

IUCN Publications new series

No. 23

bears —their biology and management

A selection of papers
and discussion from the
Second International Conference
on Bear Research and Management

held at the
University of Calgary, Alberta, Canada
6 to 9 November 1970

under the sponsorship of the
Environmental Sciences Centre (Kananaskis)
and the University of Calgary



Edited by
Stephen Herrero, Ph.D.

and published by the
International Union
for Conservation of Nature and Natural Resources,
Morges, Switzerland, 1972

Herrero 1972

5.79.78

Bear Proceedings
© IUCN, Morges, Switzerland, 1972

Prefato

Presentatio
November 1
were delive
of papers.

At the confe
'The Status
sented by D

Papers and
under the h
name of the

Four other
Uspenski—
sented duri
tional contr



PRINTED BY Unwin Brothers Limited
THE GRESHAM PRESS OLD WOKING SURREY ENGLAND

Produced by 'Uneoprint'

A member of the Staples Printing Group

(UO3614)

PANEL 4: BEAR BEHAVIOUR

Aspects of Evolution and Adaptation in American Black Bears (*Ursus americanus* Pallas) and Brown and Grizzly Bears (*U. arctos* Linné.) of North America

STEPHEN HERRERO

Research Associate, Environmental Sciences Centre (Kananaskis), and Assistant Professor, Department of Biology and Psychology, University of Calgary, Alberta.

SUMMARY

Certain behavioural, ecological, morphological, and physiological differences between grizzly/brown bears and black bears are related to the different habitats favored by each species. It is suggested that care of black bear cubs and hence reproductive success for black bears is tied to the forest biome, and that the grizzly/brown bear in branching out from the forest onto non-treed areas such as tundra, grasslands and prairie edges, gained rich new food sources, but also became more aggressive than the black bear, a behavioural adaptation to cub care in this new habitat.

INTRODUCTION

Few persons need a scientist to tell them that black bears differ from brown and grizzly bears. Still there are levels of understanding of differences as is illustrated in the following story.

A young national park naturalist, fresh from training, was lecturing to a crowd of tourists, discussing the differences between black bears and grizzly bears. The naturalist said that a good way to tell the species of a given bear was to sneak up on the bear in question and kick it in the rump, then to immediately run and climb a tree. If the bear climbs up the tree after you it is a black bear.

An old-timer in the audience thought this test too elaborate. He said all you have to do to discover the species identity is to sneak up on the bear, kick it in the rump, wait a split-second, and then if you are still alive the bear was a black.

There is both sense and nonsense in this fanciful story as there is in most "folk-knowledge" about these species.

In this paper I discuss some behavioural, ecological, morphological and physical differences between black bears and the North American brown/grizzly bear group, trying to interpret these differences in terms of the evolutionary adaptations of each species to their respective habitats.

EVOLUTION OF BLACK BEARS AND THE BROWN/GRIZZLY BEAR GROUP

The phylogeny postulated here is adapted from Kurtén (1968) and Thenius (1959). There is little original work of my own, although stress on certain relationships and errors of interpretation may be mine. Both Kurtén and Thenius, who as palaeontologists could be classified as lumpers, recognize two living sub-familial groups of bears, the Ursinae and the Tremarctinae. Simpson (1945), an even more classical lumper, is not even sure whether bears deserve familial separation as the Ursidae, from the dogs, the Canidae, and he certainly does not recognize any valid subfamilial differences among the living ursids. He points out that the ursid group is of quite recent origin, first appearing in the fossil record during the Burdigalian of the lower Miocene.

The Ursinae line, whether formally designated or not, is of importance here. The genus *Ursus*, the major modern day genus and the only genus with a well documented fossil record, first appears in the fossil record in Europe during the Astian (upper Pliocene) as the Auvergne bear, *Ursus minimus* Devèze & Bouillet. This was a small bear about the size of the Malay Bear, *Helarctos malayanus* Raffles, but anatomically it resembled the black bears. This species persisted until earliest Villafranchian (lower Pleistocene) but was gradually transformed into the typical Villafranchian species, *Ursus etruscus* Cuvier, the Etruscan bear.

The Etruscan bear is of interest for several reasons, especially if you are already interested in bears and their phylogeny. Early forms of this bear were small, about the size of the modern Asiatic black bear, but the fossil record shows that they subsequently increased in size and the terminal forms were as large as the brown bear, *Ursus arctos* Linné. The Etruscan bear was probably a forest adapted type, much like its precursor the Auvergne bear.

From the time of *Ursus etruscus*, things began to move for the bears in the theater of evolution. The geomorphology of the world was beginning to change rapidly in many areas. The age of ice was coming. In parts of the Northern Hemisphere Pleistocene glaciers advanced during cooler phases but during warmer interglacial periods the great ice sheets retreated and left bare, vast, denuded areas which because of local climatic factors probably had a tundra type of treeless vegetation. The bears responded to these and other changes with significant adaptive radiation. *U. etruscus* formed the nucleus of the middle and late Pleistocene branching of the genus which apparently led to all of the living members of the genus. The scene of this radiation was in the palaearctic region and the three species known from the nearctic are immigrants.

The Etruscan bear probably gave rise to three evolutionary lines. The first and second were localized in Asia and led to the brown bears and the black bears; the third line started and ended in Europe and was represented by the endemic cave bears *Ursus spelaeus* Rosenmüller & Heinroth. Only the brown and black bears will be of concern here.

The Asiatic black bear might almost be regarded as a surviving but slightly modified Etruscan bear, resembling especially the early, small variety of the middle Villafranchian. By 2-Mindel the black bears had entered North America where the earliest forms date from D-Holsteinian (a cave find near Port Kennedy in Pennsylvania). This form is still very similar to the Asiatic mother species.

The earliest members of the brown bear line are recognized from remains in Choukoutien in China during 2-Mindel. The brown bear group did not cross to North America until 4-Würm and even then it appears to have been confined to

Ursus maritimus. Phipps, the polar bear, is the most recent bear in the fossil record and appears to have evolved from a coastal brown bear population which specialized for life on the sea ice margins of the far north.

APPROXIMATE AGE IN MILLIONS OF YEARS	DIVISIONS		EVOLUTION OF CERTAIN URSID GROUPS
	EPOCH OR AGE	CLIMATIC PHASE	
25	MIOCENE	AQUITAINIAN	<p>AGRIOTHEREIINAE</p> <p><i>Ursus</i> sp. (dashed line)</p> <p><i>Indolestes</i> sp. (dashed line)</p> <p><i>Arctotherium</i> sp. (dashed line)</p>
		BURDIGALIAN	
		HELVETIAN	
		TORTONIAN	
		SARMATIAN	
		PONTIAN	
13	PLIOCENE	PLACEZAN	<p>?</p> <p>URSINAE</p> <p><i>Ursus</i> sp.</p> <p><i>U. minimus</i></p> <p>TREMARCTINAE</p> <p><i>Pliomarctos</i> sp.</p>
		ASTIAN	
3	VILLAGENIAN		<p><i>U. strussens</i></p> <p><i>Arctodus</i> sp.</p> <p><i>Tremarctos</i> sp.</p>
1			
		GÜNE	
		MINDEL	
		RISS	
100,000	PLEISTOCENE LATE	WÜRM-RISS	<p><i>U. variator</i></p> <p><i>U. spelaeus</i></p> <p><i>U. hibernicus</i></p> <p><i>U. americanus</i></p>
		WÜRM	
10,000	RECENT		<p><i>U. maritimus</i></p>

brown bears inhabiting the Alaskan Islands of Kodiak, Afognak, and Shuyak, he claims are reproductively isolated and 'possess distinctive cranial characteristics. . . .'. He suggests that this group be designated as *U. arctos middendorffi*. All mainland North American brown bears and grizzly bears he places in one subspecific group *U. a. horribilis*. My comments in this paper with respect to *Ursus arctos* in North America apply to all island and mainland representatives of the species usually referred to by the common names of (big) brown bears and grizzly bears.

The bears evolved from the Miacidae which were a family of small, carnivorous, tree climbing mammals. While the bears ultimately became much larger in size than their miacid ancestors and most bear species became omnivorous,

they did not in general cease their association with the forest or lose their tree climbing ability.

The earliest representative of the Ursinae group, *U. minimus*, was probably a forest adapted type, for anatomically it resembled the black bears although it was smaller (Kurtén 1968). *U. minimus* gave rise to the Etruscan bear from which the three lines I have mentioned diverged. One of these lines, the black bears, remained a pure forest specialist and another led to the brown bears. I regard *U. arctos* as a basically forest adapted type that ventured often into a new habitat, open tundra areas, left bare by retreating ice during pleistocene interglacials. Entry into this new habitat resulted in significant changes from the pure forest type ancestor and these changes will be discussed in detail later. The climax of this trend away from the forest biome appears to have been reached with the polar bears.

PAST AND PRESENT DISTRIBUTION OF THE BLACK BEAR AND BROWN/GRIZZLY BEAR GROUP IN NORTH AMERICA

Today as in the past there is significant overlap in the ranges of the American black bear and the brown/grizzly bear group. Typically however the black bear occupies forested areas, preferably somewhat open, and the brown/grizzly bear group occupies more open areas such as tundra (arctic and alpine), although individuals of the brown/grizzly bear group may sometimes be found in the forest. An examination of the extremes of the two ranges and the specific habitats occupied is revealing (Figs. 2 and 3).

In the far north while the grizzly ranges onto the actual barrengrounds, a treeless tundra area, it more often is found in association with open wooded and watered areas such as lakes, delta channels, and rivers. At the eastern extent of the barren-grounds grizzlies are rarely seen away from or beyond the Thelon, Back, Dubawnt and Kazan rivers (MacPherson 1965).

A map of the northern extent of the forests of North America reasonably well defines the northern extent of the black bear distribution (Fig. 2). Recent observations by Jonkel & Miller (1970) suggest that on parts of the barren-grounds of Canada and on the Ungava Peninsula the black bear may be extending its range somewhat onto treeless areas. This they tentatively attribute to the possible extinction of the Ungava grizzly (a questionable population according to Elton 1954) and to a general decline in the numbers of barren-ground grizzlies (Harrington *et al.* 1962).

In the southwestern extreme of the range we find another interesting situation in the grassland, and in some of the chaparral (sclerophyllous scrub) of California. Here, prior to its recent extinction, the grizzly once was numerous, extending fully to the coast and even ranging onto the beaches. Areas that were not forested seem to have been avoided by the black bears but if productive they were favored by grizzlies (Fig. 4).

In the interior of North America the grizzly found at least the edges and river bottoms of the great plains suited to his habits. Here the grizzlies' range probably extended eastward to the great bend of the Missouri River in the present North Dakota, southward to the Moreau River in South Dakota (record for Kansas and Minnesota, Hall & Kelson 1959, are probably aberrant), and possibly eastward to the Red River region (Stebler 1972). Buffalo carrion, supplemented with occasional kills, and a steady availability of grasses and forbs must have made this an area containing high quality food for grizzlies.

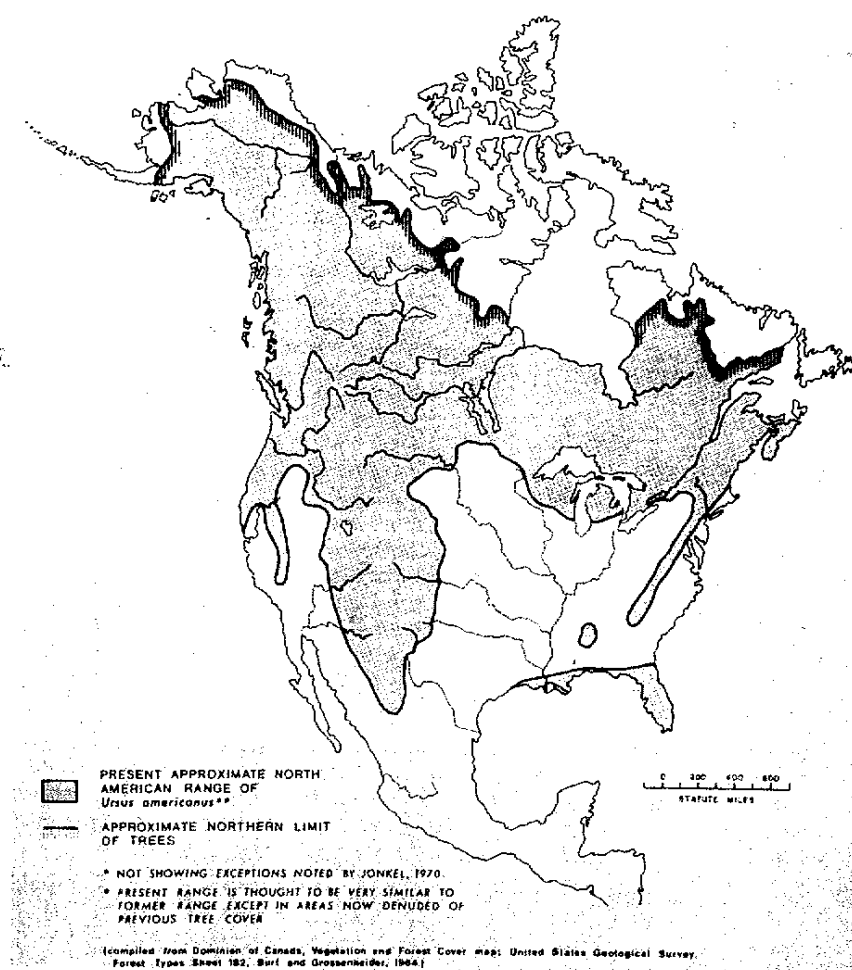
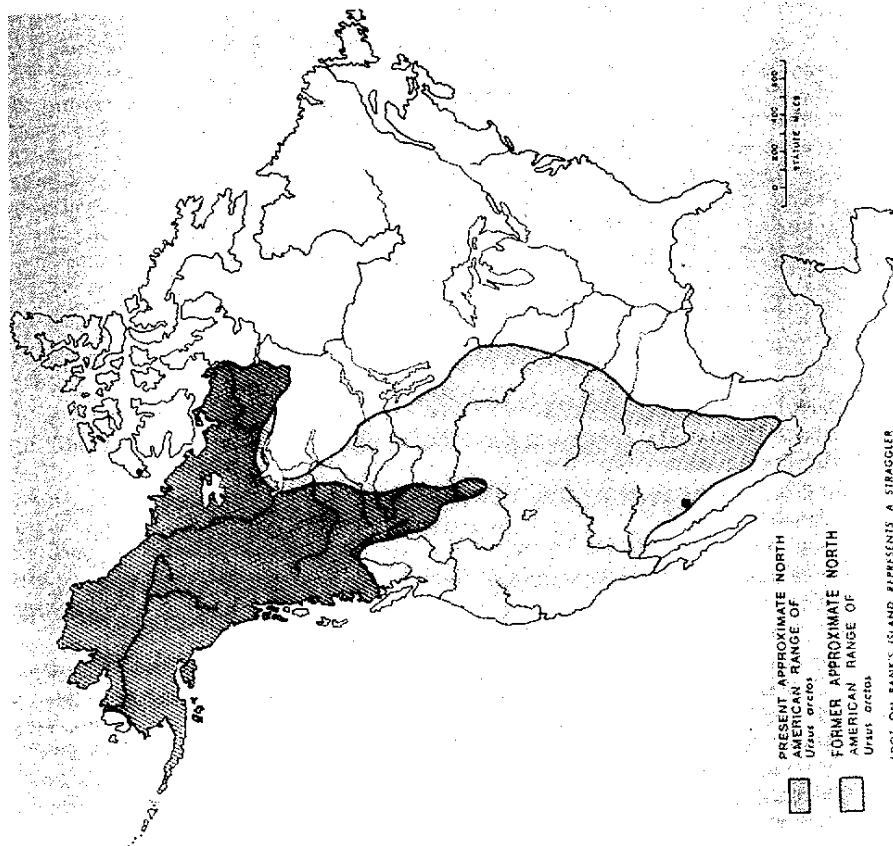


Fig. 2

Leopold (1970) regards the grizzly as primarily adapted to river valleys, foothills and brush lands. The black bear seldom ventured onto the open plains areas as did the grizzly.

In certain mountainous areas during the summer we find grizzly/brown bears frequently above the treeline on the open alpine tundra meadows and other open areas. Black bears seldom visit these seasonally rich habitats. The observations of Frank Craighead (1968) could be interpreted as giving partial support to this generalization. Based on 10 years of study of the grizzly in Yellowstone he says:

All the ranges plotted from radio fixes or bearings embraced both open country and timber. The factor largely influencing range selection and location is the open country habitat composed of grass, sagebrush, and forbs. This is a sagebrush grass subclimax type. Very little of this Yellowstone vegetation type is uninhabited by grizzlies, but there are large stretches of mature timber, dominated by the lodgepole pine type, where grizzlies are seldom found except for short periods while traveling.



226

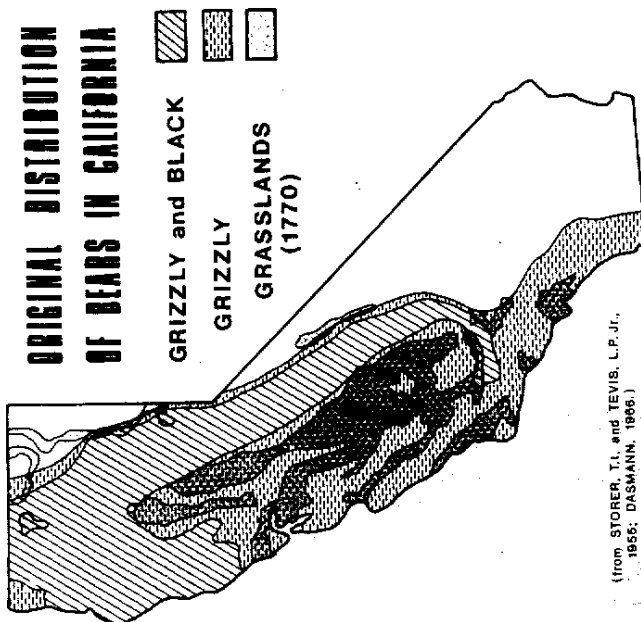


Fig. 4

In summary, data show that in North America the black bears range is mostly limited to treed areas wherever the grizzly is also found. In certain areas such as the Ungava Peninsula, the present day absence of grizzly bears is coupled with occasional black bear venturing onto the tundra. The grizzly/brown bear on the other hand may sometimes visit or live in forest areas, but mainly utilizes semi-open areas, such as the barren grounds or the alpine-tundra meadows of the mountains.

ADAPTATIONS OF THE BLACK BEAR TO THE FOREST BIOME

Black bears after reaching a certain minimum age are capable of expert tree climbing. This ability is reflected anatomically when they are compared to the grizzly: they have shorter and more narrow front claws, which are also more curved and are not much longer than their hind claws. The black bears' hind feet are also relatively shorter than those of the grizzly. The black bear is on the average lighter in body weight than the grizzly, although occasional old males may be larger than female grizzlies. This latter fact is not surprising since both species show significant sexual dimorphism with respect to body weight. Other morphological differences between the species suggest that the body of the black bear is adapted to climbing whereas that of the grizzly is not. Conversely the longer front claws of the grizzly are more specialized for digging than are those of the black bear.

Over the course of several field seasons of observing black bears, I came to appreciate how significant trees can be for the day to day existence of the black bear (Herrero, unpublished observation). The ability to climb matures early in young black bears, probably around three months of age. In cold temperate regions climbing ability is probably developed in cubs by the time the family leaves the winter den (Herrero 1970a). Cubs climb in response to a variety of intrusions, especially close approach by non-family bears or by human beings. Thus they climb in response to potentially dangerous situations created by the presence of other animals, although they also climb for what seem to be many other reasons. Immediately or soon after perceiving an intruder, young cubs climb and, if the sow is nearby, she often positions herself near the base of the tree that the cubs occupy, or may even climb the tree herself. I believe that defense of cubs is intimately related to their climbing trees. Defense against what?—conspecifics, grizzly bears, or other carnivores both present day and extinct. As the cubs grow older the tendency to climb at the slightest disturbance seems to diminish, and more direct possible threats are required to tree them. Sub-adult animals (1½ to 4½ years) still climb, especially when directly threatened. Most old boars are able to climb as is shown by the ability of hunting dogs to tree them; however, in several years of field observations I have never observed a fully mature boar climbing or in a tree. The implied 'safety-factor' of tree climbing may last to a significant degree until a black bear matures and the behaviour patterns of the adult bear develop.

Black bears, however, also often climb trees when no intruder or obvious disturbance is present. I concluded that they also climb for the implied functions of shelter, sleeping, nursing, playing and protection (Herrero, unpublished observation). While difficult to quantify it seemed that alert vigilance often shown on the ground would be relaxed once in a tree. I believe that the main significance of tree climbing to black bears was that it led to a position of relative safety.

Many field observations suggest that black bears are very reluctant to venture far from trees. Erickson (1965) noted that garbage dumps in Alaska if located in open areas tended not to be visited by this species. Conversely dumps close to forested areas where there are black bear populations are almost always used for feeding. The distribution of black bears being correlated with the forest zone has been mentioned in this context. Meadows and forest edges are often choice feeding spots and will be utilized provided they are not too far from trees. Over a period of six months I repeatedly observed black bears crossing an open slope several hundred meters in extent. The slope contained several isolated large trees, and the path used by the bears commonly zig-zagged across the slope so as to go nearby these trees.

By contrast the grizzly/brown bear, while willing to enter the forest and to travel through it or shelter and feed in it, is more often found in more open habitats as already mentioned. Young grizzlies/browns are capable of tree climbing (reflecting this ability of their tree climbing ancestors) but this trait is lost by the time the animal becomes a sub-adult. There is no indication that trees are an integral element for the grizzly life style as they are for the black bear.

ADAPTIVE BEHAVIOURAL AND PHYSIOLOGICAL DIFFERENCES BETWEEN BLACK AND GRIZZLY/BROWN BEARS

I hypothesize that black bears are less aggressive, or less inclined to serious actual attack than are grizzly/brown bears, because of different selective pressures that acted in the past and are acting today on these two species.

First I want to try to establish and clarify my claim that the two species differ in their use of serious actual attack. The best evidence that I know of that is relevant to this claim comes from analyzing records of interspecific encounters between black bears and human beings, and grizzly bears and human beings. In the entire history of the North American National Parks which shelter the grizzly bear there have been at least 20 clearly documented cases of persons hiking in backcountry areas, suddenly coming on a grizzly sow with cubs, and the sow charging and subsequently injuring member(s) of the hiking party (Herrero 1970b). I have found no recorded instances of a black bear sow with cub(s) being involved in such an incident. However, each year many more persons are injured in parks by black bears than by grizzlies. This reflects a totally different factor—the willingness of black bears to associate closely with humans, and to beg or steal man's food or garbage. While not as aggressive as is the grizzly, the black bear is still a very powerful animal and is strongly motivated towards food.

Further support for aggressive differences between black bears and grizzly/brown bears comes from examining North American hunting records. No one needs to tell a keen and experienced hunter that grizzly bears are more dangerous than are black bears. Many hunters have been injured by brown/grizzly bears (Anonymous 1969 a & b), whereas even wounded black bears are seldom dangerous to man (Page 1969).

Analysis of very limited data on intraspecific interactions also supports the contention of differences in aggression between black bears and grizzly/brown bears. While intraspecific physical encounters are rare for both species because of highly ritualized agonistic behaviour, when such encounters do occur they probably more often lead to significant injury in grizzly/brown bears than in black bears. Limited data suggest the existence of more extensive facial

and body scarring, and bone and tooth damage in grizzly/brown bears than in black bears. This question is now under study by the author.

Interspecific encounters between black bears and grizzly bears usually show that black bears avoid or flee from encounters with grizzlies. Cahalane (1947) has observed grizzlies to tree blacks. Grizzlies have also been observed to prey on blacks (Jonkel 1962), although the converse situation has not been seen. Black bears have been observed to leave dump areas when grizzlies arrive (Finley & Finley 1940; Herrero, unpublished observations). In some feeding competition situations, however, black bears may show dominance over grizzly bears (Barnes 1967). The general situation is that grizzlies dominate or even may on rare occasions kill black bears, and this I attribute to differences in aggression between the species.

I postulate that because of the use of trees it has been phylogenetically advantageous for black bears to be much less aggressive than grizzly/brown bears. When threatened by potential predators the grizzly/brown bear sow defends her young on the ground, and because of this terrestrial habit the cubs are more vulnerable to attack than are black bear cubs. With the grizzly/brown species a highly aggressive sow is probably the most successful mother. However, this carries with it the risk of injury or death (albeit rarely) to the sow and thus decreased reproductive success. With extremely powerful animals such as bears, evolution has resulted in a minimum of serious intraspecific individual injury, and a maximum ritualization of agonistic behaviour, especially with reproductive units such as sows. However, with the grizzly/brown, given its habitat requirements and other characteristics, an incidence of injury must still exist because the cub(s) are defended upon the ground.

Because of possible injury to the bear sow during defense of the cubs it would be advantageous to have low violent aggressiveness provided that the cubs are still well protected. This has been possible with black bears because of the protective function of tree climbing. Aggressive tendencies shown by each species have probably been genetically transferred from sows to the species as a whole.

Given the significant difference in aggressiveness between the species, which I conclude is an adaptive specialization to different habitats, we may ask whether there are other related differences.

The answer is a tentative yes. Certain differences in reproduction may be related to the basic difference in habitat specialization and its by-product, aggression. Firstly, black bear cubs only stay with the sow for their first year and then part of the second year, until they are about $1\frac{1}{2}$ years of age (Jonkel 1962, Cahalane 1947). Brown/grizzly bear cubs, in contrast, often remain with the sow for about $2\frac{1}{2}$ years (Hensel *et al.* 1969; Craighead *et al.* 1969). As Cowan (1972) has pointed out there must be some advantage to remaining with the sow for $2\frac{1}{2}$ years or those sows who wean at $1\frac{1}{2}$ would come to dominate the population. This reproductive difference between black and brown/grizzly bears might be related to the evolutionary differences which I have postulated. Grizzly/brown bear cubs which remain with the sow for an additional year might be receiving among other things physical protection from grizzly/brown bear boars since they do not have the assured self-protection of tree climbing.

Additionally there is evidence that grizzly bear populations feeding extensively at dump areas have high mortality rates especially in young age groups (Craighead & Craighead 1967), compared to mortality rates in young age groups of more naturally existing populations (Hensel *et al.* 1969). There is limited evidence that black bears do not show this sharp rise in mortality in young age

groups even with very frequent dump feeding (Herrero, unpublished observations). In order to feed on a dump crowded with other grizzlies, a sow grizzly with cubs must either leave her cubs on the periphery of the dump or take them into a potentially dangerous congestion. Either situation is dangerous to the cubs, and is stressful for the sow. Grizzly bear boars have on more than four occasions been observed to prey on cubs in this situation (Craighead, J., pers. comm.). The Craigheads have also observed predation on cubs taking place in areas of more natural habitat. More important, I believe, would be the effect of stress on the sows, this in turn affecting the overall care of the cubs. A black bear sow, even with very young cubs, needs only to leave them up a convenient tree to assure their safety while she goes and feeds at a congested dumpsite where many conspecifics are feeding. Hence direct mortality from boars or other predators would be infrequent and non-specific stress would be less. Of course, this is only one of many possible interpretations of the observed species mortality differences in dump areas.

REFERENCES

- ANONYMOUS 1969a. Newspaper articles from the Anchorage News. 27 Aug. 1955; 17 April 1956; 9 Sept. 1957; 6 Sept. 1958; 28 July 1959; 17 Sept. 1962; 30 Oct. 1963; 21 Oct. 1968. Anchorage, Alaska.
- 1969b. Newspaper articles from the Calgary Herald. 13 Oct. 1959; 25 Mar. 1960; 14 Sept. 1961; 5 Nov. 1968. Calgary, Alberta.
- BARNES, V. G. 1967. Activities of black bears in Yellowstone National Park. M.Sc. Thesis, Colorado State University, Fort Collins, 116 pp.
- BURT, W. H. & GROSSENHEIDER, R. P. 1964. *A field guide to the mammals*. Houghton Mifflin Company, Boston. 284 pp.
- CAHALANE, V. H. 1947. The bears—black bear; Pp. 134-143; in *Mammals of North America*. The McMillan Co., New York, 682 pp.
- COUTURIER, M. A. J. 1954. *L'ours brun, Ursus arctos* L. Grenoble, Isère, France, Marcel Couturier. 905 pp.
- COWAN, I. McT. 1972. Panel discussion on: Ecology, population characteristics, movements, and natural history in *Bears: their biology and management*. I.U.C.N., Morges, (this volume)
- CRAIGHEAD, F. C. Jr. 1968. Radiotracking of grizzly bears in Yellowstone National Park, Wyoming. Natl. Geogr. Soc. Research Repts., 1963 Projects, Washington, D. C., Pp. 59-67.
- CRAIGHEAD, J. J. & CRAIGHEAD, F. C. Jr. 1967. Management of bears in Yellowstone National Park. Unpublished Manuscript. 113 pp.
- CRAIGHEAD, J. J., HORNOCKER, M. G. & CRAIGHEAD, F. C. Jr. 1969. Reproductive biology of young female grizzly bears. *J. Reprod. Fert. Suppl.* **6**, 447-475.
- DASMANN, R. F. 1966. *Wildlife biology*. John Wiley and Sons, Inc., New York. 231 pp.
- ELTON, C. S. 1954. Further evidence about the barren-ground grizzly bear in Northeast Labrador and Quebec. *J. Mamm.* **35**: 345-357.

- ERICKSON, A. 1965. The black bear in Alaska. Alaska Dept. of Fish and Game, Juneau. 19 pp.
- FINLEY, W. & FINLEY, I. 1940. To feed or not to feed, that is the bear question in Yellowstone National Park. *Amer. Forest* 46(8): 344-347, 368, 383-384.
- HALL, E.R. & KELSON, K.R. 1959. *The mammals of North America*. The Ronald Press Co., New York. 1083 pp.
- HARRINGTON, C. R., MacPHERSON, A. H. & KELSALL, J. P. 1962. The barren-ground grizzly bear in northern Canada. *Arctic* 15: 294-298.
- HENSEL, R. J., TROYER, W. A., & ERICKSON, A. W. 1969. Reproduction in the female brown bear. *J. Wildl. Mgmt.* 33(2): 357-365.
- HERRERO, S. M. 1970a. A black bear and her cub. *Animals* 12(10): 444-447.
- 1970b. Human injury inflicted by grizzly bears. *Science* 170: 593-598.
- JONKEL, C. J. 1962. Black bear population study. Montana Fish and Game Dept., Job Completion Rept., Fed. Aid. Project, W-98-R-2. 18 pp.
- & MILLER, F. L. 1970. Recent records of the black bears (*Ursus americanus*) on the barren grounds of Canada. *J. Mamm.* 51(4): 826-828.
- KURTÉN, B. 1968. *Pleistocene mammals of Europe*. The world naturalist series. Weidenfeld and Nicolson, London. 317 pp.
- LEOPOLD, A. S. 1970. Weaning grizzly bears. *Natural History* 79(1): 94-101.
- MACPHERSON, A. H. 1965. The barren-ground grizzly bear and its survival in Canada. *Can. Audub.* 27(1): 2-8.
- PAGE, W. 1968. The black bear—trophy or nuisance? *Field and Stream* LXXIV(6): 39, 68, 70, 72.
- RAUSCH, R. L. 1963. Geographic variation in size in North American brown bears, *Ursus arctos* L., as indicated by condylobasal length. *Can. J. Zool.* 41: 33-45.
- SIMPSON, G. G. 1945. The principles of classification and a classification of mammals. *Bull. Amer. Museum of Natur. Hist.* 85: 224-225 (Ursidae); 349 pp.
- STEBLER, A. M. 1972. Conservation of the grizzly-ecologic and cultural considerations in *Bears—their biology and management*. I.U.C.N., Morges, pp. (this volume).
- STORER, T. I. & Tevis, L. P. 1955. *California grizzly*. University of California Press, Berkeley. 335 pp.
- THENIUS, E. 1959. Ursidenphylogenese und biostratigraphie. *Zeitschr. Säugertierkunde* 24: 78-84.