass and sedge. Based on microhistological examination of plant fragments in scats, bluejoint reedgrass, which grew abundantly throughout both areas, accounted for 76% of the grass–sedge component of the diet. Other species consumed in lesser amounts were tufted fescue (*Festuca altaica*), sweetgrass (*Hierochloe* spp.) (representing 5%), and sedge (*Carex* spp.) (accounting for 14%). Scats from bears in the 1947 burn area also contained considerable quantities of clover (*Trifolium* spp.), introduced species planted along roadsides and rehabilitated oil exploration trails.

Berries were more frequent in spring scats of bears in the 1947 burn than the 1969 burn area. Bears in the 1947 burn area ate lowbush cranberries when available. These berries were persistent on the plant over the winter, and in many years were available in the spring. Most lowbush cranberry was killed by the 1969 burn, so bears fed on cranberry in the remnant unburned forests where production was similar to the 1947 burn.

Animal matter, including both vertebrates and invertebrates, composed the second major food group for both areas during the spring period. Major vertebrates included moose (calf and adult), snowshoe hare (*Lepus americanus*), and birds. Moose calves were prey items (Franzmann et al. 1980, Franzmann and Schwartz 1986), whereas adult moose probably were scavenged from winter and wolf kills. It was difficult to determine if snowshoe hares and birds were consumed as prey items or scavenged. The presence of eggshells in some scats indicated nest predation. The occurrence of snowshoe

hares in scats, particularly from the 1947 burn area where we had several years of data, indicated an increased frequency of occurrence that followed the general trend in hare abundance. For example, the percent frequency of occurrence of hare remains in scats from the 1947 burn area from 1979 through 1983 was as follows: 4.7, 3.3, 8.6, 14.4, and 30.0%, respectively. Hare numbers peaked in 1984 (Kesterson 1988). The presence of white, winter hair in some scats indicated that some of the hares consumed were eaten as carrion.

Invertebrates occurred in 13–17% of all scats examined during the spring period (Table 15). Carpenter ants (*Camponotus herculeanus*) and field ants (*Lasius* spp.) were common in scats during the spring and summer periods. During the late spring (mid-May) through early summer (early Jul), bears in the 1947 burn area often were observed actively feeding on ants. During this period, it was not uncommon to observe rotten logs that had been ripped open by bears. The burned trees in the 1947 burn were ideal habitat for carpenter ants. The burned wood from the 1969 fire was still sound (i.e., not rotted) and consequently contained fewer ants. The frequency of occurrence of ants in scats from the 1947 burn area was higher (58%) than that from the 1969 burn area (21%); ant availability probably accounted for the difference.

Moose Calf Predation

Concurrent to our bear studies, we investigated moose calf mortality in the 1947 burn area during the years 1977 and 1978 (Franzmann et al. 1980) and in the 1969 burn area during the years 1982 and 1983 (Franzmann and Schwartz 1986). Predation rates of neonatal moose (i.e., collared calves killed by black bears) were nearly identical (i.e., 34 vs. 35%) in the 1947 and 1969 burn areas, respectively. However there were fewer calves consumed by black bears in the 1947 burn area because the absolute density of calves there was much less. This difference equated to approximately 1.4 calves eaten per bear (range

0.4–2.5) in the 1947 burn area, compared to >5.4 (range 4.5–6.4) calves eaten per bear (older than cub) in the 1969 burn area. Assumptions and data used for calculations in the above estimate are shown in Appendix F.

Moose calves represented a source of protein and energy to bears during spring when other foods (e.g., grasses and other green plants) were insufficient to meet maintenance requirements (Jonkel and Cowan 1971, Poelker and Hartwell 1973, Rogers 1976). The digestible energy contained in a moose calf provided 5–10 days ($\bar{x} = 7.5$) worth of energy to an adult female bear, depending on her requirements (Appendix G). This equated to 10.5 (1.4 × 7.5) versus 40.0 (5.3 × 7.5) days of energy requirements for an adult female bear in the 1947 and 1969 burn areas, respectively.

Most moose calf predation by black bears occurred from birth to about 30 days of age. Franzmann et al. (1980) and Franzmann and Schwartz (1986) indicated that predation was virtually over by 1 July when moose calves were capable of outrunning a pursuing black bear. During this period (i.e., 25 May–30 Jun), we observed black bears on 5 kills in the 1947 burn area (yrs 1978–84) and 8 kills in the 1969 burn area (yrs 1982–84). These 13 kills were made by 3 male and 10 female bears all ≥2 years of age. We made these observations from 383 and 160 visual sightings of bears ≥2 years old in the 1947 and 1969 areas, respectively. We observed lone males, lone females, and females with cubs or yearlings on kills. We compared the frequency of kills by area and sex using a logit log-linear model (Agresti 1984). There was a significant difference in number of kills ($G^2 = 5.62$, 1 df, $P = 0.018$) between areas but not between sexes of bears making the kills ($G^2 = 0.001$, 1 df, $P = 0.974$), supporting the contention that bears in the 1969 burn area were killing more moose calves. The lack of a significant sex effect suggested that both male and female bears (except for cub and yearling) were killing moose calves proportionate to their occurrence in our marked population.

The early literature suggested that black bears played a minor role as predators (Seton 1929, Bradt 1946, Chatelain 1950, Erickson 1965, and Juniper 1978). Animal remains in scats of black bears have been presumed to be carrion (Hatler 1967) often with no supportive evidence. Other early researchers (W. G. Culver, 1923, Report on moose on the Kenai Peninsula, Kenai Natl. Wildl. Refuge, Soldotna, Alas., 18pp., unpubl.; L. J. Palmer, 1939, Kenai Peninsula moose, Res. Proj. Rep., Bur. of Biol. Serv., Sep–Oct 1938, Kenai Natl. Wildl. Refuge, Soldotna, Alas., 24pp., unpubl.; H. R. Saber, 1944, Report of the moose studies, National Moose Range, Kenai Peninsula, Alaska, Kenai Natl. Wildl. Refuge, Soldotna, Alas., 10pp., unpubl.) and more recent information (Franzmann et al. 1980, Franzmann and Schwartz 1986) have implicated black bears as major predators of moose calves. Of 241 scats examined from both areas during the spring period, 69% contained no remains of moose calves and 23% contained a volume <25%. Only 8% of all the scats we examined contained a large quantity of moose calf remains.

Calf predation studies and our observations of black bears substantiated that bears killed more moose in the 1969 burn, yet the frequencies of occurrence of moose calf remains found in scats in the 1947 (31%) and 1969 (29%) burn areas were not significantly different (χ^2 = 0.06, 1 df, P = 0.806). Similarly, the distribution among volume categories (i.e., 0, >0–5, >5–25, >25–50, and >50%) of moose calf in scats in the 1947 burn (69, 14, 9, 3, and 5%) was not significantly different (χ^2 = 2.26, 4 df, P = 0.133) from the volume in the 1969 burn (71, 7, 14, 4, and 4%). Also, in the 1947 burn where we collected scats over a 5-year period (1979–83) while moose numbers in the area were declining, we could not detect a significant difference (χ^2 = 1.80, 4 df, P = 0.772) in the frequency of occurrence of moose calf remains in scats. We detected a difference (χ^2 = 13.8, 4 df, P = 0.008) in the percent volume of moose calf remains among years (1979–83) in the 1947 burn, but there was no consistent trend. The fluctuation likely represented variation in sampling scats

containing trace to high volumes of moose calf. Our data suggested that because of extreme variation in calf remains in bear scats, it was almost impossible to detect differences in calf consumption rates based on fecal analysis. Supplemental data (observations of marked bears, calf mortality studies, and bear and moose demographics) verified differences in consumption rates.

Digestion of foods eaten by bears was greater for animal material than herbaceous vegetation (Hewitt 1989), and the volume of animal matter in feces often was less than that consumed (Hatler 1967). In brown bears, digestion of protein and fat was 92.2 and 91.8%, respectively (Bunnell et al. 1978), and thus a few dozen hairs potentially represented several kg of consumed meat. This was particularly true for bears eating moose calves where varying amounts of hide and hair were consumed at kills (Ballard et al. 1979). In our studies of black bear predation of moose calves, almost the entire hide was intact at 34% of examined kills (n = 35), only part of the hide was consumed (i.e., ears, head, part of back or belly) at 46%, but the hide was completely consumed at 20%.

Hewitt (1989) developed correction factors for estimating intake of bear foods from fecal samples. For herbaceous material, the correction factor was 0.25 (i.e., for every 100 g dry matter consumed, 250 ml of undigested material was passed in the feces). For white-tailed deer fawns (*Odocoileus virginianus*) the correction factor varied from 1.5 when the entire carcass was consumed to 15 if the skin and hair were not ingested. Using these correction factors, if a bear scat contained 10% moose remains and 90% vegetation, the dietary intake of moose represented close to 40% of the diet when the entire carcass was consumed and 87% of the diet when skin and hair were not ingested. It was apparent that predicting the amount of moose calf consumed based upon the proportion remaining in feces was subject to error because it was impossible to determine the amount of hide and hair consumed when examining a scat.

Based on the number of times we sight-

ed black bears on calf kills and the relatively low occurrence of moose calf in scats, it was easy to understand why other researchers concluded that black bears were not important predators. It was only when we radio collared the prey that we learned the significance of this predation to the moose population (Franzmann et al. 1980, Franzmann and Schwartz 1986).

Schwartz and Franzmann (1989) discussed the implications of black bear predation on moose population dynamics on the Kenai Peninsula. Moose numbers have fluctuated with habitat quality and rates of predation. However, it was difficult to determine which agents (predation and/ or habitat) influenced moose population change at any given time. Schwartz and Franzmann (1989) concluded that predation and habitat quality operated in concert to control moose numbers. Mortality by either agent acted in a compensatory or noncompensatory fashion depending upon habitat quality, predator density, or winter weather.

Summer Foods

Summer diet generally was transitional between the spring diet and that of the fall. In general there was an increase in the amount of fruit and berries consumed and a decrease in the consumption of green vegetation. The occurrence of moose calves declined in scats, which was consistent with data from Franzmann et al. (1980) and Franzmann and Schwartz (1986), who indicated that most calf predation by black bears ceased by July. Consumption of insects, mainly carpenter ants, was high in summer. Diversity of diets was not significantly different ($t = -1.48$, 687 df, $P = 0.070$) between the 1947 burn ($J = 0.73$) and the 1969 burn ($J = 0.75$) areas.

Summer Feeding Areas

In summer, bears from both study areas migrated to their traditional summer feeding areas (*see* Migration and Summer Feeding Areas). Individuals from both study areas used the same summer areas, and we believe that food habits of both

groups of bears (i.e., the 2 study areas) during this period were essentially identical. Consequently, food habits from summer feeding areas represent foods consumed by both groups of bears (Table 15).

Foods eaten in the summer feeding areas were almost entirely American devilsclub and claspleaf twistedstalk berries (*Streptopus amplexifolius*). Of all the foods identified in this study, American devilsclub fruit was probably the single most-often-observed dietary item. American devilsclub represented (1) the first fruit available in summer, (2) food sufficient in quantity and quality for hyperphagia and fat deposition, and (3) a generally reliable food source each year. The abundance of American devilsclub appeared to influence reproduction (*see* Effects of Food on Reproductive Success) and timing of migration back to traditional use areas (*see* Migration and Summer Feeding Areas). In years of abundant fruit production, many bears returned from their summer feeding area and immediately denned; this suggested that American devilsclub fruit provided adequate energy for winter hibernation.

Fall Foods

When bears returned to their traditional use areas, fall food habits differed between the 2 areas. Bears in the 1947 burn area consumed mainly lowbush cranberry until denning. Because cranberry was not abundant in the 1969 burn, bears consumed American devilsclub and claspleaf twistedstalk in the unburned remnant forests surrounding this burn (Table 15). Diet diversity did not differ ($t = 1.46$, 503 df, $P = 0.072$) between the 1947 burn ($J = 0.70$) and the 1969 ($J = 0.66$) burn areas.

Food Abundance and Distribution

There are only 2 plant groups consumed as green vegetation that occurred frequently in bear scats: *Equisetum* spp. and bluejoint reedgrass. Both of these were widely distributed throughout both study areas and were available in almost every habitat type. Because of the high density

and universal distribution of these plants, they did not limit bears.

Equisetum has been commonly reported as an important spring food of bears in both northern and western areas of North America (Chatelain 1950, Tisch 1961, Hatler 1967, McIlroy 1970, Schaffer 1971, Zytaruk and Cartwright 1978, Modafferi 1982, Miller 1983, MacHutchon 1989). Mealey (1975) calculated that *Equisetum* contained about 15% crude protein and had an apparent digestibility of 31%. Stelmock (1981) found 32 and 26% crude protein in *Equisetum* in samples collected in May and June, respectively.

Nutrient quality of vegetation can increase after fire, although hot fires (i.e., 1969 burn) volatilize organic nitrogen resulting in a net loss of nutrients (Spurr and Barnes 1973:188). Regelin et al. (1987) found a lower crude protein (i.e., the difference between same species in the 2 areas, $\bar{x}$ = 2.7%, range 0.9–4.2%) and higher fiber content (neutral detergent fiber) ($\bar{x}$ = −1.1%, range 0.5 to −5.3%) for browse and forbs examined in June in the 1947 versus 1969 burn areas. Pritchard (1989) indicated that bears digested plant proteins at about 88% and that for each percentage increase in dietary fiber there was a 1.4% decline in dry matter digestibility. Assuming similar changes occurred in grasses and *Equisetum* spp. between burns, this would equate to about a 2.3% increase in protein and 1.5% increase in dry matter digestion for herbaceous materials in the 1969 burn. This represented only a slight increase in diet quality and could not have accounted for the major differences in reproduction, growth, and survival that we observed.

Although bluejoint reedgrass, other grasses, and sedges were common in scats collected in spring, their occurrence was 2–4 times lower than that reported from other studies (Tisch 1961, Hatler 1967, Zytaruk and Cartwright 1978, Grenfell and Brody 1983). The nutrient quality of bluejoint reedgrass declines rapidly from early growth stages in May through boot stage in mid-June (McKendric et al. 1977).

The other major plant foods consumed by bears were berries of American devilsclub, lowbush cranberry, and claspleaf twistedstalk. Very little is known about American devilsclub, though it has been identified as an important food of brown bears on Afognak Island (Clark 1957) and of black bears in Washington (Poelker and Hartwell 1973), British Columbia (Lloyd and Fleck 1978), and the Susitna River area in Alaska (Miller 1983). Estimated abundance of American devilsclub berries varied over the 7-year period; there were abundant berries in 1979 and almost none in 1985 (Table 16).

On the northern Kenai lowlands, American devilsclub was associated with old-growth forest, particularly with black cottonwood and mixed mature white spruce and paper birch. Based on our field experiences, this plant species was extremely fire sensitive. There was no American devilsclub growing within the area burned in 1969, and it only occurred in unburned mature forest stands within the 1947 burn (Fig. 10). Immediately adjacent to both the 1947 and 1969 burns there were stands of mature forest with American devilsclub, further substantiating that this plant was fire sensitive.

We do not know when American devilsclub invades a burn, but based on our observations, the interval must be >40 years. Site requirements for American devilsclub include a mature forest overstory (Viereck and Little 1972); however, much of this forest type on the northern Kenai Peninsula did not contain an American devilsclub understory. Distribution of American devilsclub used by our marked bears on the northern Kenai lowlands occurred in a band from Point Possession south to the northern boundary of the 1947 burn area and around the perimeter of the 1969 burn area (Fig. 10); however, most stands were small (<2 km²).

Black bear density in some American devilsclub stands was high. For example, in 1 stand on the northern boundary of the 1947 burn area, it was not unusual to have 4–8 radio-collared bears within a 2.5-km² area; bear density was much higher than this because we commonly sighted uncol-

Table 16. Abundance of American devilsclub fruit in old-growth forest and lowbush cranberry fruit in the 1947 burn area on the Kenai Peninsula, Alaska, 1979–86.

| | | Abundance of lowbush cranberry | | | |
| | | | | Production[c] (kg/ha) | |
Year	Devilsclub estimate[a]	Estimate[a]	Quantity purchased[b] (kg)	$\bar{x}$	SE
1979	Abundant	Abundant	1,827		
1980	Scarce	Common	491		
1981	Scarce	Common[d]	491		
1982	Common	Common	609	28.5	8.0
1983	Common	Common	709	17.6	6.6
1984	Scarce	Scarce	272		
1985	Almost none	Common	1,300		
1986	No Data	Abundant	1,827		

[a] Abundance was determined by visually estimating the amount of fruit present.

[b] The quantity (kg) of lowbush cranberry purchased by Alaska Wild Berry Products, Homer, is given to show general trends in berry production throughout the Kenai Peninsula.

[c] Cranberry production (kg/ha) was measured in the 1947 burn area by picking plots in 1982 and 1983.

[d] Locally abundant in some habitat types.

lared bears within the area. Bears observed in American devilsclub stands appeared to tolerate each other.

Lowbush cranberry is generally killed by moderate-to-high-intensity fires. Such was the case in the 1969 burn area where the distribution of lowbush cranberry was associated with unburned forests (Table 17). There was some cranberry growing in the burned areas in upland stands of hard-
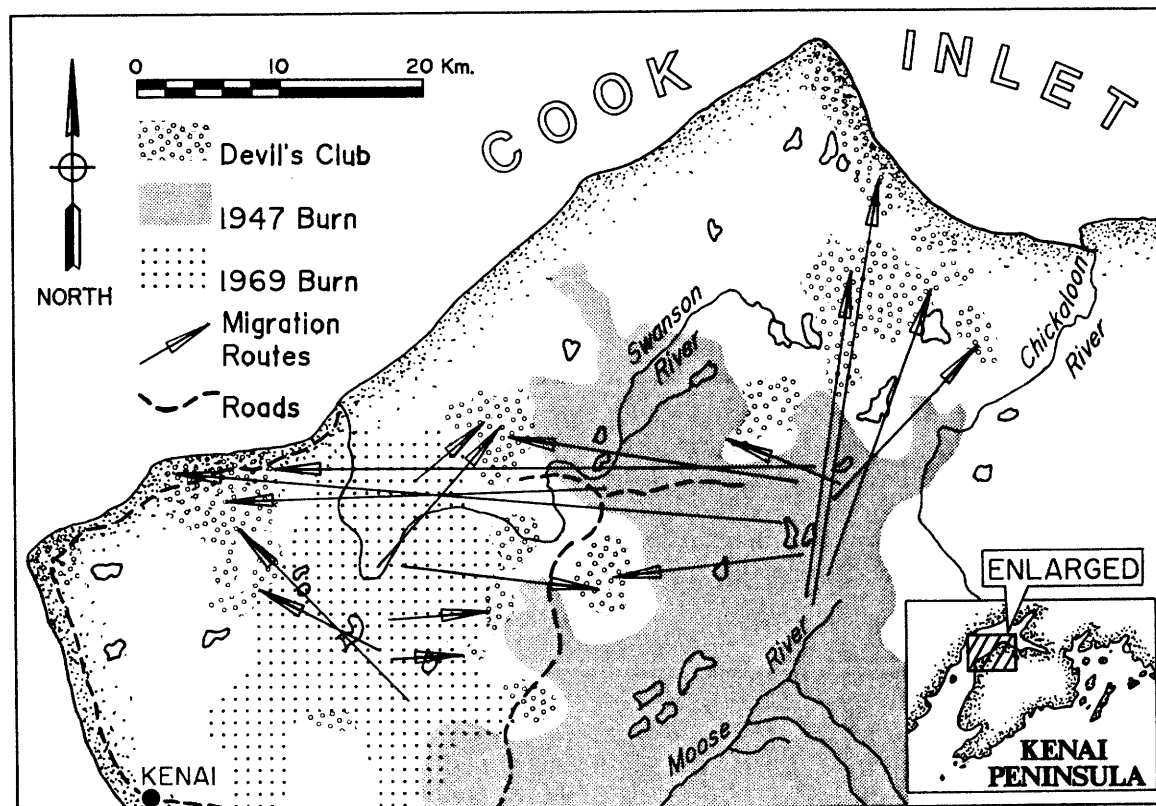

Fig. 10. Location of the 1947 and 1969 burn boundaries, the distribution of American devilsclub stands, and migration routes and locations of summer feeding areas for black bears radio collared in the 1947 and 1969 burn areas, Kenai Peninsula, Alaska, 1982–86.

Table 17. Dry matter and biomass estimates of lowbush cranberry fruit production and the frequency of occurrence of the plants (freq) by forest type on the northern Kenai Peninsula lowlands, Alaska, 1982–83.[a]

	1982			1983			
Burn age and habitat type	Dry matter (%)	Biomass (kg/ha)	SE	Dry matter (%)	Biomass (kg/ha)	SE	Freq[b]
Unburned forest							
Mature spruce	17.1	0.6	0.4				1.0
Hemlock	20.5	1.7	1.2				0.7
Mixed mature	16.0	4.0	2.8				0.6
1947 burn							
Mature deciduous	16.5	18.3	8.5	15.8	6.9	4.9	0.9–1.0
Mature spruce	17.1	0.6	0.3	17.0	1.4	1.0	0.9
Mixed mature	16.0	0.0	0.0	16.0	0.0	0.0	0.7–0.9
Mixed regrowth	15.8	3.0	0.6	16.3	3.1	0.8	1.0
Spruce regrowth	17.2	6.4	2.8	16.5	5.4	1.7	1.0
Crushed	15.9	0.1	0.03	15.9	0.2	0.2	0.9–1.0
1969 burn							
Mature deciduous	17.3	1.3	1.0				0.8
Mature spruce	16.5	1.7	0.7				0.8
Mixed mature	14.8	1.6	0.8				0.7
Deciduous regrowth	14.9	0.5	0.3				0.4

[a] Berry abundance and plant frequency of occurrence were measured in 80-m^2 plots in the 1947 and 1969 burn areas and on 40-m^2 plots in old-growth forest.

[b] Frequency of occurrence: 1 = 100% of plots contained plants; 0 = no plots contained plants.

wood regrowth; this probably represented invasion into the area and/or possibly remnant stands not killed by the fire. Plants of lowbush cranberry occurred on all upland sites that were forested (Table 17). Plants did not occur in wet bogs or areas subjected to seasonal flooding, but they did grow in bogs where there were hummocks or raised areas with dry soil.

Estimated production of lowbush cranberry fruit varied each year (Table 16). Our production estimates from the 1947 burn area paralleled the amount of fruit purchased by Alaska Wild Berry Products (Homer, Alas.), indicating that our estimates were reasonable. Harvesting of berries for sale on the Kenai Peninsula varied according to fruit production and not demand for the product. In the 2 years when >1,800 kg of cranberries were purchased, our estimates of production were abundant, and in the 1 year when <300 kg were purchased, we ranked production as scarce.

Measured production in the 1947 burn area in 1982 and 1983 varied from 28.5 to 17.6 kg/ha; our estimates for both of these years were "common," indicating that our

estimates were only general and large differences were required before they changed.

Production of fruit (kg/ha dry matter) of lowbush cranberry was greatest in the 1947 burn area in mature deciduous forest stands (18.3) (i.e., mainly mature birch forests that were burned by ground fires), regrowth of mixed hardwoods and spruce (3.0), and spruce regrowth (6.4) (Table 17). Berry production was poorest in recently burned 1969 deciduous regrowth (0.5) because of the low frequency of plants (Table 17). Although the frequency of occurrence of lowbush cranberry plants was high (0.6–1) in old-growth forests (i.e., unburned mature spruce, mixed mature in the 1947 burn, and western hemlock, *Tsuga heterophylla*), these plants were growing with several species of mosses and produced poor crops of fruit (Table 17). Lack of plants in early seral stages (1969 burn regrowth) precluded fruit production, whereas competition and reduced light associated with a closing of the forest canopy reduced fruit production in old-growth forests (Hall and Shay 1981, Holloway 1981).

Biomass (kg/ha wet weight) of fruit pro-

duced by lowbush cranberry was greatest in the deciduous forest (248), followed by spruce forest (74) and tundra (32.7) in interior Alaska (Hatler 1967:70–71). Estimated cranberry production (kg/ha wet weight) in natural habitats in Russia (Sautin et al. 1975) ranged from 6 to 74, whereas in tree plantations, production ranged from 41 to 246; production was inversely related to tree density. Our wet weight estimates ranged from as low as 0.07 to 111 kg/ha and variance estimates were generally high. With few exceptions, production estimates varied greatly within and between habitats (Table 17). Yields for cranberries reported in the literature differed widely, and high variability appeared universal.

Chatelain (1950), Hatler (1967), McIlroy (1970), Rogers (1976), Lloyd and Fleck (1978), Zytaruk and Cartwright (1978), Modafferi (1982), Miller (1983), and MacHutchon (1989) all reported that black bears used berries from the genus *Vaccinium* heavily. Only MacHutchon (1989) indicated that lowbush cranberry, *V. vitis-idaea*, occurred more often than other species of this genus. In some of the reports, species were not differentiated, whereas in others the abundance of lowbush cranberry was less than that of other species in this genus.

Like American devilsclub, claspleaf twistedstalk grew in old-growth forests. Unlike American devilsclub and lowbush cranberry, claspleaf twistedstalk was never found in high densities and there were relatively few berries per plant. We had no estimates of the abundance of claspleaf twistedstalk fruit by year.

Claspleaf twistedstalk occurred more frequently in scats from summer feeding areas and from the 1969 burn area in the fall. Because claspleaf twistedstalk grew in association with American devilsclub, its high occurrence in scats from summer feeding areas was not surprising. High use in the fall by bears in the 1969 burn area indicated that they spent much time feeding in remnant old-growth stands of timber within and surrounding the burn during the fall season. Radioed bears in the

1969 burn area substantiated this as 62% of all locations were in mature forest, yet only about 8% of the area was remnant mature forest. McIlroy (1970) reported that bears from the Prince William Sound area of Alaska fed on claspleaf twistedstalk. Although the frequency of occurrence in scats was relatively high for claspleaf twistedstalk, percent volumes were low (Table 15). Fruit of this species was high in water content and contained small seeds (hence the alternate name of watermelon berry) compared to American devilsclub.

Effects of Food on Reproductive Success

Reproduction in black bears is controlled mainly by food abundance in a density-independent fashion (Rogers 1976, 1983, 1987; Bunnell and Tait 1981; Elowe 1987; Elowe and Dodge 1989). Lowbush cranberry and/or American devilsclub were the major fall foods in the 2 areas. We compared cub production relative to the previous fall's abundance of these fruits (Table 18). In the 1947 burn area, cub production appeared related to the abundance of American devilsclub the previous fall, where 9 of 12, 10 of 15, and 14 of 28 females produced cubs in years following abundant, common, and scarce crops of American devilsclub, respectively (Table 18); however, the values were not different ($x^2 = 2.569$, 2 df, $P = 0.277$). When we compared pregnancy rates of poor versus average and abundant crops of American devilsclub combined, the frequencies still were not different ($x^2 = 2.377$, 1 df, $P = 0.123$). An abundance of lowbush cranberry did not improve cub production (Table 18).

Similarly, there was no apparent relationship between cub production and either American devilsclub or lowbush cranberry abundance in the 1969 burn area (Table 18). We suspect any possible relationship was obscured by the volume of moose calf meat consumed earlier in the season in that area.

During the years 1982–85, fewer adult females produced cubs in the 1947 burn

Table 18. Effects of American devilsclub and lowbush cranberry fruit abundance on cub production the next spring by adult females (age ≥3 yrs not already accompanied by cubs) and cub survival the same year in the 1947 and 1969 burn areas on the Kenai Peninsula, Alaska, 1978–85.

Fruit and abundance	Year	1947 burn		1969 burn		Cub survival	
		n	No. with cubs	n	No. with cubs	1947 burn	1969 burn
Devilsclub							
Abundant	1978	5	4				
	1979	7	5			1.0	
Mean (SE)		6 (1.2)	4.5 (0.6)			1.0 (0)	
Common	1982	7	4	6	5	1.0	1.0
	1983	8	6	6	5	0.75	1.0
Mean (SE)		7.5 (0.6)	5 (1.2)	6 (0)	5 (0)	0.88 (0.12)	1.0 (0)
Scarce	1980	4	0			1.0	
	1981	10	5	7	6		
	1984	7	6	6	5	0.79	1.0
	1985	7	3	3	3	0.52	0.50
Mean (SE)		7 (1.2)	3.5 (1.3)	5.3 (1.2)	4.6 (0.9)	0.66 (0.13)	0.75 (0.25)
Lowbush cranberry							
Abundant	1979	7	5 (0)			1.0	
Mean (SE)		7 (0)	5 (0)			1.0 (0)	
Common	1980	4				1.0	
	1981	10	5	7	6		
	1982	7	4	6	5	1.0	1.0
	1983	8	6	6	5	0.75	1.0
	1985	7	3	3	3	0.52	0.5
Mean (SE)		7.2 (1.0)	3.6 (1.0)	5.5 (0.9)	4.8 (0.6)	0.82 (0.12)	0.83 (0.17)
Scarce	1978	5	4				
	1984	7	6	6	5	0.79	1.0
Mean (SE)		7 (0)	5 (1.2)	6 (0)	5 (0)	0.79 (0)	1.0 (0)
Grand mean (SE)[a]							
	1978–85[b]	6.9 (0.6)	4.1 (0.7)			0.84 (0.08)	
	1982–85	7.3 (0.1)	4.8 (0.8)	5.3 (0.8)	4.5 (0.5)	0.76 (0.10)	0.88 (0.12)

[a] These values were the same for both fruits.
[b] Years 1978–85 for cub production and years 1979–85 for cub survival.

area (66%) than in the 1969 burn area (85%) (Table 18). These percentages reflect age of first reproduction and reproductive interval, which were older and longer, respectively, in the 1947 burn area. Cub survival in the 1947 burn area appeared related to American devilsclub fruit abundance (Table 18), although we do not believe this to be the case. Survival rates in years of abundant, common, and scarce crops of American devilsclub fruit were 100, 88, and 66%, respectively. However, 4 of 9 cubs died before American devilsclub was available in the fall, and 3 of 5 cub mortalities in the fall occurred because the females were shot.

We also looked at the relationship between cub survival and the year after excellent, average, or poor American devilsclub crops, but there was no relationship.

MIGRATION AND SUMMER FEEDING AREAS

Most radio-tracked bears left their traditional use areas and migrated some distance to stands of mature forest that contained American devilsclub in summer. Summer feeding areas for bears living in the 1947 burn area were geographically distinct from traditional use areas. Distance ($\bar{x} \pm$ SE) of summer feeding areas from traditional use areas was 31.4 $\pm$ 1.7 km for males and 17.2 $\pm$ 0.7 km for females during 1978–81 for 87% of the bears ($n = 124$) we monitored. The remaining individuals ($n = 18$, 13%) used an area of mature forest with American devilsclub in a season other than midsummer, and their summer feeding area was not geographically distinct from their traditional use area.

Table 19. Dates of departure and return for black bears migrating to summer feeding areas on the Kenai Peninsula, Alaska, 1978–84.

Year and burn area	n	Departure			Return		
		x̄	Earliest	Latest	x̄	Earliest	Latest
1978							
1947 burn	17	10 Aug	4 Aug	15 Aug	8 Oct	18 Sep	18 Oct
1979							
1947 burn	14	30 Jul	22 Jul	21 Aug	22 Sep	6 Sep	10 Oct
1980							
1947 burn	11	4 Aug	31 Jul	5 Aug	7 Sep	5 Aug	16 Oct
1981							
1947 burn	9	30 Jul	30 Jul	31 Jul	1 Sep	24 Aug	22 Sep
1982							
1947 burn	14	31 Jul	14 Jun	21 Aug	24 Sep	17 Sep	6 Oct
1969 burn	6	31 Jul	29 Jun	10 Aug	1 Oct	24 Sep	11 Oct
1983							
1947 burn	19	26 Jul	20 Jul	29 Aug	7 Sep	17 Aug	21 Sep
1969 burn	6	2 Aug	22 Jul	17 Aug	21 Sep	26 Aug	4 Oct
1984							
1947 burn	8	22 Jul	9 Jul	30 Aug	26 Aug	10 Aug	17 Sep
1969 burn	7	20 Jul	3 Jul	10 Aug	4 Sep	10 Aug	18 Sep

Although most bears (87%) from the 1947 burn area migrated to summer feeding areas, only 43% ($n = 39$) from the 1969 burn area were migratory and 57% ($n = 29$) fed in summer feeding areas that were not geographically distinct from their traditional use area. The primary reason for these differences was the proximity of American devilsclub stands to the 1969 burn area (Fig. 10). Most of the forest surrounding this burn was old growth containing American devilsclub. Consequently, bears living in the 1969 burn area did not have to migrate far to these stands. Bears that migrated from the 1969 burn area used some of the same stands of old growth used by bears from the 1947 burn area (Fig. 10).

In both areas, a few bears used different summer feeding areas in different years, but they generally demonstrated fidelity for the same area each year. Regardless of whether bears were migratory or not, they all fed almost exclusively on American devilsclub during this period (*see* Feeding Ecology, Table 15).

Timing of migration to and from summer feeding areas varied among years (Table 19), but most bears generally departed

for their summer feeding area in late July to early August and returned to their traditional use areas by late September. Timing of departure was not different for the 1947 and 1969 burn areas in 1982 (Bonferroni $t = 0.01$, $P = 0.990$), 1983 (Bonferroni $t = 2.17$, $P = 0.04$), and 1984 (Bonferroni $t = 0.29$, $P = 0.777$) (Please recall that for an overall experimental-wise error of $P = 0.05$, the P value for Bonferroni t must be <0.017 to be significant).

Bears from the 1969 burn area remained in their summer feeding areas longer than bears from the 1947 burn area (Table 19), but only 1983 was significantly different (Bonferroni $t = 2.92$, $P = 0.007$). Significant differences were not detected in 1982 (Bonferroni $t = 2.21$, $P = 0.04$) and 1984 (Bonferroni $t = 0.81$, $P = 0.433$). Longer use of the summer feeding areas by bears in the 1969 burn reflected both the close proximity of traditional use areas to summer feeding areas and the lack of lowbush cranberry within the 1969 burn.

Return from summer feeding areas to traditional use areas was influenced by abundance of American devilsclub fruit (Tables 16, 19). For example, in years with abundant or common crops of American

devilsclub (i.e., 1979, 1982, and 1983), bears remained in their summer feeding areas until mid-September or early October, which was just prior to den entrance (Schwarz et al. 1987a). In years of scarce American devilsclub fruit crops (i.e., 1980, 1981, and 1984), bears returned from their summer feeding areas in late August or early September.

In 1985 there was an almost complete failure in fruit production in American devilsclub stands (Table 16) on the Kenai lowlands. Several bears from the 1947 burn were radio tracked to their traditional summer feeding area, but they did not remain there for much more than a week. Instead they wandered to mountains in search of bog or early blueberry (*Vaccinium uliginosum* or *V. ovalifolium,* respectively) and crowberry (*Empetrum nigrum*) or remained in the lowlands and ate blueberries, which were abundant that year in open bogs. This shift in bear distribution from dense cover of American devilsclub stands to open mountain tundra or bogs was reflected in hunter harvest statistics from the Kenai Peninsula ($\bar{x}$ harvest during 1980–84 = 184 ± SE 19; 1985 harvest = 374) and in survival rates of marked bears (Table 14).

Bears in the 1969 burn area were essentially nonmigratory in 1985, when there was a failure in American devilsclub fruit production. Instead of moving to mountain stands of blueberry and crowberry, they obtained blueberries in the extensive bogs within the 1969 burn area. Like bears in the 1947 burn area, they suffered high hunting mortality (Table 14) in the open bogs. Mortality was particularly high in the 1969 burn area because of high moose hunter use in the area. Because of the excellent habitat in the burn, moose numbers were high, and most of the hunting pressure for moose occurred within the 1969 burn.

CONCLUSIONS

The major objective of this study was to compare black bear population characteristics in the 1947 and 1969 burn areas and relate them to the stages of forest succession following fire. Originally, we believed that there were more bears in the 1947 burn area and that bear reproductive performance was greater in the 1947 burn. We thought this to be true because of the vast difference in the amount of lowbush cranberry in the 2 areas. We further hypothesized that these differences (more bears and better food) likely explained why the moose population in the 1969 burn was at a high density and growing while the 1947 burn moose population was at a lower density and declining. Based on our findings presented here, we must reject this original hypothesis (i.e., H_0: bear population dynamics were similar in the 2 burn areas). We did not demonstrate that bear demographics were superior in the later stage of forest succession (i.e., 1947 burn area) but did show that the earlier seral stage (i.e., 1969 burn area) produced more bears.

Comparative statistics discussed in this report are summarized (Table 20) for easy reference. The habitat in the 1947 burn area was in an intermediate stage (>35 yrs old) of plant succession; the regrowth areas were poor moose habitat. Moose numbers peaked in the 1947 burn area in 1971, and moose density declined during our study. Density of moose was approximately 1.3 moose/km² in 1981, compared with 0.3 moose/km² by 1987. Twinning rates (22%) in the moose population reflected the poor quality of the habitat. However, the 1969 burn area habitat was in early stages (>13 yrs old) of forest succession and excellent moose habitat. Moose density was 3.3 moose/km² in 1981–82; the population peaked in 1984–85; in 1987 density was 3.6 moose/km². Reproductive rates reflected the high quality moose habitat in the 1969 burn area; the twinning rate for moose was 70%, the highest ever recorded for a moose population (Franzmann and Schwartz 1985) in North America. Studies of predation of neonatal moose calves indicated that the percentage of calves taken by black bears, the major predator identified, was similar (34 vs. 35%), but the absolute number of calves consumed per

Table 20. Summary of vital statistics for moose and black bears from the 2 study areas on the Kenai Peninsula, Alaska.[a]

| Vital statistic[b] | Study area | | P |
	1947	1969	
Forest age (yrs)	>35	>13	
Moose			
Density (moose/km²)	1.3–0.3	3.3–3.7	
Population trend during study	down	peaked	
Population peak (yrs)	1970–71	1984–85	
Twinning rate (%)	22	70	
Neonatal predation by black bears (%)	34	35	
Black bears			
Density (bears/1,000 km²)	205	265	>0.05
Cubs (% of population)	25	25	>0.05
Yearlings (% of population)	14	23	0.003
Adult males (% of population)	18	13	0.049
Adult females/adult male	1.5	1.8	0.399
Food habits (similar except)			
Moose calves eaten/bear >1 year old	1.4	5.3	
Lowbush cranberry use	high	low	
Major summer foods	devilsclub	devilsclub	
Age of first litter production (yrs)	5.8	4.6	0.03
Reproductive interval (yrs)			
Cubs	2.2	2.1	0.348
Yearlings	2.4	2.0	0.03
Young/female			
Cubs/litter (all litters)	2.2	2.3	0.65
Yearlings/litter (first litter)	1.7	2.0	
Yearlings/litter (subsequent litters)	1.9	2.3	
Yearlings/all litters	1.9	2.2	0.265
Body size (kg)			
Adult males	116	96	0.045
Adult females	56	62	<0.001
Yearling males in den	20	26	0.001
Yearling females in den	16	22	0.001
Survival estimates of cubs	0.74	0.91	0.047
Blood constituents	similar		0.778

[a] The study areas were located in 2 different-aged stands of northern coniferous forest.
[b] All comparative statistics were during 1982 to 1986, except where earlier data (1978–81) from the 1947 burn were not different for the later years.

bear was 4 times greater in the 1969 burn (1.4 vs. 5.3 calves/bear).

Densities of bears in the 2 areas were similar (Table 20). There were significantly fewer adult males than adult females in both areas, but the sex ratio was not different between areas. In both areas, cubs composed approximately 25% of the population. Age structure was significantly different with more yearlings in the 1969 burn population. Food habits of the 2 populations were similar, except bears in the 1947 burn area consumed more cranberries and fewer moose calves than bears in the 1969 burn area. Both populations were migratory and ate American devilsclub

fruit in late summer. Bears in the 1947 burn area were smaller.

Females in the 1947 burn produced litters at an older age and had a longer interval between weaning of yearlings than females in the 1969 burn. Litter size was similar between areas, but cub survival was lower in the 1947 burn area (Table 20).

Statistically, we could not detect a difference in the ratio of adult male to female bears between the 2 areas. However, the absolute percentage of adult males in the 1969 burn area was less (13%) than that in the 1947 burn area (18%). Young and Ruff (1982) demonstrated that after the removal of adult male bears from their study

area in Alberta, there was an increase in recruitment of subadult bears. Based on their work and on a reanalysis of Yellowstone brown bear data (McCullough 1981, Stringham 1983), it has been hypothesized that adult males played a role in population regulation through infanticide, social and physiological stress, and/or competition for food. These effects were manifested inversely (i.e., increased cub survival and subadult recruitment followed a decrease in the number of adult males). This hypothesis could be used to partially explain higher cub survival in the 1969 burn area (0.91) compared with that at the 1947 burn area (0.74). However, we do not believe this was the case because (1) the difference in numbers of adult males between the 2 areas was small and nonsignificant, (2) cub mortality was high in both areas in 1985, suggesting other environmental controls, and (3) most cub deaths were attributed to causes other than black bear predation (i.e., brown bears, hunters).

Our data concerning subadult males were less useful. Because some subadult males were transient and roamed in search of a secure home range, we only radiocollared bears that we were sure were residents. Consequently, we had a poor understanding of recruitment of subadult males into the 2 study areas. Dispersal from each study area was the same; all surviving subadult males born in the 2 study areas dispersed.

Bears from both areas migrated to old-growth forest and ate American devilsclub, the major food source in summer and fall. Rogers (1987) and Elowe (1987) both documented superior reproductive performance in black bear populations consuming high quality fall foods compared to poor fall diets. Their data suggested that fall diets largely controlled cub production the following spring. Our observations support these findings. Reproductive performance, measured as cubs per litter and interval between production of cubs, was not different between the 2 areas, suggesting similar environmental controls. We

observed a failure in cub production in the 1947 burn in 1980, a year following a scarce American devilsclub crop, and a positive but nonsignificant difference in pregnancy rates in years of abundant versus common versus scarce crops of American devilsclub fruit.

Reproduction and growth generally were linked to superior nutrition (Rogers 1976, 1983, 1987; Bunnell and Tait 1981). Herbaceous food consumption was similar for the 2 populations during spring. Any possible improvement in diet quality due to the more recent fire in the 1969 burn did not account for the superior performance of bears in the 1969 burn. Nutritionally, diets of bears in the 1969 burn area were superior because of the greater consumption of moose calves. This source of high-quality protein and energy represented 40.5 days of energy requirements for an adult female in the 1969 burn, compared to only 10.5 days in the 1947 burn. Because black bears are monogastric animals (Rogers 1977), they require all of the essential amino acids in their diets. Animal protein represented an excellent source of these amino acids. Moose calves also represented a highly digestible source of dietary energy; bears consuming herbaceous diets insufficient to meet maintenance energy requirements shifted to positive energy balance when eating moose.

The availability of this high-quality food source probably explained the larger body size of bears in the 1969 burn area, particularly in yearlings. Weights of yearlings in the winter dens reflected growth as cubs. Yearling bears in the 1969 burn area were significantly larger than yearling bears in the 1947 burn area, indicating they had access to a higher level of nutrition for their first year of life.

Our findings suggested that high quality food in the form of moose calves, in spring and early summer influenced population demographics by regulating cub survival and growth. The higher reproductive success observed on the 1969 burn area probably was due to better nutrition rather than to the presence of fewer adult males. If

adult males had imposed physiological stress or competed for food, as suggested by Stringham (1983), we would have witnessed male aggression toward females; we did not. Furthermore, many of the migrating adult males from the 1947 burn area fed in American devilsclub stands used by females in the 1969 burn area. Competition for spring and summer foods probably did not exist, and on most occasions only a single bear or family group was located in a remnant stand of forest in the 1969 and the 1947 burn areas, indicating spatial separation of individuals. Spring and summer food was generally abundant.

Vigor of black bear populations on the Kenai Peninsula was linked to moose abundance. Black bear predation rates of neonatal moose were independent of moose density (Franzmann and Schwartz 1986). Black bear predation may have been a proximal cause of population control for moose on the Kenai Peninsula, but habitat quality ultimately influenced moose density and population trend (Schwartz and Franzmann 1989). Many studies (Schlegel 1976, Franzmann et al. 1980, Ballard et al. 1981, Gasaway et al. 1983, Franzmann and Schwartz 1986) have focused on the potential effects of bear predation on ungulate population dynamics. This study was the first to our knowledge to demonstrate a link between predation of neonatal moose and demographics of bear populations.

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APPENDIXES

Appendix A. Data used to calculate moose densities in the 1947 and 1969 burn areas on the Kenai Peninsula, Alaska. Calculations and symbols were defined by Gasaway et al. (1986:38–40). Each area was stratified (strata) divided into survey units (SU's) based on moose densities, and a sample of these units was counted.

Year and variable	Area and strata					
	1947 burn			1969 burn		
	Low	Medium	High	Low	Medium	High
1971						
A_i (area of stratum, mi^2)	13	291	134	121	14	4
n_i (no. SU's surveyed)	3	14	21	3[a]	38[a]	21[a]
N_i (total no. SU's)	13	291	134	121	14	4
d_i (observed density, moose/mi^2)	0	7	15.3	0	4.3	15.3
s^2_{qi} (sample variance)	0	52.8	67.8	0[a]	0[a]	0[a]
Density estimate ± 80% CI (moose/km^2)[b] for all strata		3.61 ± 0.70			0.34 ± 0.0[a]	
1982						
A_i (area of stratum, mi^2)	105	300	32	105	62	45
n_i (no. SU's surveyed)	8	44	4	8	13	4
N_i (total no. SU's)	105	300	32	105	62	45
d_i (observed density, moose/mi^2)	1.8	3.6	6.5	1.8	6.7	24.5
s^2_{qi} (sample variance)	6.5	22.5	51.7	6.5	25.1	318.3
Density estimate ± 80% CI (moose/km^2)[b] for all strata		1.31 ± 0.28			3.10 ± 1.08	
1987						
A_i (area of stratum, mi^2)	256	202	0	14	36	77
n_i (no. SU's surveyed)	4	4	0	2	2	6
N_i (total no. SU's)	21	14	0	2	4	6
d_i (observed density, moose/mi^2)	0.2	0.8	0	0.8	5.0	7.8
s^2_{qi} (sample variance)	13.1	2,272	0	6,816	2,577	3,121
$\bar{x}_i$ ($\bar{x}$ mi^2 of all SU's surveyed)[c]	11.4	13.3	0	11.0	47.2	12.8
Density estimate ± 80% CI (moose/km^2)[b] for all strata		0.30 ± 0.03			3.65 ± 0.32	

[a] There were insufficient SU's counted in the 1969 burn in 1971; therefore, the estimate was derived from count information from all of Unit 15A. For this reason, no variance estimate was available.

[b] Areas in 1971 and 1982 were surveyed for an average of 12 min/mi^2; therefore, no sightability correction factor (SCF$_o$) was used. Gasaway et al. suggest searching for 4–6 min/mi^2 and 12 min/mi^2 during intensive searches to generate the correction factor. The SCF$_o$ for counts in 1987 was 1.32.

[c] The mean mi^2 of all SU's in 1971 and 1982 was 1.

Appendix B. Number of radiolocations and the fate of black bears monitored in the 1947 burn area (B) and the 1969 burn area (C) on the Kenai Peninsula, Alaska, 1978–87.

Bear no.	Year of birth	Sex	Year										Fate	Date
			1978	1979	1980	1981	1982	1983	1984	1985	1986	1987		
B1	1974	F	30	28		11	25	5					Hunter-killed	27 Jul 85
B2	1975	F	27	34	21	19	24	25	3	13	4	1	Alive	18 May 87
B3	1975	M	18										Unknown	17 Jun 82
B4	1975	M											Capture mortality	6 May 78
B5	1973	M	29										Radio malfunction	3 Oct 78
B6	1972	M	11										Hunter-killed	1 Sep 78
B7	1970	F											Capture mortality	9 May 78
B8	1968	M	30										Natural mortality	18 Oct 78
B9	1974	M	1	31	18	6		10	11				Hunter-killed	24 Aug 84
B10	1969	M	26	31	10	16	18						Radio malfunction	15 Oct 82
B11	1970	M			15	17	23	25	6				Unknown cause; hunting loss suspected	29 Jun 84
B12	1975	F	30	37	22	20	24	25	18	9			Hunter-killed	1 Sep 85
B13	1975	F	30	37	13								Hunter-killed	4 Sep 80
B14	1976	F	30	37	21	20	24	25	20	13	4		Alive	22 Oct 86
B15	1976	F	10	36	22	20	26	25	18	11			Unknown causes; hunting loss suspected	9 Sep 85
B16	1971	M	18	31	17	20	23	23	2				Hunter-killed	26 Sep 85
B17	1968	M	17										Hunter-killed	6 Sep 81
B18	1972	F	21	35	1								Hunter-killed	6 Sep 83
B19	1975	M	22	25									Hunter-killed	18 Sep 81
B20	1969	F		33	19	18	13						Radio malfunction	14 Jul 82
B21	1978	F		20	7								Radio malfunction	26 Aug 80
B22	1978	M											Unknown; suspected transient, not collared	1 Jun 80
B23	1978	F		19									Radio malfunction	14 Mar 80
B24	1969	F		23	21	20	25	25	20	11			Radio malfunction	29 Oct 85
B25	1973	M		23	21	15	10	18	6				Radio malfunction	20 Jun 84
B26	1975	M											Hunter-killed; suspected transient, not collared	24 May 80
B27	1977	M				8	14	13	20	12	2		Alive	20 May 86
B28	1977	M											Hunter-killed; suspected transient, not collared	18 May 80
B29	1977	M			9								Unknown causes; hunting loss suspected	11 Sep 80
B30	1976	F		20	13								Hunter-killed	3 Sep 80
B31	1975	F		17	21	8							Hunter-killed	20 May 81
B32	1979	M			5								Black bear predation	18 Jun 80
B33	1976	M			9	2							Hunter-killed	7 Sep 85
B34	1978	M				4	12						Hunter-killed	28 Aug 82
B35	1974	F				11	25	25	20	12	4	1	Alive	18 May 87
B36	1979	F			2								Radio malfunction	1 May 80
B37	1979	M			15								Radio malfunction	1 Sep 80
B38	1979	F			21	18	23	25	20	14	4	1	Alive	18 May 87
B39	1979	M			21	9	15		11	5			Hunter-killed	24 May 88
B40	1978	M											Hunter-killed; suspected transient, not collared	20 May 81
B41	1980	M				11	18	7					Hunter-killed	12 Oct 83
B42	1980	F				11	25	24	13				Hunter-killed	29 Aug 84
B43	1980	M											Capture mortality	13 May 81
B44	1980	F				5							Starvation	14 Jul 81
B45	1980	M				1							Capture mortality	18 May 81
B46	1980	F				3							Starvation	11 Jun 81

Appendix B. Continued.

Bear no.	Year of birth	Sex	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	Fate	Date
B47	1979	M				2	5						Radio malfunction	11 May 82
B48	1977	F					10	19	20	10	4		Alive	22 Oct 86
B49	1982	M						21					Hunter-killed	4 May 84
B50	1982	F						25	20	11	4	1	Alive	18 May 87
B51	1977	F					16	7					Black bear predation	16 May 83
B52	1978	M											Hunter-killed	30 Jun 82
B53	1982	M						27	6	1			Wolf snare	1 Jun 85
B54	1982	F						27	21	5			Radio malfunction	16 Jul 85
B55	1982	F						15					Radio malfunction	20 Jul 83
B56	1982	F						25	20	13	4		Alive	22 Oct 86
B57	1982	F						11	9				Hunter-killed	15 Sep 84
B58	1982	F						27	19	6	3	1	Unknown	13 Jun 85
B59	1979	F						16	19	13	3	1	Alive	18 May 87
B60	1969	M						9					Radio malfunction	17 Aug 83
B61	1980	M							3				Hunter-killed	8 Sep 85
B62	1970	M						8					Hunter-killed	1 Sep 85
B63	1980	M						1					Hunter-killed	3 Jun 85
B64	1980	M						1					Unknown	1 Oct 83
B65	1980	M											Hunter-killed	23 May 85
B66	1968	F						2	1				Radio malfunction	27 Jun 84
B67	1980	M								6	4		Hunter-killed	1 May 87
B68	1980	M											Unknown	28 Jun 83
B69	1983	M							12				Hunter-killed	22 May 85
B70	1983	F							17	13	2		Hunter-killed	22 Aug 86
B71	1983	F							19				Capture mortality	27 Feb 85
B72	1981	M											Hunter-killed	5 Jun 85
B73	1975	F							13	7	1	1	Alive	18 May 87
B74	1976	M											Unknown; not resident of study area	4 Jun 84
B75	1981	M											Hunter-killed	19 Sep 84
B76	1973	M											Unknown	7 Jun 84
B77	1982	M											Hunter-killed	25 May 86
B78	1984	F							3	3			Radio malfunction	15 May 85
B79	1984	M							13	2			Alive	20 May 86
B80	1984	F							13	4			Hunter-killed	1 Sep 87
B81	1984	M											Capture mortality	1 Mar 85
B82	1984	F							13	4			Alive	22 Oct 86
B83	1984	M							13	3			Alive	22 Oct 86
B84	1984	F							13	3			Alive	28 Aug 86
B85	1984	M							11	2			Alive	28 Aug 86
B86	1984	F							8				Natural mortality	1 Jun 85
B87	1980	F							8	2	1		Alive	18 May 87
B88	1985	M											Brown bear predation suspected; no collar	1 Sep 85
B89	1985	M											Brown bear predation suspected; no collar	1 Sep 85
B90	1985	F							5				Brown bear predation; collared	1 Sep 85
C1	1972	M					18	23	2				Radio malfunction	23 Apr 84
C2	1973	F					20	27	20	15			Radio malfunction	29 Oct 86
C3	1971	M					22	21					Hunter-killed	2 Sep 85
C4	1979	F											Hunter-killed	14 May 82
C5	1980	M					3						Hunter-killed	13 Aug 82
C6	1973	F					22	25	20	15	3	1	Alive	18 May 87
C7	1981	M					15						Hunter-killed	13 Aug 84
C8	1978	F					16						Natural mortality	1 Aug 82
C9	1970	F											Capture mortality	18 May 82
C10	1975	F					22	27	20	15	3	1	Alive	18 May 87

Appendix B. Continued.

Bear no.	Year of birth	Sex	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	Fate	Date
C11	1980	M					7	5					Hunter-killed	15 Sep 83
C12	1979	F					16	27	20	15			Radio malfunction	29 Oct 85
C13	1980	M					5						Hunter-killed	17 Oct 87
C14	1977	F					16	28	4				Hunter-killed	19 May 84
C15	1980	M											Unknown	24 May 82
C16	1977	M					17	6					Hunter-killed	2 Sep 85
C17	1976	F					19	28	20	14			Radio malfunction	16 Oct 85
C18	1976	F					16	26	18	14			Natural mortality	16 Oct 85
C19	1977	F					16	27	20	15	2		Radio malfunction	7 Aug 86
C20	1982	F						16					Hunter-killed	7 Aug 86
C21	1982	M						27	2				Radio malfunction	8 Jun 84
C22	1982	F						21					Hunter-killed	30 May 84
C23	1982	M						18					Hunter-killed	18 May 85
C24	1982	F						17					Hunter-killed	27 May 84
C25	1982	F						24	7				Hunter-killed	13 Sep 84
C26	1982	F						27	13				Unknown	1 Jun 85
C27	1982	F						10					Hunter-killed	27 Aug 85
C28	1975	M						21	2	5	2		Alive	7 May 86
C29	1968	F						14					Hunter-killed	12 Aug 83
C30	1979	M						4					Hunter-killed	26 Jun 84
C31	1970	F						21	20	11			Hunter-killed	8 Sep 85
C32	1971	F						21	20	13	3	1	Alive	18 May 87
C33	1982	M						15					Hunter-killed	26 Aug 83
C34	1982	F						21	16	6			Radio malfunction	29 Oct 85
C35	1982	M						15	2				Radio malfunction	9 May 84
C36	1980	M											Hunter-killed	2 Oct 84
C37	1982	M											Unknown	1 Oct 83
C38	1982	F						2					Capture mortality	1 May 83
C39	1975	M						17	20	3			Hunter-killed	9 May 85
C40	1979	F						19	20				Capture mortality	13 Mar 85
C41	1980	F						10					Hunter-killed	26 May 86
C42	1971	M						14					Hunter-killed	30 May 85
C43	1981	F											Capture mortality	27 May 83
C44	1983	F							12	1			Hunter-killed	22 Jun 85
C45	1983	M							4				Hunter-killed	9 May 84
C46	1983	F							12	8	2		Alive	7 May 86
C47	1983	M							4				Radio malfunction	23 May 84
C48	1983	F							21	7			Hunter-killed	28 Jul 85
C49	1983	M							13				Hunter-killed	13 Jul 86
C50	1983	M							12				Hunter-killed	12 May 85
C51	1983	M							15	4			Hunter-killed	2 Sep 85
C52	1983	M							17	1			Hunter-killed	3 Sep 85
C53	1983	M							16	2			Radio	23 Sep 85
C54	1978	F							4				Unknown	23 May 84
C55	1983	M							20	4			Radio malfunction	28 May 85
C56	1983	F							4	9	1		Natural mortality	1 May 86
C57	1980	M								9	3		Alive	22 Oct 86
C58	1980	F								7			Unknown cause; hunting loss suspected	1 Sep 85
C59	1984	M								8			Hunter-killed	27 Jul 85
C60	1984	F								15	3		Alive	22 Oct 86
C61	1984	M								4			Hunter-killed	30 May 86
C62	1984	F								14	3		Alive	22 Oct 86
C63	1984	M								11			Hunter-killed	1 Sep 85
C64	1984	F								10			Hunter-killed	1 Sep 85
C65	1984	M								12			Hunter-killed	17 Sep 85
C66	1984	F								15	3		Alive	22 Oct 86
C67	1984	M								9			Hunter-killed	31 Aug 85

Appendix B. Continued.

Bear no.	Year of birth	Sex	Year										Fate	Date
			1978	1979	1980	1981	1982	1983	1984	1985	1986	1987		
C68	1983	F								8	3	1	Alive	18 May 87
C69	1984	M								15	1		Hunter-killed	4 Jun 86
C70	1983	F								2			Wolf snare	6 Jun 85
C71	1982	M								2			Hunter-killed	5 Jul 85
C72	1983	M								1			Radio malfunction	23 Sep 85
C73	1976	F								1			Hunter-killed	29 Jun 85

Appendix C. Assumptions made about bears in the 1947 (1979–85) and 1969 (1982–85) burn areas on the Kenai Peninsula, Alaska.

Assumptions made in the 1947 burn area included the following:

1. An adult female (B35) captured in 1981 was assumed to be in the area in 1979 and 1980. An unmarked female with 2 cubs was sighted numerous times in 1980 and later with yearlings in 1981. When B35 was captured, her home range occurred where this unmarked female was sighted, and we never spotted the uncollared female subsequent to B35's tagging. We also included her 2 cubs and yearlings in the estimates.

2. A male and female yearling of female B24 were included in our estimate in 1979. This female was captured in 1979 before she separated from her 2 yearlings, but we were unable to capture and tag these offspring. We assumed that if these yearlings did not disperse, they would be captured later.

3. Cubs born to females in 1985 ($n = 12$) were not tagged and sex was assigned assuming a 50:50 sex ratio.

Assumptions made in the 1969 burn area included the following:

1. For sex ratio and age structure data in 1982, we assumed adults C28, C29, C31, C39, and C42 were in the area in 1982. All of these bears were tagged in 1983 as adults, and their home ranges were within the area.

2. We assumed adult female C58 was in the area in 1983 and 1984; this bear was captured in 1985. Her home range did not overlap the core of the area used to determine density, but we counted her as part of the area population for population sex and age structure estimates.

3. We assumed adult female C41 was in the area in 1984 and 1985. This bear was captured in 1983, but her radio failed that same year. She was harvested in 1986 in the area she occupied in 1983. We observed an ear-tagged bear within the known home range area of C41 in both 1984 and 1985; this bear was probably C41 as no other marked bear was missing.

4. The cubs born in 1985 ($n = 13$) were not tagged; sex was assigned assuming a 50:50 sex ratio.

Appendix D. Reproductive history for female bears in the 1947 burn area on the Kenai Peninsula, Alaska, from 1978 to 1987. Reproductive status was as follows: C = cubs of the year, Y = yearlings, OPEN = not accompanied by offspring, DEAD = bear died and no data available, LOST = radio contact lost with bear, and UNK = status unknown. Successful litter production was measured after females emerged from their winter dens, so pre-emergence mortality of cubs was not reflected in these results.

Bear no.	Year of birth	Age at first litter (yrs)	Year									
			1978	1979	1980	1981	1982	1983	1984	1985	1986	1987
B1	1974	4	C 2a	Y 2a	C ?	Y ?	OPEN	C 3	Y 1	C 3	DEAD	
B2	1975	4	OPEN	C 2	Y 2	OPEN	C 2	Y 2	C 3	Y 3	C 2	Y 2
B7	1970	UNK	C 3	DEAD	Y 2	OPEN	C 2	Y 2	C 1	Y 1	DEAD	
B12	1975	4	OPEN	C 2	Y 1	DEAD						
B13	1975	4	OPEN	C 1	C 2	Y 2	OPEN	C 2	Y 2	C 2	Y 2	
B14	1976	4	OPEN	OPEN	C 2	Y 2	OPEN	C 1+	Y 1	OPEN	DEAD	
B15	1976	4	OPEN	OPEN	Y 2	LOST						
B18	1972	UNK	UNK	C 2	C 2	Y 2	C 1	Y 1	C 1	C 2	Y 2	LOST
B20	1969	UNK	UNK	Y 2	C 2	Y 2	C 2	LOST				
B24	1969	UNK	UNK	UNK	OPEN	DEAD						
B30	1976	>4b		OPEN	OPEN	OPEN	DEAD					
B31	1975	>6		OPEN	UNK	UNK	C 3	Y 3	C 3	Y 3	C 2	Y 2
B35	1974	UNK	UNK	UNK	OPEN	OPEN	OPEN	OPEN	OPEN	C 2	Y 1	C 3
B38	1979	6		OPEN	OPEN	OPEN	OPEN	OPEN	C 3	Y 2	UNK	
B42	1980	>4					OPEN	OPEN	OPEN	DEAD		
B48	1977	7		OPEN	OPEN	OPEN	OPEN	OPEN	OPEN	OPEN	OPEN	OPEN
B50	1982	>5				UNK	OPEN	C 2	DEAD			
B51	1977	6					OPEN	OPEN	OPEN	OPEN	LOST	
B54	1982						OPEN	OPEN	OPEN	OPEN	LOST	
B55	1982						OPEN	OPEN	OPEN	OPEN	OPEN	OPEN
B56	1982	>4					OPEN	OPEN	OPEN	OPEN	OPEN	LOST
B58	1982	>5					UNK	OPEN	C 3	Y 2	OPEN	OPEN
B59	1979	5						OPEN	OPEN	OPEN	C 2	Y 2
B70	1983	>3							C 2	UNK	OPEN	DEAD
B73	1975	UNK						UNK	C 1	OPEN	C 2	
B87	1980	5									OPEN	

a Number after C or Y denotes number of cubs and yearlings, respectively.
b Females, whose age at first litter is preceded by a > sign, died prior to first litter production.

Appendix E. Reproductive history for female bears in the 1969 burn area on the Kenai Peninsula, Alaska, from 1982 to 1987. Reproductive status was as follows: C = cubs of the year, Y = yearlings, OPEN = not accompanied by offspring, DEAD = bear died and no data available, LOST = radio contact lost with bear, and UNK = status unknown. Successful litter production was measured after females emerged from their winter dens, so pre-emergence mortality of cubs was not reflected in these results.

Bear no.	Year of birth	Age at first litter (yrs)	Year					
			1982	1983	1984	1985	1986	1987
C2	1973			C 3[a]	Y 3[a]	C 3	LOST	
C6	1973		C 2	Y 1	C 3	Y 3	C 2	Y 2
C8	1978	>4[b]	OPEN	DEAD				
C9	1970		C 1	DEAD				
C10	1975		C 2	Y 2	C 1	Y 1	C 1	Y 1
C12	1979	4	OPEN	C 2	Y 2	C 3	DEAD	
C14	1977	4	Y 2	C 3	Y 3	DEAD		
C17	1976		C 2	Y 2	C 2	Y 2	LOST	
C18	1976		C 3	Y 3	OPEN	C 2	LOST	
C19	1977	4	Y 2	C 3	Y 3	C 3	Y 3	LOST
C29	1968			Y 1	DEAD			
C31	1970			C 2	Y 2	OPEN	DEAD	
C32	1971		C 3	Y 3	C 3	Y 3	C 2	Y 2
C40	1979	5	OPEN	OPEN	C 3	Y 3	DEAD	
C41	1980			OPEN	LOST			
C46	1983			OPEN	OPEN	OPEN	OPEN	LOST
C54	1978	5			Y 1	LOST		
C58	1980	5				C 2	DEAD	
C68	1983						OPEN	OPEN

[a] Number after C or Y denotes number of cubs and yearlings, respectively.
[b] Females, whose age at first litter is preceded by a > sign, died prior to first litter production.

Appendix F. Data and calculations used to determine the number of moose calves consumed per bear (excluding cubs) in the 1947 burn and 1969 burn areas on the Kenai Peninsula, Alaska.[a]

	Calculated as	Area 1947	Area 1969
ADF&G composition count area		15A6, 15A7	15A2
Count area size (km²)		273, 352	271
Moose counted (n)		24–96	283–460
Years counted		1977–87	1982–87
Herd composition[b]			
Bulls (% herd)		6–14	9–14
Calves (% herd)		18–23	25–29
Calf sex ratio[c]	% females/100	0.38	0.36
Cows (% herd > calf)	100 − (% bulls + % calves)	63–76	57–66
Yearling females (% herd)	% calves × calf sex ratio × 0.9[d]	6–8	8–9
Adult females (% herd)	% cows − % yearling females	55–70	48–58
Moose density (moose/km²)[e]			
Year 1981–82		1.3	3.1
Year 1986–87		0.30	3.7
Calf production (calves/cow)[f]		1.22	1.71
Predation rate by black bears (%)[g]		34.0	35.1
Calves/km²	moose/km² × (% adult females ÷ 100) × calf production	0.2–1.1	2.5–3.6
Bear density (km²/bear)[h]		6.6	4.9
No. calves eaten/bear (age > 0)	calves/km² × (% predation rate ÷ 100) × km²/bear	0.4–2.5	4.3–6.2

[a] Data ranges represent variation among years in composition counts and are presented to show the possible variation within an area.
[b] Moose composition counts were conducted by the Alaska Department of Fish and Game during early winter to determine the composition of the moose herd. These data were used to calculate the number of breeding females in each study area. They were not used to determine density.
[c] Sex ratio of calves was determined during tagging operations for moose calf mortality studies. Data were presented by Franzmann and Schwartz (1986).
[d] Assumed a 0.9 survival of calves counted in the fall recruited as yearlings for calculations of percent yearling females in the herd. Yearling females could not be separated from adult cows during composition counts, and they did not produce calves.
[e] Density was calculated by the Alaska Department of Fish and Game and the Kenai National Wildlife Refuge using a stratified census technique described by Gasaway et al. (1986). Two censuses were conducted—one in the winter of 1981–82 and a second in the winter of 1986–87. Densities represented approximate moose numbers in the 2 study areas.
[f] Twinning rates in the 2 study areas were determined during calf tagging operations. Data were presented by Franzmann and Schwartz (1985).
[g] Data on predation rates were from Franzmann et al. (1980) and Franzmann and Schwartz (1986).
[h] Densities for the year 1985 when we conducted a mark–recapture census in both areas following procedures of Miller et al. (1987).

Appendix G. Calculations used to estimate the energetic return that a moose calf provided a female black bear.

Variable	Calculated as	x̄	Range
Adult female bear body weight (BW in kg)		57	55–59
Metabolic body weight (BW^0.75)[a]		21	20.2–21.3
Basal metabolic requirement (BMR in kcals/day)	70 × BW^0.75[a]	1,452	1,414–1,490
Activity cost (AC)[b] (kcal/day)			
(1.5 × BMR)		2,178	2,121–2,235
(3.0 × BMR)		4,356	4,242–4,470
Moose calf weight[c] (kg)		23	14.2–32.7
Energy content of calf (kcal/g of wet weight)[d]		1.03	
Kcals/calf		24,152	14,625–33,681
Efficiency of digestion[e]		0.9	
Digestible energy (DE/calf in kcals)		21,737	13,162–30,313
Days of energy provided/calf	DE/calf ÷ AC		
For 1.5 × BMR	21,737 ÷ 2,178	10	
For 3.0 × BMR	21,737 ÷ 4,356	5	

[a] There were no data for metabolic rates of bears during the nondenning period. We calculated basal metabolism using a standard equation for eutherian mammals developed by Kleiber (1947).
[b] There were no estimates for costs of activity above BMR for bears. Robbins (1983:136) listed daily energy expenditure for large mammals of 85–190 kcal/kg^0.75/day. This equated to roughly 1.2–2.6 BMR (i.e., 85 ÷ 70 = 1.2, 190 ÷ 70 = 2.6).
[c] Schwartz et al. (1987b) estimated the mean weight of calf moose at birth from the Kenai Peninsula at 14.2 kg. Growth equations for male and female calves indicate that at 30 days of age they would weigh 37.8 and 27.6 kg, respectively. The mean of these is 32.7 kg.
[d] Caloric content of full-term white-tailed deer (Odocoileus virginianus) fetus (Robbins 1983:175).
[e] Bunnell and Hamilton (1984) listed the digestibility of protein and energy fed to several species of carnivores, including bears. A digestive efficiency of 0.9 was a close approximation.