

DEMOGRAPHIC RESPONSE OF BLACK BEARS AT COLD LAKE, ALBERTA, TO THE REMOVAL OF ADULT MALES

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Abstract: Previous reports described an increase in population density following the removal of 23 adult and 3 subadult male black bears (*Ursus americanus*) from a 218-km² study area near Cold Lake, Alberta (the CLSA). This finding plays a central role in continuing debates over population regulation in bears, but has been criticized because density estimates were based on assumptions that were not met. Moreover, subsequent discussion has been predicated on conjecture that human exploitation had minimal influence on population dynamics. We used improved methods of mark-recapture and survival analysis with a combination of new and previously published data to resolve these issues. Jolly-Seber estimates suggest numbers of females using the CLSA were relatively stable from 1969 to 1971, then more than doubled when males were captured and euthanized during 1971–72. Numbers remained high until 1975, when they declined abruptly. Similarly, numbers of subadult males captured annually increased disproportionately in 1972 and remained high until 1976, when they also declined. Changes in numbers of subadult males captured indicated changes in local density because they were not caused by changes in capture or settling rates. These findings support previous descriptions of trends in bear density at Cold Lake. However, survival records of 56 bears radiomarked during 1974–77 revealed heavier exploitation than previously suspected. Annual mortality rates of radiomarked bears ranged from 14 to 51%, and humans caused at least 25 of 30 observed deaths. Consequently, an underlying assumption of previous interpretations—that the Cold Lake bear population was naturally regulated near carrying capacity—no longer seems reasonable. Our results suggest that adult males deterred bears in other sex-age groups from using the CLSA; however, we found no evidence that birth or death rates were affected. Thus, the observed increase in local density should not be construed as a density-dependent response. Abrupt changes in local density might not have occurred if males had been removed from a larger area encompassing the CLSA.

Ursus 12:59–68

Key words: Alberta, black bear, compensatory mortality, density dependence, limiting factors, mark-recapture, population dynamics, population regulation, *Ursus americanus*

Natural regulation of bear populations ultimately involves density-dependent processes (Taylor 1994). These processes, however, are poorly understood and a subject of continuing controversy. Some have suggested that adult males regulate bear populations by killing or evicting younger males and, to a lesser extent, females (Bunnell and Tait 1981, McCullough 1981, LeCount 1993). If so, removing adult males by hunting might increase survival rates of subadult and female bears. Others contend that evidence of density dependence is lacking for black bears and warn against harvest strategies that anticipate increases in survival or reproduction when populations are reduced (Miller 1990a,b; Garshelis 1994; Taylor 1994).

Interpretations of an experiment begun by Kemp (1972, 1976) and continued by Young and Ruff (1982) are central to this ongoing debate (Garshelis 1994). To determine whether adult males mediated density-dependent changes in demographic parameters of a black bear population at Cold Lake, Alberta, Kemp (1976) and Young and Ruff (1982) used mark-recapture to estimate population size before (1968–70), during (1971–72), and after (1973–75) an experimental removal of adult males. The population was thought to be unexploited and naturally regulated prior to the removal (Kemp 1976). After 4 years of relative stability before the removal, population estimates more than doubled from 1971 to 1973 and remained relatively high through 1975. Moreover, disproportionately large numbers of subadult males were captured an-

nually during 1972–75. Kemp (1976) and Young and Ruff (1982) concluded that adult males regulated population density by controlling recruitment of subadults. These results are often cited as evidence of density dependence in black bears (Garshelis 1994).

Garshelis (1994) subsequently identified potential sources of bias in population estimates of Kemp (1976) and Young and Ruff (1982): Perceived changes in population might have resulted from (1) age- and sex-related differences in recapture probabilities, combined with the removal of adult males from the population, and (2) increased numbers of transient bears passing through the area when male density was low. Though Kemp (1976) inferred an increase in settling rates of subadults from increased recapture rates following the removal, Garshelis (1994) pointed out that these high rates were observed in only 1 year; thus the data did not support inferences about changes in emigration, immigration, or settling rates. Garshelis (1994) concluded that Kemp (1976) and Young and Ruff (1982) reached unjustified and possibly erroneous conclusions about changes in the Cold Lake black bear population and called for a re-analysis of their data.

We analyzed data first presented by Kemp (1972, 1976) and Young and Ruff (1982), unpublished mark-recapture records for 1976 and 1977, and unpublished survival records for bears radiomarked during 1974–77. Objectives of this paper are to (1) use improved methods of mark-recapture analysis to reassess evidence for an in-

crease in bear densities following the removal of adult males from the CLSA; (2) estimate mortality rates, identify causes of death, and reconsider the conjecture that bear densities were naturally regulated prior to the removal; (3) determine whether numbers of subadult males captured on the CLSA were indicative of trends in numbers using the area; and (4) reinterpret the Cold Lake study with respect to density-dependent population regulation in black bears.

STUDY AREA

The 218-km² Cold Lake bear study area (CLSA) was located along the Alberta–Saskatchewan border, 240 km northeast of Edmonton, Alberta (Fig. 1). Boundaries of the CLSA were defined by Cold Lake and the province of Saskatchewan to the east, the Medley River and Marie Lake to the west, the Primrose Lake Air Weapons Range to the north, and by agricultural lands to the south. The CLSA was closed to sport hunting, but bears could be taken by native people. Some bears that used the CLSA also used areas where they could be killed by hunters or to control depredations.

Topography of the CLSA was generally flat except near the Medley and Martineau rivers. Elevation ranged from 535 to 702 m. Vegetation was dominated by aspen (*Populus tremuloides*) and mixed stands of aspen and spruce (*Picea glauca*), which occupied 66% of the landscape. Dominant understory plants in these areas included alder (*Alnus* spp.), rose (*Rosa* spp.), and lowbush cranberry (*Viburnum edule*). The remaining third of the area consisted primarily of muskeg (24%) and spruce (6%), habitats that also dominated the landscape to the east and west of the CLSA. The climate was northern continental, with average monthly temperatures ranging from -19°C in January to 17°C in July. Annual snowfall averaged 138 cm, and snow cover usually persisted from late October to early April. More detailed descriptions of the study area have been presented by Kemp (1972, 1976), Tietje and Ruff (1980, 1983), Young and Ruff (1982), and Pelchat and Ruff (1986).

METHODS

Bears were captured from April through December, 1968–77, with Aldrich foot snares (Aldrich Animal Trap

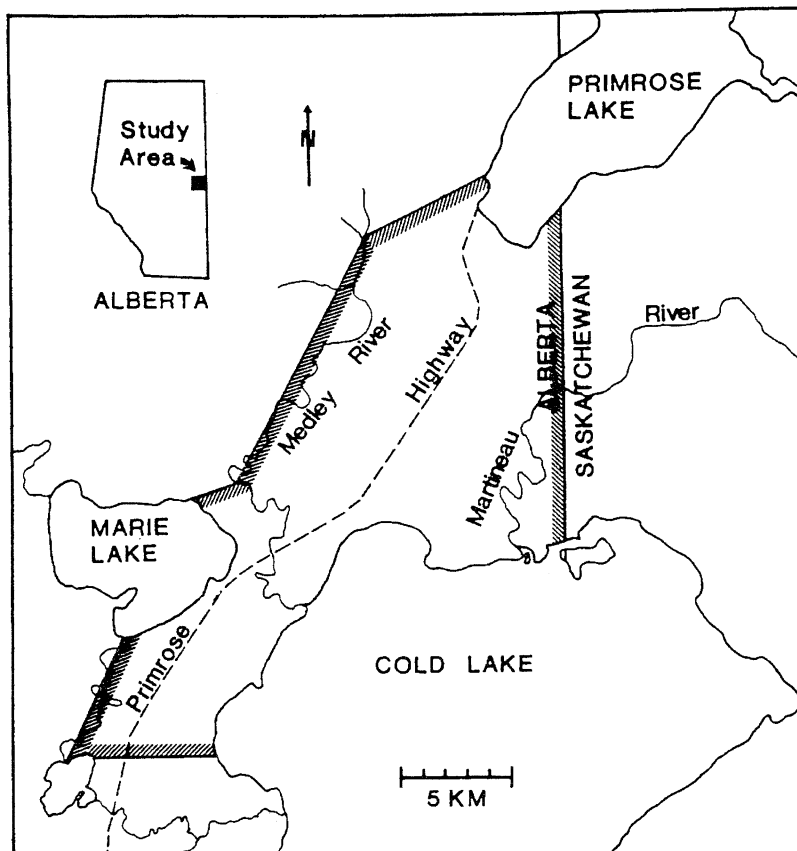


Fig. 1. The Cold Lake bear study area (CLSA). Reproduced with permission from *The Journal of Wildlife Management* (Tietje and Ruff 1980).

Co., Clallam Bay, Washington, USA), in culvert traps, by hand (cubs), in dens, and with tranquilizer dart guns. Captured bears were immobilized with phencyclidine hydrochloride and weighed. In 1971 and 1972, males >90 kg were euthanized. Bears that were released were marked, when first captured, with colored ear tags and a permanent tattoo, and a premolar tooth was extracted for age determination (Willey 1974). Hereafter, 2- and 3-year-old bears are referred to as subadults and bears ≥ 4 years of age are called adults.

During 1974–77, 56 captured bears were equipped with radiocollars and located daily by triangulation when they were within radio range of roads (~5 km). When collared bears moved farther from roads, they were relocated from aircraft within 1 week.

We used captures of bears ≥ 2 years of age that occurred during annual capture periods of May 1–September 30 for mark–recapture analyses. For these analyses, we used only captures accomplished with snares and culvert traps because other methods sometimes targeted specific individuals.

We used Jolly-Seber (J-S) open-population models (Pollock et al. 1990) to estimate numbers of female bears using the CLSA during 1969–76. By limiting this portion of our analysis to females, we eliminated bias resulting from sex-related differences in capture probabilities. To investigate possible effects of age-related differences in capture probabilities, we compared results for all females with a second set based only on adult females. Finally, to guard against spurious increases in estimates that might result from the temporary departure of marked bears from the CLSA, we computed a third set of estimates from capture histories truncated in 1974. To facilitate visual comparisons of trends resulting from these analyses, which were based on different-sized groups of bears, we plotted standardized deviates of estimates (Sokal and Rohlf 1981) instead of estimates themselves.

We could not estimate numbers of males by mark–recapture methods because the experimental removal of males resulted in the marking, release, and recapture of too few. Thus, we used indirect methods to determine whether numbers of subadult males captured annually on the CLSA indicated numbers residing in the area. We inferred trends in numbers of subadult males that were present at least temporarily from numbers of individuals captured and mark–recapture estimates of capture probabilities. We then estimated settling rates of subadult males (probabilities of surviving from 1 capture period to the next while continuing to use the CLSA) from generalized mark–recapture models (Lebreton et al. 1992). Finally, we considered trends in numbers of subadults and settling rates concurrently to determine whether numbers of subadults captured reflected numbers that used the study

area on a continuing basis.

We depicted capture histories of individual bears as vectors of 0's and 1's, with 1's indicating capture. Our models represented probabilities of possible capture histories as combinations of settling and recapture probabilities (e.g., Lebreton et al. 1992:71). Settling rates were represented by $\Phi_{i,k}$ and recapture parameters by $P_{i,k}$, where subscript i denoted the capture period and k indexed age class (sa = subadults, ad = adults). Thus, $\Phi_{i,k}$ was the probability a bear in age class k would survive from capture period i to $i+1$ and still be using the CLSA during capture period $i+1$. $P_{i,k}$ was the probability a bear in age class k would be captured during period i if it was using the CLSA.

Our full model was constrained by 4 sets of equalities:

$$\begin{aligned} \Phi_{1968,k} &= \Phi_{1969,k} = \Phi_{1970,k} = \Phi_{1971,k} = \Phi_{1976,k} = \Phi_{\text{pre},k}; \\ \Phi_{1972,k} &= \Phi_{1973,k} = \Phi_{1974,k} = \Phi_{1975,k} = \Phi_{\text{post},k}; \\ P_{1969,k} &= P_{1970,k} = P_{1971,k} = P_{1976,k} = P_{1977,k} = P_{\text{pre},k}; \\ P_{1972,k} &= P_{1973,k} = P_{1974,k} = P_{1975,k} = P_{\text{post},k}. \end{aligned}$$

Constraints divided the study into 2 periods dictated by the volume of data available, which precluded separate estimation of every $\Phi_{i,k}$ and $P_{j,k}$. Periods corresponded with the pre-removal (1968–71) and post-removal (1972–75) periods described by Young and Ruff (1982), except that we placed previously unpublished data for 1976–77, when relatively few subadult males were captured, in the pre-removal period. We used nested models and likelihood ratio tests to test for significant differences between parameters of our full model. We used SURGE 4.2 computer software to compute maximum-likelihood estimates of model parameters and likelihood ratio tests (Lebreton et al. 1992).

We used the staggered-entry Kaplan-Meier (K-M) estimator (Pollock et al. 1989) to estimate survival rates of radiomarked bears and ratios of age- and sex-specific survival rates. For known or suspected mortalities, we used the date of last radio contact as the date of death. Records for bears with unknown fates were terminated (right censored) at the date of last radio contact. A log-rank test, stratified by year and age class, was used to compare rates for males and females. Age classes were compared after stratifying by year and sex. We used 1-tailed tests because we anticipated higher mortality rates for males and subadults than for females and adults. We used SAS PROC PHREG (Allison 1995), for survival analyses.

RESULTS

Our criteria for mark–recapture modeling (age ≥ 2 , captured during May–Sep) were met by 692 captures of 276 individual bears. However, only the first capture within each annual capture period was relevant to our analysis. After removing duplicate captures within periods, we were

left with 65 females captured 123 times as adults, 40 females captured 46 times as subadults, 93 males captured 136 times as adults, and 125 males captured 146 times as subadults. Twenty-three adult males and 3 large subadult males captured during 1971–72 were euthanized.

We used Jolly-Seber models with time-specific survival and capture probabilities to estimate numbers of females (Model A of Pollock et al. 1990) because they fit better than models with constant survival probabilities (Model B: all females $\chi^2_5 = 12.3$, $P = 0.03$; adults only $\chi^2_3 = 10.9$, $P = 0.01$; truncated capture histories $\chi^2_3 = 8.6$, $P = 0.03$) and models with constant survival and recapture probabilities (Model D: all females $\chi^2_{13} = 27.3$, $P = 0.01$; adults only $\chi^2_{13} = 25.84$, $P = 0.02$; truncated capture histories $\chi^2_8 = 14.4$, $P = 0.07$). Further, goodness-of-fit was satisfactory only for Model A (all females $\chi^2_9 = 4.07$, $P = 0.91$; adults only $\chi^2_5 = 3.52$, $P = 0.62$; truncated capture histories $\chi^2_4 = 3.28$, $P = 0.51$). Estimated numbers of females (Table 1) were relatively stable from 1968 to 1970, increased abruptly during 1971–72, remained high through 1974, then declined abruptly (Fig. 2).

The abrupt nature of the increase in estimated numbers of female bears suggests a change in spatial distribution, rather than a change in reproduction or survival. Survival records of radiomarked bears suggest that mortality may have been partially responsible for the abrupt decline in 1975 (Table 2). K-M estimates of mortality caused by humans were similar for radiomarked male and female bears (M:F risk ratio = 1.05, $\chi^2_1 = 0.014$, $P = 0.91$) and were not significantly lower for subadults than for adults (ad:sa risk ratio = 0.80, $\chi^2_1 = 0.20$, $P = 0.66$).

Table 1. Estimated numbers of black bears using a 218-km² area near Cold Lake, Alberta, 1968–77. Estimates of total numbers (all bears) are from Young and Ruff (1982) unless otherwise noted. Estimates for females are from this study and are based on Jolly-Seber models with time-specific survival and recapture probabilities.

Year	All bears	All females		Adult females	
	\hat{N}	\hat{N}	SE	\hat{N}	SE
1968	84	— ^a	— ^a	— ^a	— ^a
1969	71	15.9	2.88	16.1	3.11
1970	92	21.4	4.36	17.1	3.51
1971	75	31.6	9.49	18.9	5.80
1972	117	45.8	11.38	40.4	15.63
1973	175	46.7	15.60	31.5	19.42
1974	136	59.1	24.61	41.4	27.02
1975	137	25.5	5.85	22.9	7.24
1976	123 ^b	34.2	5.26	25.0	— ^c
1977	99 ^b	— ^c	— ^c	— ^c	— ^c

^aNot estimable by Jolly-Seber method

^bR. L. Ruff, unpublished data

^cLimited data precluded estimation

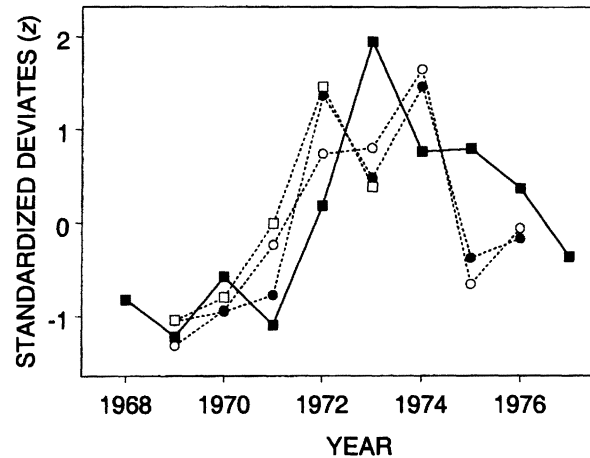


Fig. 2. Trends in estimated numbers of bears using the CLSA during 1968–77, standardized for comparison. Estimates from Young and Ruff (1982) are based on male and female bears aged ≥ 2 years (■). Others are Jolly-Seber estimates for females (age ≥ 4 years [○]; age ≥ 2 years [●]; captures prior to 1975, age ≥ 2 years [□]).

Human activity was the proximate cause of at least 25, and probably 28, of 30 deaths that befell radiomarked bears during 1974–77. Principal causes of mortality were depredation control (11 deaths) and a combination of legal hunting by native people and poaching (11 deaths), which could not be distinguished. Legal sport hunting, a drug overdose, a collision with a train, another bear, and other natural causes each caused 1 death. Fates of 3 bears could not be confirmed by recovery of a carcass or radiocollar, but each was rumored to have been shot.

The number of subadult males captured on the CLSA was larger during each year of 1972–75 (range = 21–25) than during any year of 1968–71 or 1976–77 (range = 2–17; Table 3). We believe this result indicates a difference in the number of subadults that were at least temporarily present on the study area because estimated capture probabilities of subadults were not significantly higher ($\chi^2_1 = 1.13$, $P = 0.29$) during the post-removal period ($\hat{P}_{\text{post,ca}} = 0.55$, SE = 0.11) than during the pre-removal period ($\hat{P}_{\text{pre}} = 0.72$, SE = 0.13).

Table 2. Kaplan-Meier estimates of mortality rates from deaths due to all agents and natural agents only for radiocollared black bears at Cold Lake, Alberta, 1974–77.

Year	Natural mortality		All mortality		Bears	Deaths
	Rate	SE	Rate	SE		
1974	0		0.14	0.122	11	1
1975	0		0.51	0.086	36	16
1976	0.08	0.079	0.28	0.087	30	7
1977	0.03	0.077	0.24	0.080	26	6

Moreover, estimated settling rates did not differ enough between periods ($\hat{\phi}_{pre,sa} = 0.49$, $SE = 0.10$; $\hat{\phi}_{post,sa} = 0.49$, $SE = 0.07$) to offset the increase in captures. Thus, numbers of subadult males using the study area were probably larger during 1972–75 than during other years.

DISCUSSION

Changes in Density

Studies of black bears embody most limitations of mark–recapture analysis: sample sizes are usually small, capture rates are often low, and necessary assumptions are seldom met. Thus, estimates of abundance are often biased and imprecise. In the case that inspired this work, Kemp (1976) and Young and Ruff (1982) estimated bear numbers for each year by averaging 6 Lincoln-Petersen estimates, 3 capture efficiency estimates (Meslow and Keith 1968), and 1 estimate obtained from the distribution of capture frequencies (Hartley 1958). Estimates were stable from 1968 to 1971, increased abruptly from 1971 to 1973, then declined from 1973 to 1977.

Garshelis (1994) subsequently showed how the Lincoln-Petersen estimates could have been influenced if (1) age class and sex-related differences existed in capture rates and (2) the composition of the population changed over time. According to Garshelis (1994), the Lincoln-Petersen estimates were severely biased and had so much influence on results that trends in bear numbers could have been misinterpreted.

Unlike previous analyses, our J-S estimates for female bears were not affected by sex-related differences in capture rates. We believe perceptions of trends were robust to age-related differences because they were affected only slightly when we restricted our analysis to adult females. Estimates were similar from 1969 through 1970, increased abruptly during 1971–72, remained high through 1974, and declined abruptly in 1975. Thus, our results, like those of Kemp (1976) and Young and Ruff (1982), suggest bear

density increased when adult males were removed (Fig. 2). However, neither their results nor ours should be used to calculate actual densities (i.e., bears/km²). The CLSA was small relative to home range sizes of bears; consequently, the effective area sampled was not known with sufficient accuracy for density estimation (White et al. 1982).

Changes in estimated numbers of females could have resulted from (1) parallel changes in the effective area sampled by trapping or (2) the temporary departure of bears marked prior to 1975; however, these alternative explanations seem comparatively unlikely. First, distances between capture locations suggest movements of females may have been more extensive during 1968–71 than during 1972–75 (Young and Ruff 1982). Resulting changes in the effective area trapped would have dampened, rather than produced, the trends in our estimates. Second, the abrupt increase in estimates during 1971–72 persisted even when we made departures effectively permanent by truncating capture histories in 1974. Finally, our results are consistent with subjective perceptions of field staff from the Cold Lake study, who reported a notable increase in the frequency of bear sightings after males were removed.

An abrupt increase during 1971–72 in the number of females using the CLSA nevertheless seems surprising. Typically, adult females monitored for ≥ 2 years occupy the same home range in successive years (e.g., Alt et al. 1980, Reynolds and Beecham 1980, Powell 1987). Emigration by females is thought to be uncommon for reasons related to reproductive fitness (Rogers 1987). However, shifts in home ranges of adult females are not unprecedented. For example, adult females monitored by Lindzey et al. (1986) on Long Island, Washington, USA, adjusted home ranges and increased their use of the adjacent mainland as bear densities and competition for resources increased. Moreover, the removal of adult males probably subjected bears to abrupt changes in social pressure or competition for resources that were more extreme than typically occur while individual bears are being monitored.

Female bears radiomarked within the CLSA during 1974–77 sometimes made long-range exploratory movements (Pelchat and Ruff 1986, R.L. Ruff unpublished data). Presumably, bears living near the CLSA did so as well and were aware the area comprised primarily aspen and aspen–spruce habitats, a better source of food (Pelchat and Ruff 1986), preferred over muskeg and spruce that dominated the surrounding area (Young and Ruff 1982, Pelchat and Ruff 1986). Thus, habitat differences may have motivated female bears from the surrounding area to make greater use of the CLSA after adult males were removed. Subadult males may have been attracted to potential mates as well as by habitat.

Table 3. Numbers of individual black bears captured annually at Cold Lake, Alberta, May–Sep, 1968–77.

Year	Males		Females		Total
	Subadults	Adults	Subadults	Adults	
1968	2	14	3	14	33
1969	5	9	0	14	28
1970	14	15	4	12	45
1971	7	14	5	6	32
1972	21	17	6	14	58
1973	25	8	8	5	46
1974	24	7	6	7	44
1975	22	12	3	12	49
1976	17	31	6	25	79
1977	13	13	7	18	51

Settling and Survival

Kemp (1972, 1976) and Young and Ruff (1982) noted an increase in numbers of subadult bears caught on the CLSA after males were removed. However, Garshelis (1994) pointed out that it was impossible to tell, from their results, whether subadults captured on the CLSA settled there. Recent advances in mark-recapture analysis (Lebreton et al. 1992) enabled us to estimate capture and settling rates. Neither changes in trapping effectiveness nor changes in settling rates offset the increased number of subadults captured. It thus seems likely that removing adult males did, in fact, encourage continuing use of the CLSA by an increased number of subadults.

Settling rates were probabilities that marked bears would survive from 1 capture period to the next and continue using the study area. They were not annual survival rates and did not distinguish mortalities from departures. Thus, we were able to estimate annual mortality rates only for bears marked with radios during 1974–77. Results were surprising because the CLSA was closed to sport hunting. Mortality rates were much higher than those of previously studied un hunted populations (Bunnell and Tait 1985, Clark and Smith 1994, Doan-Crider and Hellgren 1996). During 1975–77, mortality rates equaled or exceeded estimates of the maximum sustainable by black bears (22–24%; Bunnell and Tait 1981).

Annual variation in survival rate estimates was substantial, but regulations governing human exploitation of bears did not change during the study. Thus, immigration may have played an important role, even prior to the removal of adult males, in sustaining bear densities within the CLSA. This new finding has important implications, because previous interpretations of this study have been predicated on the belief that human exploitation was negligible. Bear densities may not have been naturally regulated at the outset of the Cold Lake study, and high rates of human-caused mortality may have contributed to the abrupt decline in density that occurred in 1975. Young and Ruff (1982) previously reported a more gradual decline resulting from changes in social structure as males matured on the study area.

Density Dependence and Population Regulation

Up to this point, we have used such terms as *population*, *density dependence*, and *regulation* in the same context as they were used by our predecessors (Kemp 1972, 1976; Young and Ruff 1982). However, these terms are frequently used to mean different things (Sinclair 1991, Wells and Richmond 1995). Semantic misunderstandings result so frequently that evaluating the concept of density-dependent population regulation is largely a problem of determining what ecologists mean by it (Murray

1994). In this section, we hope to define our meaning, and that of our predecessors, in a way that will clarify previous discussion and prevent future misunderstandings of events at Cold Lake.

Our predecessors described a population that comprised bears using the CLSA (Kemp 1972, 1976; Young and Ruff 1982). Thus, population growth rates were determined by 4 processes: reproduction, mortality, immigration, and emigration. Density-dependence was indicated if any of these processes were influenced by abundance. Unfortunately, this common perspective (e.g., Caughley 1977, Shenk et al. 1998) poses 2 difficulties for interpretation when small “populations” are arbitrarily spatially delimited from larger groups of individuals (Harrison and Cappucino 1995). First, the occurrence of immigration, emigration, and changes in density are scale-dependent (Fig. 3; Wells and Richmond 1995). Second, dynamics of population numbers over time are not distinguished from movements of individuals (Allen and Hoekstra 1992), although the distinction is of critical importance for bear management.

To resolve semantic difficulties, we believe bear biologists should reserve population status for disjunct (Wells and Richmond 1995) or, minimally, much larger groupings (e.g., local populations; Goodwin and Fahrig 1998) of bears than was studied at Cold Lake. When populations are defined this way, the critical processes of population dynamics are birth and death (Allen and Hoekstra 1992); movements of individuals are no less important, but are said to influence local densities and metapopulation dynamics.

Regardless of how they are defined, populations cannot increase without limit and seldom dwindle to extinction. Regulation is perhaps best defined as the tendency of populations to fluctuate, over the long term, about stationary mean densities (Turchin 1995). Limiting factors influence these means (Sinclair 1991). Direct density dependence is an inverse relation between per capita population growth rates and present or past population densities (Murdoch and Walde 1989, Turchin 1995). Direct density-dependence is a necessary (but not sufficient) condition for population regulation (Murdoch and Walde 1989).

Like most studies of black bears, the Cold Lake experiment was not controlled. Thus, the removal of adult males was confounded with other influences on bears of the CLSA. However, the timing, magnitude, and duration of changes in numbers of bears using the CLSA strongly suggest that the presence of adult males influenced local bear densities. In keeping with their use of *population*, our predecessors interpreted this effect as evidence of density dependence. However, we note that (1) effects were documented only for a localized area; (2) adult males

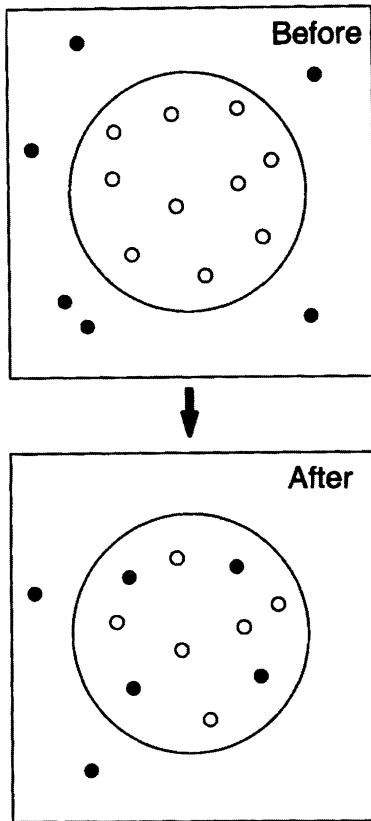


Fig. 3. Demographic concepts are ambiguous when small study populations are arbitrarily delimited. Removing individuals from the circle causes the actual density to decline in the square, but immigration maintains the actual density in the circle. Relative local densities are increased within and reduced outside the circle.

depressed densities of bears in other sex and age classes; and (3) interactions with conspecifics are 1 of many factors that may operate on local densities in a relative sense, across a wide range of actual densities. Thus, in keeping with our synthesis of terminology, we conclude that adult males limited relative local densities of female and subadult male bears. Our results do not permit inferences about density dependence or population regulation, as we defined these terms. We could not estimate population growth rates, test for changes in survival or reproduction, or estimate population densities across an area large enough to encompass effects of the experimental treatment.

Implications for Research and Management

Until effects on survival or reproduction can be documented, we support the views of Miller (1990*a,b*) and Taylor (1994): Sustainable yield projections should not be based on anticipated increases in vital rates that might result from reductions in black bear population density. Although removing adult males encouraged bears in other

sex and age classes to use the CLSA, implications for bear harvest management are not obvious. Other than reports of a few bears killed by conspecifics (Kemp 1976, Young and Ruff 1982), we have no evidence that adult males influenced rates of population growth. Moreover, the CLSA was unusual because most hunted areas are not adjacent to large, unhunted reservoirs of potential immigrants (Garshelis 1994).

At Cold Lake, adult males were removed from a restricted area during a short period. The removal of bears from broad geographic areas over long time spans is more typical of hunted black bear populations. In such cases, hunter harvests of adult males are unlikely to cause sudden changes in the dispersion of subadult and female bears. Further, the response observed at Cold Lake may have occurred only because the CLSA was a population sink comprising aspen and spruce habitats, which bears preferred over surrounding muskeg. Removing males from less desirable habitats might not have a similar effect.

Density-dependent population regulation is a topic of special interest to bear biologists interested in maximizing sustainable harvest rates (McClellan 1993, 1994; Derocher and Taylor 1994; Garshelis 1994; Taylor 1994), but efforts to conclusively demonstrate density dependence within black bear populations may be doomed to failure. Formidable logistical barriers limit the accuracy and precision of density estimates. Unambiguous detection of density dependence is difficult (Pollard and Lakhani 1987), even with error free estimates, and some tests designed to accommodate sampling error are invalid (Shenk et al. 1998). Moreover, most black bear populations are studied at moderate densities, where changes in density probably have little effect on reproduction or survival (Fowler 1981*a,b*; Strong 1986). Finally, even at high densities, regulatory agents may reduce survival or suppress reproduction at irregular intervals, so that a "vague" (Strong 1986) relationship between density and demographic performance of a population should be expected.

Similarly, density dependence is difficult to detect by comparing the demographic performance of different populations that vary in density. Garshelis (1994) noted some obstacles, including the difficulty of measuring relevant parameters with sufficient accuracy, complications that arise from methodological differences among studies, and factors other than density that influence vital rates. More important, however, is the fact that carrying capacity varies among populations. Thus, density alone is likely to be a poor predictor of demographic performance, even if compensatory responses are strong and population density can be estimated accurately.

In large mammals, strong density-dependent responses usually occur only when populations near carrying capacity are reduced (Fowler 1981*a,b*). Probably few man-

aged bear populations are near carrying capacity (Taylor 1994). Thus, much current interest in density dependence and population regulation might more profitably be directed toward factors that limit growth rates of populations at low densities. The management significance of such factors may be much greater. Relief from factors that limit growth rates can buffer low populations from overharvest and increase sustainable yields, whether or not density-dependent responses occur (Gasaway et al. 1992, Van Ballenberghe and Ballard 1994). Although we could not assess effects of adult males on population growth rates, their influence on relative local densities should encourage further study of this issue, especially with respect to mortality rates and causes of death during juvenile dispersal.

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LITERATURE CITED

- ALLEN, T.F.H., AND T.W. HOEKSTRA. 1992. Toward a unified ecology. Columbia University Press, New York, New York, USA.
- ALLISON, P.D. 1995. Survival analysis using the SAS system: a practical guide. SAS Institute, Inc., Cary, North Carolina, USA.
- ALT, G.L., G.J. MATULA, JR., F.W. ALT, AND J.S. LINDZEY. 1980. Dynamics of home range and movements of adult black bears in northeastern Pennsylvania. *International Conference on Bear Research and Management* 4:131–136.
- BUNNELL, F.L., AND D.E.N. TAIT. 1981. Population dynamics of bears—implications. Pages 75–98 in C. W. Fowler and T. D. Smith, editors. *Dynamics of large mammal populations*. John Wiley and Sons, New York, New York, USA.
- , AND ———. 1985. Mortality rates of North American bears. *Arctic* 38:316–323.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley and Sons, London, UK.
- CLARK, J.D., AND K.G. SMITH. 1994. A demographic comparison of two black bear populations in the interior highlands of Arkansas. *Wildlife Society Bulletin* 22:593–603.
- DEROCHER, A.E., AND M.K. TAYLOR. 1994. Density-dependent population regulation of polar bears. Pages 25–30 in M. Taylor, editor. *Density-dependent population regulation in black, brown, and polar bears*. *International Conference on Bear Research and Management Monograph Series* 3.
- DOAN-CRIDER, D.L., AND E.C. HELLGREN. 1996. Population characteristics and winter ecology of black bears in Coahuila, Mexico. *Journal of Wildlife Management* 60:398–407.
- FOWLER, C.W. 1981a. Comparative population dynamics of large mammals. Pages 437–455 in C.W. Fowler and T.D. Smith, editors. *Dynamics of large mammal populations*. John Wiley and Sons, New York, New York, USA.
- . 1981b. Density dependence as related to life history strategy. *Ecology* 62:602–610.
- GARSHELIS, D.L. 1994. Density-dependent population regulation of black bears. Pages 3–14 in M. Taylor, editor. *Density-dependent population regulation in black, brown, and polar bears*. *International Conference on Bear Research and Management Monograph Series* 3.
- GASAWAY, W.C., R.D. BOERTJE, D.V. GRANGAARD, D.G. KELLEYHOUSE, R.O. STEPHENSON, AND D.G. LARSEN. 1992. The role of predation in limiting moose at low densities in Alaska and Yukon and implications for conservation. *Wildlife Monographs* 120.
- GOODWIN, B.J., AND L. FAHRIG. 1998. Spatial scaling and animal population dynamics. Pages 193–206 in D.L. Peterson and V.T. Parker, editors. *Ecological scale*. Columbia University Press, New York, New York, USA.
- HARRISON, S., AND N. CAPPUCINO. 1995. Using density-manipulation experiments to study population regulation. Pages 131–147 in N. Cappucino and P. W. Price, editors. *Population dynamics: new approaches and synthesis*. Academic Press, San Diego, California, USA.
- HARTLEY, H.O. 1958. Maximum likelihood estimation from incomplete data. *Biometrics* 14:174–194.
- KEMP, G.A. 1972. Black bear population dynamics at Cold Lake, Alberta, 1968–1970. *International Conference on Bear Research and Management* 2:26–31.
- . 1976. The dynamics and regulation of black bear *Ursus americanus* populations in northern Alberta. *International Conference on Bear Research and Management* 3:191–197.
- LEBRETON, J.D., K.P. BURNHAM, J. CLOBERT, AND D.R. ANDERSON. 1992. Modeling survival and testing biological hypotheses using marked animals: a unified approach with case studies. *Ecological Monographs* 62:67–118.
- LECOUNT, A.L. 1993. Intrinsic population regulation among black bears. Pages 103–110 in J.A. Keay, editor. *Proceedings of the Fourth Western Black Bear Workshop*. U.S. Department of Interior National Park Service Natural Resources Publication Office, Technical Report NPS/NRWR/NRTR-93/12.
- LINDZEY, F.G., K.R. BARBER, R.D. PETERS, AND E.C. MESLOW. 1986. Responses of a black bear population to a changing environment. *International Conference on Bear Research and Management* 6:57–63.
- MCCLELLAN, B.N. 1993. A summary of the discussion on the natural regulation of black bears. Pages 117–119 in J.A. Keay, editor. *Proceedings of the Fourth Western Black Bear*

- Workshop. U.S. Department of Interior National Park Service Natural Resources Publication Office, Technical Report NPS/NRWR/NRTR-93/12.
- MCCLELLAN, B. 1994. Density-dependent population regulation of brown bears. Pages 15–24 in M. Taylor, editor. Density-dependent population regulation in black, brown, and polar bears. International Conference on Bear Research and Management Monograph Series 3.
- MCCULLOUGH, D.R. 1981. Population dynamics of the Yellowstone grizzly bear. Pages 173–196 in C.W. Fowler and T.D. Smith, editors. Dynamics of large mammal populations. John Wiley and Sons, New York, New York, USA.
- MESLOW, E.C., AND L.B. KEITH. 1968. Demographic parameters of a snowshoe hare population. *Journal of Wildlife Management* 32:812–834.
- MILLER, S.D. 1990a. Impact of increased bear hunting on survivorship of young bears. *Wildlife Society Bulletin* 18:462–467.
- . 1990b. Population management of bears in North America. International Conference on Bear Research and Management 8:357–373.
- MURDOCH, W.W., AND S.J. WALDE. 1989. Analysis of insect population dynamics. Pages 113–140 in P.J. Grubb and J.B. Whittaker, editors. Towards a more exact ecology. Blackwell, Oxford, UK.
- MURRAY, B.G. 1994. On density-dependence. *Oikos* 69:520–523.
- PELCHAT, B.O., AND R.L. RUFF. 1986. Habitat and spatial relationships of black bears in boreal mixedwood forest of Alberta. International Conference on Bear Research and Management 6:81–92.
- POLLARD, E., AND K.H. LAKHANI. 1987. The detection of density-dependence from a series of annual censuses. *Ecology* 68:2046–2055.
- POLLOCK, K.H., J.D. NICHOLS, C. BROWNIE, AND J.E. HINES. 1990. Statistical inference for capture–recapture experiments. *Wildlife Monographs* 107.
- , S.R. WINTERSTEIN, C.M. BUNCK, AND P.D. CURTIS. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53:7–15.
- POWELL, R.A. 1987. Black bear home range overlap in North Carolina and the concept of home range applied to black bears. International Conference on Bear Research and Management 7:235–242.
- REYNOLDS, D.G., AND J.J. BEECHAM. 1980. Home range activities and reproduction of black bears in west-central Idaho. International Conference on Bear Research and Management 4:181–190.
- ROGERS, L.L. 1987. Factors influencing dispersal in the black bear. Pages 75–84 in B.D. Chepko-Sade and Z.T. Halpin, editors. Mammalian dispersal patterns: the effects of social structure on population genetics. University of Chicago Press, Chicago, Illinois, USA.
- SHENK, T.M., G.C. WHITE, AND K.P. BURNHAM. 1998. Sampling-variance effects on detecting density dependence from temporal trends in natural populations. *Ecological Monographs* 68:445–463.
- SINCLAIR, A.R.E. 1991. Science and the practice of wildlife management. *Journal of Wildlife Management* 55:767–773.
- SOKAL, R.R., AND F.J. ROHLF. 1981. *Biometry*. W.H. Freeman and Company, New York, New York, USA.
- STRONG, D.R. 1986. Density-vague population change. *Trends in Ecology and Evolution* 2:39–42.
- TAYLOR, M., EDITOR. 1994. Density-dependent population regulation in black, brown, and polar bears. International Conference on Bear Research and Management Monograph Series 3.
- TJETJE, W.D., AND R.L. RUFF. 1980. Denning behavior of black bears in boreal forest of Alberta. *Journal of Wildlife Management* 44:858–870.
- , AND ———. 1983. Responses of black bears to oil development in Alberta. *Wildlife Society Bulletin* 11:99–112.
- TURCHIN, P. 1995. Population regulation: old arguments and a new synthesis. Pages 19–40 in N. Cappuccino and P.W. Price, editors. Population dynamics: new approaches and synthesis. Academic Press, San Diego, California, USA.
- VAN BALLEMBERGHE, V., AND W.B. BALLARD. 1994. Limitation and regulation of moose populations: the role of predation. *Canadian Journal of Zoology* 72:2071–2077.
- WELLS, J.V., AND M.E. RICHMOND. 1995. Populations, metapopulations, and species populations: what are they and who should care? *Wildlife Society Bulletin* 23:458–462.
- WHITE, G.C., D.R. ANDERSON, K.P. BURNHAM, AND D.L. OTIS. 1982. Capture–recapture and removal methods for sampling closed populations. LA-8787-NERP UC-11, Los Alamos National Laboratory, New Mexico, USA.
- WILLEY, C.H. 1974. Aging black bears from first premolar tooth sections. *Journal of Wildlife Management* 38:97–100.
- YOUNG, B.F., AND R.L. RUFF. 1982. Population dynamics and movements of black bears in east-central Alberta. *Journal of Wildlife Management* 46:845–860.