

IS GRIZZLY BEAR CUB MORTALITY RATE ELEVATED BY
AGGREGATING AT CONCENTRATED FOOD SOURCES?

S. F. STRINGHAM. Wildwatch Ecological Center, P.O. Box 35, Browning, MT 59417,
USA

Abstract: Social strife is elevated at sites where grizzly bears (*Ursus arctos*) aggregate. Stokes (1970) and Glenn et al. (1976) hypothesized that this increases COY (cub-of-the-year) mortality. They noted that rates were over 30% at Yellowstone National Park (YNP) and at McNeil Falls (MF), whereas the rate averaged no more than 10% in dispersed populations. However, re-examination of those data, and consideration of a larger sample of dispersed populations, show that the difference they found is an artifact. Mortality rates at YNP and MF, where bears were known individually, were estimated from actual numbers of cubs lost between ages COY to yearling. By contrast, rates for the dispersed populations were estimated by comparing relative sizes of COY vs. yearling litters, which omits all losses of entire COY litters. When all mortality is taken into account, rates in YNP and MF are not significantly higher than in dispersed populations (34% vs. 31%, $t_{2,8} = -0.2$ x $t_{2,8} P=0.88$). Data do not support claims that aggregation is harmful and that bears can benefit from elimination of ecocenters, as when "developers" destroy groves of nut-producing trees or dumps are closed.

Key words: Aggregation, cub, dispersal, ecocenter, food concentration, mortality, (*Ursus arctos*).

During 1987-88, I estimated potential impacts on black bears (*Ursus americanus*) by planned expansion of Killington Ski Area in Vermont. New ski slopes were to be cut through a large grove of beech (*Fagus grandifolia*) where bears foraged for nuts during the occasional years when a good crop was produced. The bark of some trees was so heavily scarred from bear claw punctures that individual sets of scars could not be distinguished. Dissection of some scars down through the annular rings indicated that the trees had been heavily used for at least the past half-century. Heavy use of the site was probably typical too in earlier centuries before the ancestors of these trees were harvested by European colonists.

Beech nuts are undoubtedly an important source of nutrition for bears, as were the nuts of other species originally found in the area. Better nutrition can elevate reproductive rate and nutrition-related survivorship (see reviews by Rogers 1987 and Stringham 1985, 1986, 1989). But the net effect on population dynamics is unclear. When nut-producing trees were common in New England, bears could have fed on nuts while avoiding one another. But now that groves are scarce, and numerous bears are drawn near one another

(e.g., Garshelis and Pelton 1981), benefits of enhanced nutrition might be outweighed by the detriments of elevated social strife.

Stokes (1970) hypothesized that aggregation of bears at ecocenters aggravates strife, lowering reproductive rate by females and survivorship of their young. At ecocenters, cubs seem unusually exposed to dangerous conspecifics and many are killed (Craighead and Craighead 1967; Craighead 1972; Glenn et al. 1976; Bledsoe 1987). Large bears, particularly adult males, are known to frequent ecocenters and to be aggressive towards cubs (see reviews by Stringham 1980, 1983, 1985; McCullough 1981; Bledsoe 1987). So elimination of an ecocenter and dispersal of the bears could supposedly benefit cubs or entire populations, despite reduced nutrition (Cole 1976).

I had to consider this issue with regard to bears that aggregated in the Killington beech grove. It was not possible to test the hypothesis empirically. So testing was approached through review and analysis of data in the literature. Only for grizzly bears are there enough data to support this kind of analysis. Stringham (in press b) refuted the reproductive suppression hypothesis; this paper refutes Stokes' COY mortality hypothesis.

Observations of infanticide (see Discussion) were most common at 2 sites where aggregations of over 30 bears have been a tradition spanning decades: (a) McNeil Falls in Alaska's McNeil River Game Sanctuary (Glenn et al. 1976), and (b) garbage dumps open from about 1900 until 1968-72 in or near Yellowstone National Park (Craighead 1972). Mortality was also observed near a dump in Denali National Park (Murie 1981).

Craighead and Craighead (1967) reported 39% COY mortality while the Yellowstone dumps were still open to bears. Following closure of the dumps, grizzly bears dispersed and COY mortality decreased (Cole 1976). Glenn et al. (1976) reported 38% mortality among 13 COY litters seen at MF, but no more than 10% mortality for at least 42 other litters dispersed elsewhere in the McNeil River State Game Sanctuary. Likewise, for other populations where the bears were typically dispersed, estimated COY mortality averaged about 10%. Glenn et al. (1976) interpreted the above comparisons between YNP and MF vs. dispersed populations as confirming Stokes' (1970) hypothesis that COY mortality rate is elevated several-fold in populations forming large aggregations, due to aggravated social strife.

The strife-aggravated mortality hypothesis was reevaluated here, using an alternative method of estimating cub mortality rate and data from more dispersed populations. With data from only 2 aggregated populations, I could not test the general hypothesis that aggregation elevates cub mortality. But data did suffice to refute the claim that mortality rate in dispersed populations was a mere fraction of that in YNP and MF, and thus to undercut the argument that degradation of the Killington beech grove was likely to benefit black bears.

My work was supported by Wildwatch, the Society of the Sigma Xi, and the Shikar-safari Club International; the Ecology Program, University of Tennessee, Knoxville; the State University of New York, College of Environmental Science and Forestry; Anne, Jeanette, Joyce, and Robert Stringham; Christine and Vladimir Nicolayeff; Helen Strauss and Laura Lippincott.

METHODS

Estimating Mortality Rate

Data on litter size and numbers of cubs in each age-class were taken from the literature, then used to estimate cub mortality rates. The "litter size" (LS) method compares mean numbers of COYs vs. yearlings *per litter* (CL vs. YL): $100\% \times (CL - YL)/CL$. The "age-class size" (ACS) method compares total numbers of COYs vs. yearlings: $100\% \times (C - Y)/(C)$.

With either the LS or ACS method, comparison can be made within cohorts (COYs in year t vs. yearlings in $t+1$) or across cohorts (COYs in year t vs. yearlings in year t).

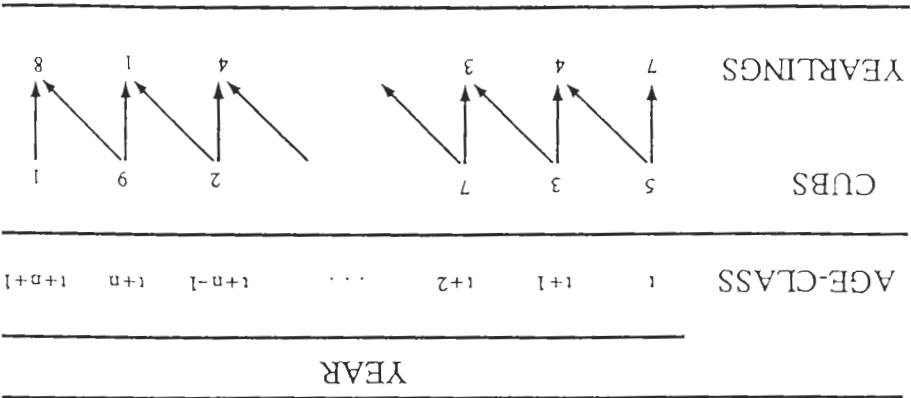
Across-cohort comparison can introduce bias (Caughley 1977; Stringham 1980, 1985; Bunnell & Tait 1985; Reynolds and Hechtel 1984). For instance, if COY litters born in year t are larger than those born in $t+1$, then in year $t+1$ litter size for yearlings could exceed that for COYs. Other problems are illustrated with an hypothetical example (Fig. 1).

COYs in year t become yearlings in $t+1$; COYs in $t+n$ become yearlings in $t+n+1$. Mortality rate is properly estimated within cohorts (diagonal lines), comparing total numbers of COYs in years t to $t+n$ vs. yearlings in years $t+1$ to $t+n+1$. In the hypothetical example, if $N=4$, mortality is 23% ($=6/26$); this contrasts to the 0% ($=0/27$) figure obtained by comparing total numbers of COYs in years t to $t+n+1$ vs. yearlings in all of those same years (i.e., across cohorts, vertical lines). The calculation across cohorts differs from that within cohorts in that crossing cohorts includes the (7) yearlings from t and the (1) COY from $t+n+1$, whereas the within-cohort method does not. The larger n is, the smaller the fraction of the total COYs were present in year $t+n+1$ and yearlings in year t ; so the smaller the bias produced by the across-cohort method tends to be. Underestimation or exaggeration of mortality estimates from across-cohort comparison can occur with either the LS or ACS methods. Across-cohort comparison can lead to cases where estimates of mortality rate are higher with the LS method than with the ACS method (Table 1); but generally, the ACS method produces higher estimates of COY mortality, as explained below.

A bias unique to the LS method, which can cause serious underestimation of mortality rate, is omitting entire litter losses -- yearling litters of size 0 -- from calculation of mean litter size. Such litters have died or dispersed before they could be censused as yearlings. This bias can be avoided if cubs or litters are known individually. Consider 2 examples: (a) Reynolds and Hechtel (1984) reported on fates of known grizzly litters from several cohorts in the Western Brooks Range of Alaska. Of 31 litters with 59 COYs, only 19 litters with 33 COYs survived until fall. Whereas litter size fell only 8% (1.90 to 1.74), COY mortality rate was actually 44%. (b) At Denali National Park, Murie (1981) noted a 7% decline in COY litter size contrasted to a 31% mortality rate.

The LS method has been preferred in cases where relative litter sizes seemed much more reliably documented than relative numbers of COYs vs. yearlings. Because adult females tend to be more secretive with COYs than with yearlings or older cubs, the number of litters censused is sometimes lower for COYs than for yearlings; across-cohort comparison can have that effect too. The LS method is also preferred where only mean LS was published, not the numbers of litters or of cubs. Overall, the LS method tends to be much less reliable than the ACS method.

Fig. 1. Numbers of COYs and yearlings over several successive years in a hypothetical population. These figures are used to illustrate how artefacts arise when mortality rate is estimated by cross-cohort comparisons (see text). Diagonal lines represent the changes in cohort size between successive years (e.g., of 5 COYs in year 1, 4 survive to be yearlings in +1. Encircled numbers (7 and 1) are omitted when calculating mortality rate but included when comparing total numbers of yearlings vs. COYs.



Statistical Techniques
 Data are available on 2 highly aggregated and 16 dispersed grizzly populations. The Student *t*-test was used to assess differences between the aggregated vs. dispersed populations.

RESULTS

Findings are presented first by considering mean estimates of mortality across all the populations for which litter sizes or age-class sizes were documented (N=17 and 9, respectively), and then by comparison across the smaller number of populations for which both types of data are available (N=9). The various sets of results are then compared and interpreted.

Relative Sizes Of COY vs. Yearling Litters

In grizzly populations where the bears tend to be well dispersed (and where, generally, few litters were known individually), litters averaged only 7% smaller for yearlings than for COYs--by contrast to 38% at YNP and MF. After closure of the garbage dumps at YNP, and dispersal of those bears, the within-cohort COY-to-yearling litter size decline was only 15% (Table 1). At McNeil River State Game Sanctuary, the litter size decline was only 10% for litters that did not frequent the Falls (data from Glenn et al. 1976).

Contrasting these LS declines between the aggregated vs. dispersed populations: their variances do not differ significantly ($P = 0.10$), but the mean for the 2 aggregated populations is over 5-fold higher than that for the 15 dispersed populations (38.5% vs. 6.9%, $t_{2,15} = -3.8, P=0.001$).

Relative Numbers Of COYs vs. Yearlings

Aggregated Populations

At MF, only 16 of 26 COYs survived to become yearlings, a decline of 38%. For YNP grizzly bears, mean cohort size dropped 31% between ages 0.5-1.5 years, and 22% between ages 1.5-2.5 years; this occurred during 1959-68, prior to closure of the major garbage dumps (data from Craighead et al. 1974; Table 1).

Dispersed Populations

By the early 1980's, after the YNP bears had dispersed, COY mortality had dropped to 12%; yearling mortality rate was nearly unchanged at 24% (Knight et al. 1985; Table 10). Mortality rates for COYs and yearlings in Denali National Park were 31% and 17% (Murie 1981). For another 6 dispersed populations (GNP, KI, AK, WBR, CMP, and USSR; Table 1), relative numbers of COYs vs. yearlings (across cohorts) yielded a mean COY mortality rate estimate of about 35%. In a dispersed population of black bears in Minnesota, COY mortality averaged about 25% (data from Rogers 1977; Table 3).

Contrasting the aggregated ($\bar{N} = 2$) vs. dispersed ($\bar{N} = 8$) grizzly populations, ACS estimates of mortality rate do not differ significantly in either variance ($F = 0.29$) or mean (34.5% vs. 31.4%, $t_{2,8} = -0.2, P=0.88$).

This contradiction to the Cole/Glenn et al. conclusion is not an artifact of lacking ACS mortality estimates for the other 8 populations on which we have data on LS decline.

Comparison of Mortality Estimates Between Methods

If one considers just the 7 dispersed populations for which both LS and ACS values can be calculated, mean estimates of mortality by the LS and ACS methods are, respectively, 5.7% and 15.2%. Both LS and ACS mortality rate estimates are also available from the 2 aggregated populations (38% vs. 34%). Combining data from all 9 of these populations, there is no overall correlation between LS vs. ACS estimates ($r^2 < 4\%$, $P > 0.35$). Neither index cannot be used to estimate the other.

DISCUSSION

Sampling Different Sets of Populations With LS vs. ACS Methods: What Artifacts Does This Generate?

LS and ACS data are available for 17 and 10 populations, respectively. Could the difference in mortality rate estimated by the 2 methods (LS:7% vs. ACS:38%) be primarily an artifact due to the LS method encompassing 8 populations which the ACS method doesn't? No. The difference is only reduced (LS:6% vs. ACS:15%), not eliminated for the 7 dispersed populations to which both methods can be applied.

Aggregated vs. Dispersed Populations

Litter Size Decline

Glenn et al. (1976) reported that COY-to-yearling litter size declines were several-fold higher at YNP and MF than in dispersed populations. That is confirmed using the larger sample sizes now available; the decline averages over 5-fold higher for YNP and MF than dispersed populations. However, this difference may be only a statistical artifact of lacking data on entire-litter losses for many dispersed populations.

These results do not confirm the conclusion by Glenn et al. (1976) that the difference in litter size declines reflected more than 3-fold higher mortality rates at YNP and MF. Their conclusion was based on what is here shown to be an artifact from interpreting litter size decline as an index of mortality rate even though decline data from dispersed populations generally ignored entire-litter losses. Using the more reliable ACS method of estimating mortality, one finds no significant difference in rates between these aggregated vs. dispersed populations.

Available data suffice to refute the interpretation of Glenn et al. (1976), and to throw doubt on Stokes' (1970) hypothesis that aggregation elevates COY mortality; however, a definitive test requires data on more aggregated populations. Furthermore, the dichotomy between aggregated vs. dispersed populations should be replaced by a gradient for degree of aggregation/dispersion. Analysis should consider size of the aggregation, and age-sex ratios among bears at ecocenters vs. the total habitat.

Observations of Bears Killing One Another.

Even if COY mortality is not elevated in populations which regularly form dense aggregations, one might question whether mortality is higher at ecocenters than in areas

where bears are widely dispersed -- as hypothesized by Stokes (1970). Confirmation for that hypothesis seems implicit in the data of Glenn et al. (1976) and Cole (1976); but they did not address the issue of why so few of the mortalities at YNP and MF were known to have occurred at ecocenters; indeed, most mortality of McNeil COYs happened during the time of year when bears were dispersed (Bledsoe 1987, pers. commun.).

McNeil Falls.--Glenn et al. (1976:387) reported 3 instances of juvenile mortality near MF. In one instance, a female with 3 cubs was carrying a salmon from the river to an alder patch on higher ground.

One cub in the lead took a different trail than the others and was not seen again. The female was later seen with the other cubs and never appeared to be searching for the 3rd cub. In another instance, 3 cubs became separated from their mother when she was attempting to drive off a large male. She found one cub immediately and another 3 days later. After a week, she still had only the 2 cubs. No other female was observed with an extra cub. In the 3rd instance, a dead cub was found at a feeding area away from the Falls. Separated from its mother only 4 weeks earlier, it apparently died from a bite which crushed its esophagus and perforated its pharynx; its carcass had been partly eaten (Egbert and Luque 1975; Egbert and Stokes 1976; Bledsoe 1987).

Bledsoe (1987) cites additional mortalities observed by himself or Aumiller. Two COYs of 1 dam were killed when they approached another dam with COYs. A yearling that ventured too near a dam with COYs was attacked and killed. A 2-year-old was attacked and nearly killed after trying to steal a salmon scrap from an adult male.

Summarizing: In at least 15 years of observation, only 6 juveniles are known to have died at or near the Falls, only 4 are known to have been killed by conspecifics, and only 2 were definitely COYs rather than yearlings or 2-year-olds.

Yellowstone Dumps

McCullough (1981:183) stated that "Park Service personnel reported finding 3 dead cubs killed in 1 night at the Rabbit Creek dump" in YNP.

Previously, J. Craighead and F. Craighead (1967) reported 4 cases of infanticide. J. Craighead (1972) documented additional incidents, noting that most juveniles were killed by large males in the spring, not all in the vicinity of dumps. Indeed, he doubts that mortality is elevated at ecocenters (pers. commun.).

COYs known to have been killed at or near dumps are only a tiny fraction of the 93 that died in YNP from 1959 until the dumps were closed.

Dispersed Populations

Contrasted to the above incidents of conspecific mortality at YNP and MF with large aggregations of bears, are a few incidents at sites of smaller aggregations (Katmai and Denali), and numerous incidents where bears were dispersed. Citations given below exclude cases of victims restrained by traps, chains, or drugs (Wright 1909; Troyer and Hensel 1962; Pearson 1975) or killed by rivals during rut (Couturier 1954; J. Craighead 1972; Pearson 1975).

Although large numbers of bears now aggregate at Brooks River in Katmai National Monument (Gilbert, pers. commun.), during the early 1970's it was uncommon to see even 10 bears spread out over a mile of river (Stringham, unpubl.). In one case, a medium-sized bear was fishing when attacked and killed by a much larger bear.

George (1979) observed the disappearance of a cub whose mother had left it ashore while she fished.

Several bears commonly aggregated at the garbage dump in Denali National Park (Murie 1981). In 1963, the mother of 3 COYs was found dead of severe wounds from another bear; Murie inferred that she had been killed trying to protect her COYs. In 1961, a large bear killed a smaller bear (apparently not a cub).

Killing of juveniles away from even such small eccenters has been reported by Seton (1921), Troyer and Hensel (1962), Glenn (1971), Reynolds (1980), Reynolds and Hechel (1984), and Murie (1981). Killing of older conspecifics was reported by Seton (1921), Pearson (1975), Reynolds (1974, 1976, 1980), Stringham (1985) gave a detailed review of these incidents. Reviews for black and polar bears were provided by Rogers (1983) and Taylor et al. (1985). Data were compiled by Taylor et al. (in press).

Interpretation

Available evidence on grizzly bears killing one another does not reveal an obviously greater incidence of such mortality for either cubs or older victims at eccenters than in areas where grizzlies are dispersed. Both this finding, and lack of substantially lower mortality rates in dispersed populations, contradict Stoke's (1970) hypothesis. Also contradictory is the fact that reproductive rates at YNP and MF aren't suppressed; they have the same relationship to body size (an index of nutritional status) as do dispersed populations (Stringham, in press b). These findings also throw doubt on Cole's (1976) conclusion that closure of the YNP dumps and dispersal of the bears is responsible for the subsequent decline in mortality rate for COYs (but not yearlings). However, definitive testing of both hypotheses will require much more detailed data on the frequency of mortality from conspecific attack vs. other factors (allospecific enemies, humans, accidents, pathogens, malnutrition, etc.). For example, does aggregation increase mortality from specific causes such as social strife while reducing mortality from other causes? Intensity and duration of strife also need quantification.

Alternative Hypotheses

Research should also address alternative hypotheses as to why aggregation would not tend to increase either COY mortality or infanticide -- hypotheses based on infanticide theory or on strategies by which dams protect their cubs (see Stringham 1985, Bledsoe 1987).

LITERATURE CITED

- BALLARD, WARREN B., S. D. MILLER, AND T. H. SPRAKER. 1982. Home range, daily movements, and reproductive biology of brown bear in Southcentral Alaska. *Can. Field-Nat.* 96:1-5.
- BLEDSE, T. 1987. Brown bear summer: life among Alaska's giants. E. P. Dutton, New York. 249pp.
- BUNNELL, F. L., AND D. E. N. TAIT. 1985. Mortality rates of North American bears. *Arctic* 38:316-323.
- CAUGHLEY, G. 1977. Analysis of vertebrate populations. John Wiley and Sons. New York. 232pp.
- COLE, G. F. 1976. Management involving grizzly and black bears in Yellowstone National Park, 1970-75. *Nat. Res. Rep. 9*. U. S. Department of Interior, National Park Service. 26pp.
- COUTURIER, J. A. 1954. L'ours brun, *Ursus arctos* L. Publ. by author. Grenoble, France. 904 pp.
- CRAIGHEAD, J. J. 1972. Panel discussion. *Int. Conf. Bear Res. and Manage.* 2:245.
- , AND F. C. CRAIGHEAD Jr. 1967. Management of bears in Yellowstone National Park. Unpubl. MS. 113pp.
- , J. R. VARNEY, AND F. C. CRAIGHEAD, Jr. 1974. A population analysis of the Yellowstone grizzly bears. *Montana For. and Conserv. Exp. Stn. Bull.* 40. Univ. Montana, Missoula. 20pp.
- DEAN, F. C. 1976. Aspects of grizzly population ecology in Mount McKinley National Park. *Int. Conf. Bear Res. and Manage.* 3:111-119.
- EGBERT, A. L., AND H. M. LUQUE. 1975. Among Alaska's brown bears. *Natl. Geogr.* 148:428-442.
- , AND A. W. STOKES. 1976. The social behavior of brown bears on an Alaskan salmon stream. *Int. Conf. Bear Res. and Manage.* 3:41-56.
- FARO, J. 1977. Brown/grizzly bear survey-inventory progress report, 1975. Pages 89-93 in R. A. Hinman, ed. *Alaska Dep. Fish Game, Proj. Progr. Rep., Fed. Aid Wildl. Res. Proj. W-17-6 and W-17-7*.
- GARSHELIS, D. L., AND M. R. PELTON. 1981. Movements of black bears in the Great Smoky Mountains National Park. *J. Wildl. Manage.* 45:912-925.
- GEORGE, J. C. 1979. The Kingdom of the grizzly. *Scene Mag.* Dec: 6-15.
- GLENN, L. P. 1971. Report on 1970 brown bear studies. *Alaska Dep. Fish Game, Proj. Progr. Rep., Fed. Aid Wildl. Res. Proj. W-17-2 and W-17-3*, 67 pp.
- , 1973. Report on 1972 brown bear studies. *Alaska Dep. Fish Game, Proj. Progr. Rep., Fed. Aid Wildl. Res. Proj. W-17-6 and W-17-7*, 10pp + App.
- , J. W. LENTFER, J. B. FARO, AND L. H. MILLER. 1976. Reproductive biology of female brown bears (*Ursus arctos*), McNeil River, Alaska. *Int. Conf. Bear Res. and Manage.* 3:381-390.
- HENSEL, R. J., W. A. TROYER, AND A. W. ERICKSON. 1969. Reproduction in the female brown bear. *J. Wildl. Manage.* 33:357-365.
- KLEIN, D. R. 1958. Alaskan brown bear studies. *Alaska Dept. Fish Game, Proj. Rep., Fed. Aid Wildl. Res. Proj. W-3-R-13*, Job 1. Juneau, AK.
- KNIGHT, R. R., B. M. BLANCHARD, AND D. J. MATTSO. 1985. Yellowstone grizzly bear investigations. *Ann. Rep. Interagency Study Team*, 1983 and 1984. U. S. Department of Interior, National Park Service. 41pp.
- MARTINKA, C. J. 1974. Population characteristics of grizzly bears in Glacier National Park, Montana. *J. Mamm.* 55:21-29.
- McCullough, D. R. 1981. Population dynamics of the Yellowstone grizzly. Pages 173-196 in C. W. Fowler and T. D. Smith (eds). *Dynamics of large mammal populations*. John Wiley and Sons, New York. 477 pp.
- MUNDY, K. R. D., AND D. R. FLOOK. 1973. Background for managing grizzly bears in the national parks of Canada. *Can. Wildl. Serv. Rep. Ser.* 22. 35pp.
- MURIE, A. 1981. The grizzlies of Mount McKinley. U. S. Interior Department, National Park Service, Scientific Monograph Series No. 14. Washington, D. C. 251pp.

- NOVIKOV, G. A., A. E. AIRAPETJANTS, V. B. PUKINSKY, E. K. TIMOFEEVA, AND I. M. FOKIN. 1969. Some peculiarities of populations of brown bears in the Leningrad district. *Zool. Zh.* 48:885-901 (in Russian).
- PEARSON, A. M. 1975. The northern interior grizzly bear *Ursus arctos* L., Can. Wildl. Serv. Rep. Ser. 34. 86pp.
- REYNOLDS, H. V. 1974. North Slope grizzly bear studies. Alaska Dep. Fish Game, Final Rep., Fed. Aid Wildl. Res. Proj. Progr. Rep. W-17-6, 27pp.
- . 1976. North Slope grizzly bear studies. Alaska Dep. Fish Game, Final Rep., Fed. Aid Wildl. Res. Proj. W-17-6 and W-17-7. 14pp + App.
- . 1980. North Slope grizzly bear studies. Alaska Dep. Fish Game, Final Rep., Fed. Aid Wildl. Res. Proj. W-17-11. 65 pp.
- and J. L. HECHTEL. 1984. Structure, status, reproductive biology, movement, distribution, and habitat. Proj. Final Rep. Fed. Aid Wildl. Res. W-22-3. 29 pp.
- ROGERS, L. L. 1977. Social relationships, movements, and population dynamics of black bears in northern Minnesota. Ph.D. Thesis. Univ. Minnesota, Minneapolis. 194pp.
- . 1983. Effects of food supply, predation, cannibalism, parasites, and other health problems on black bear populations. Pages 194-211 in F. L. BUNNELL, D. S. EASTMAN, AND J. M. PEEK, eds. Symposium on natural regulation of wildlife populations. Proc. No. 14. For. Wildl. Exp. Stn. Univ. Idaho, Moscow. 225pp.
- . 1987. Effects of food supply and kinship on social behavior, movements, and population growth of black bears in northeastern Minnesota. Wildl. Monogr. 97. 72pp.
- SETON, E. T. 1929/1953. Lives of game animals. Vol. II, Part I. Charles T. Branford, Co., Boston. 367pp.
- STOKES, A. W. 1970. An ethologist's views on managing grizzly bears. *BioScience* 20(21):1154-1157.
- STRINGHAM, S. F. 1980. Possible impacts of hunting on the grizzly/brown bear, a threatened species. *Int. Conf. Bear Res. and Manage.* 4:337-349.
- . 1983. Roles of adult males in grizzly bear population ecology. *Int. Conf. Bear Res. and Manage.* 5:140-151.
- . 1985. Responses by grizzly bear population dynamics to certain environmental and biosocial factors. Ph. D. Thesis, Univ. Tennessee, Knoxville. 454pp.
- . 1986. Effects of climate, dump closure, and other factors on Yellowstone grizzly bear litter size. *Int. Conf. Bear Res. and Manage.* 6:33-39.
- . 1989. Demographic consequences of bears eating garbage at dumps. *Bear-People Conflicts* 40:4-7.
- . 1992 a. Aggregation of bears at food concentrations (ecocenters). *Int. Conf. Bear Res. and Management*, Grenoble.
- . 1992 b. Is grizzly bear reproductive rate depressed by aggregating at concentrated food sources? *Int. Conf. Bear Res. and Management*, Grenoble.
- TAYLOR, M., T. LARSEN, AND R. E. SCHWEINSBURG. 1985. Observations of intraspecific aggression and cannibalism in polar bears (*Ursus maritimus*). *Arctic* 38:303-309.
- , D. GARSHELIS, B. MCELLELLAN, A. DEROCHE, AND S. STRINGHAM. 1992. Density dependent population regulation in black, grizzly, and polar bears. *Int. Conf. Bear Res. and Management*, Grenoble.

- TROYER, A. W., AND R. J. HENSEL. 1962. Cannibalism in brown bear. *Anim. Behav.* 10:231.
- and —. 1964. Structure and distribution of a Kodiak bear population. *J. Wildl. Manage.* 28:769-772.
- WRIGHT, WM. H. 1909. The grizzly bear: the narrative of a hunter-naturalist. C. Scribner's Sons, New York. 274 pp.