ARCTIC
VOL. 38, NO. 4 (DECEMBER 1985) P. 303-309

Observations of Intraspecific Aggression and Cannibalism in Polar Bears (*Ursus maritimus*)

MITCHELL TAYLOR,[1] THOR LARSEN,[2] and R.E. SCHWEINSBURG[3]

ABSTRACT. Cannibalism in polar bears appears to occur as carrion feeding and as attacks by males on small cubs or incapacitated individuals. Direct observations indicate that intraspecific killing and cannibalism occur among polar bears throughout the Arctic. The high incidence of *Trichinella* infection and circumpolar observations of cannibalism suggest that polar bears will readily eat other polar bears when they can do so without excessive risk of injury. Speculations that intraspecific aggression and cannibalism may be an important social and ecological force are consistent with existing information on polar bear biology.

Key words: aggression, cannibalism, parasitism, polar bears, population dynamics, *Trichinella*, *Ursidae*, *Ursus maritimus*

RÉSUMÉ. Le cannibalisme chez les ours blancs semble se produire en des cas d'ingestion de charogne et d'attaques par des mâles contre des oursons ou des individus incapables de se défendre. Des observations directes signalent qu'à travers l'Arctique, les ours blancs tuent et mangent d'autre ours de leur même espèce. L'incidence élevée d'infection *Trichinella* et les observations de cannibalisme partout dans les régions polaires suggèrent que les ours blancs mangent sans hésitation d'autres ours blancs s'ils le peuvent sans recevoir de blessures graves. Des spéculations présentées selon lesquelles l'agression et le cannibalisme intraspécifique comportent une importante force sociale et écologique sont conformes à des informations connues sur la biologie des ours blancs.

Mots clés: agression, cannibalisme, parasitisme, ours blancs, dynamique des populations, *Trichinella*, *Ursidae*, *Ursus maritimus*

Traduit pour le journal par Maurice Guibord.

INTRODUCTION

Events that play important roles in determining the behaviour, distribution, and abundance of a species may be short and difficult to observe. Thus observations of polar bears attacking or eating one another have been opportunistic and mainly anecdotal. We summarize the available accounts of polar bear intraspecific killing and cannibalism into four categories: 1) infanticide by males; 2) infanticide by females; 3) adults killing other adults; and 4) carrion feeding or killing disabled bears. We also examine the likelihood that cannibalism is the primary vector of *Trichinella* propagation in polar bears.

Because direct observations of cannibalism are rare, our conclusions are necessarily speculative. All undated citations of Larsen (TL), Schweinsburg (RES), and Taylor (MT) refer to this study.

Sources of Observation

Before 1970, commercial hunters used set-guns to kill polar bears in the Svalbard archipelago. These set-guns were rifles in boxes; bait placed in front of the gun was connected to the rifle trigger. Cubs would usually stay with killed females and females would often stay with slain cubs (TL). Svalbard has long had continuously manned weather and research stations. Both hunters and weather station personnel kept diaries and submitted reports that contained accounts of polar bear cannibalism and intraspecific predation. TL conducted interviews in 1980 and 1981 with individuals who kept these diaries.

Observations by Inuit are included here, but the experience of native observers is undersampled because of a lack of written records. Many observations of cannibalism came from personnel involved in polar bear research programs. Observations have occurred during helicopter tagging studies and behavioural studies conducted from blinds. An attempt was made to find accounts of cannibalism in recent journals, but the records of early explorers and hunters were not extensively surveyed.

Some accounts of infanticide or attempted infanticide are ambiguous. We have listed some accounts as intraspecific killing or infanticide that might have been merely carrion cannibalism. Classifications were based on our field experience and the circumstances surrounding the observations (Table 1). Only verified accounts or accounts from reliable sources were listed. The following account (TL) is given as an example of the ones summarized:

> On 17 April 1980, P. Bakkenhaug, station chief at the Hopen weather station, observed a male following a female with one cub of the year (COY). Suddenly the male rushed upon the pair and seized the COY. The female also seized her COY and a grim tug-of-war ensued. The struggle continued for some minutes until the male released the COY; then the female carried her cub about 1 km onto the sea ice. As P. Bakkenhaug and his group approached, the female abandoned the cub, which was dead.

Social Behaviour and Geographical Stratification

COYs and yearlings appear to be most vulnerable to predation by other bears, particularly by large males (Table 1). If large males were perceived as a threat, females with COYs and yearlings might be expected to seek areas removed from those frequented by large males. Alternatively, females may be able to protect their cubs from attacks in most cases (Stirling, 1974). The existing data provide arguments supporting both opinions. We agree with Stirling (1974) that the most vulnerable period for cubs is just after the female has left the maternity den, and that as the cubs mature their ability to escape

[1]Department of Fisheries and Wildlife, Michigan State University, East Lansing, Michigan, U.S.A. 48824
[2]Norsk Polarinstitutt, 1330 Oslo Lufthavn, Norway
[3]Northwest Territories Wildlife Service, Yellowknife, Northwest Territories, Canada X1A 2L9

TABLE 1. Summary accounts of intra-specific aggression, infanticide, and cannibalism

Date	Observer	Location	Description	Reference
Infanticide — Attacks by Males on Cubs				
September 1896	Nansen	Franz Josef Land	Male killed 2 COYs	Nansen (1897)
1950 - 1970	Strand Forfang Torsvik	Svalbard set-gun sites	10 accounts of orphaned COYs and 7 accounts of orphaned yearlings killed by other bears after their mothers were killed at set-gun sites	Larsen (this study)
Spring 1962	Harrington	Southampton Island, N.W.T.	Large male attacked female with COYs	Harrington (1963)
February 1970	Nordes	Northwest Svalbard	Male attacked female with one yearling; killed yearling	Larsen (this study)
June 1970	Strand	Half Moon Island, Svalbard	Male attacked 3 tethered cubs; killed one, injured one	Larsen (this study)
Fall 1970	Jonkel	Cape Churchill, Manitoba	Large male attacked and killed female with 2 COYs	Jonkel (1970)
Spring 1970 - 1973	Parovshchikov	Franz Josef Land	"Most" COY mortalities in Franz Josef Land are due to attacks by large males in early spring	Parovshchikov (1964)
Spring 1976	Lentfer	Pt. Barrow, Alaska	2 COYs killed and partially consumed by a large male	Lentfer (pers. comm.)
Summer 1977	Larsen	Sea ice between Franz Josef Land and Svalbard	Attack on female with COY by a young male; no kill	Larsen (this study)
Spring 1979	Taylor	Pt. Barrow, Alaska	1 COY killed and partially consumed by a large male	Taylor (this study)
April 1980	Bakkenhaug	Hopen, Svalbard	Male attacked female with one COY; killed COY	Larsen (this study)
Spring 1980	Taylor	Pt. Barrow, Alaska	2 instances of drug immobilized females with yearlings having yearlings killed; 1 observed, 1 presumed	Taylor (this study)
Spring 1980	Taylor	Pt. Barrow, Alaska	1 COY decapitated by a large male, not eaten	Taylor (this study)
Not given	Coastal Inuit	Alaska; Canada; and Greenland	Large male bears kill and eat cubs and smaller bears; general knowledge from hunters	Schweinsburg and Taylor (this study)
Infanticide — Mother - Offspring				
Spring 1969	Kistchinski	Wrangel Island, U.S.S.R.	Malnourished female killed and ate 1 COY from a 2-COY litter	Uspenskii and Kistchinskii (1972)
Spring 1970	Uspenskii	Wrangel Island, U.S.S.R.	Malnourished female killed and ate 1 COY from a 2-COY litter	Uspenskii and Kistchinskii (1972)
Spring 1975	Belikov and Kuprijanov	Wrangel Island, U.S.S.R.	Malnourished female killed and ate 1 COY from a 2-COY litter	Belikov and Kuprijanov (1977)
Spring 1975	Belikov and Kuprijanov	Wrangel Island, U.S.S.R.	Malnourished female killed but did not eat 2 COYs	Belikov and Kuprijanov (1977)
Spring 1979	Hansson and Thomassen	Kongsoya, Svalbard	Female went into den with 2 COYs, emerged with 1 COY	Hansson and Thomassen (1982)
Spring 1979	Schweinsburg	S. Devon Island, N.W.T.	1 abandoned COY found in convulsions emaciated female with sibling COY located by tracks	Schweinsburg (this study)
Spring 1982	Lee	Clyde River, N.W.T.	Two thin females killed by Inuit were each found to have 1 COY in their stomachs	Schweinsburg (this study)
Adults Killing Other Adults				
Spring 1983	Inuit hunters	Agu Bay, N.W.T.	Adult (presumed healthy) killed and partially consumed	Schweinsburg (this study)
August 1984	Smith and Alexander	Lancaster Sound, N.W.T.	Adult male killed and partially consumed adult female, but had not killed her 2 cubs	Taylor (this study)
Feeding on Carrion or Disabled Adults				
September 1896	Nansen	Franz Josef Land	Male fed from carcass of shot female	Nansen (1897)
1950 - 1970	Svalbard set-gun hunters	Svalbard Archipelago	Cubs cannibalizing shot mother; bears of both sexes and all ages eating bear carrion at set-gun sites	Larsen (this study)

(continued)

TABLE 1. (concluded)

Date	Observer	Location	Description	Reference
April 1973	Schweinsburg	Victoria Strait, N.W.T.	Two 2-year-old cubs ate previously immobilized mother	Schweinsburg (this study)
April 1976	Schweinsburg	Tasmania Island, N.W.T.	2 large males abandoned by hunters unskinned, completely consumed in less than one week	Schweinsburg (this study)
Spring 1979	Latour	Southeastern Devon, N.W.T.	Immobilized male killed and eaten by undetermined number of bears	Taylor (this study)
August 1980	Helicopter pilot, YMER	Kongsoya, Svalbard	Possible cannibalism on previously immobilized male	Taylor (this study)
Not given	Inuit hunters	Alaska; Canada	Carrion feeding by polar bears common at skinned carcasses	Schweinsburg and Taylor (this study)

an attack increases, thereby improving the effectiveness of maternal defense.

The ability of females to defend their young is a key factor in evaluating the role of infanticide in polar bear ecology. Size appears to confer an advantage in antagonistic encounters between members of the same sex and between sexes. MT observed two female polar bears of known age and weight (both with litters of COYs) fighting over a freshly killed seal in Radstock Bay, Northwest Territories, in summer 1978. The larger, older female displaced the younger, smaller female. RES observed three polar bears at a single seal kill. The largest bear was feeding on the kill, the medium-sized bear was about 100 m distant, and the smallest bear was about 200 m away.

Adult males are typically two to three times heavier than adult females (DeMaster and Stirling, 1981), suggesting that a female would find it difficult to defend a stationary resource against an aggressive male. The fastest and smallest self-sustaining polar bears are weaned subadults (three to five years old). Yearlings and two-year-olds are nearly as fast as their mothers and certainly faster than adult males. Adult males are not as fast, nor did they appear to have the stamina, of female bears. Large males probably overheat if they attempt to run any distance at too fast a pace (Øritsland and Lavigne, 1976). This disparity is accentuated as the males grow larger and heavier. The proximate effect of age and sex differences in running speed is that young COYs are the most vulnerable to being captured by large males. Very young COYs also have difficulty making sustained progress across pack ice. Females spend several weeks after emerging from the den making small forays in the vicinity of the maternity den, presumably to strengthen the cubs for travel (Hansson and Thomassen, 1982).

Stirling (1974) also believed that, except for small COYs, young polar bears are faster than adult males and are unlikely to be captured in a chase by the heavier, older bears. He suggested that because of this disparity in running speed, intraspecific killing is an infrequent occurrence in polar bears. Stirling (1974) also suggested that adult females with large young are not subordinate to polar bears of any other age or sex class and gave an account of a female with two-year-old cubs displacing a larger male for possession of a seal kill. In a second instance (Stirling, 1974), a female, her two-year-old, and a large male all fed on a seal together. These observations were made in summer, after the breeding season and presumably just prior to weaning. Two-year-old cubs are much larger than yearlings or COYs; and male two-year-olds are sometimes larger than their mother. Svalbard hunters have documented six cases of females removing and defending young killed by set-guns: four instances of slain yearlings on Half Moon Island (winter of 1966–67 and 1967–70), and two instances of slain COYs, one on Ryke Yse and one on Hopen Island (both in winter 1967) (TL).

Polar bear tagging studies were usually conducted in April and May, which is the breeding season for adult females that either have no cubs or are weaning two-year-old cubs. Often females with two-year-old cubs have not yet weaned their offspring and the cubs remain with the female into the spring breeding season. When a female with two-year-old cubs is approached by a male, she usually does not defend the cubs. The weaned (or displaced) cubs are often observed trailing the mating pair, but clearly avoid any close contact. This behaviour is consistent with our suggestion that these large males (at least during the breeding season) pose a threat to smaller, non-estrous bears, particularly cubs.

Although the threat of intraspecific predation declines when cubs become large and active enough to be difficult to catch, females may still perceive the larger males as a threat to their offspring. Indications of spatial segregation of females with COYs or yearlings from other bears are consistent with this hypothesis.

In Hudson Bay, polar bears are forced onto land during summer when the ice melts. These bears are spatially segregated; groups of large males tend to be found in coastal areas and family groups farther inland (Stirling *et al.*, 1977; Latour, 1981). In autumn the bears congregate in the area of Cape Churchill, Manitoba, to await formation of the first winter ice. As the density of bears increases, the degree to which subadults are segregated from adults also increases (Latour, 1981). Wounded subadults have been observed in high density areas. It is possible that these wounds occurred merely from play bouts (Latour, 1980, 1981). Only one determined attack was observed during autumn in the Cape Churchill area (Jonkel, 1970).

Fifty-six polar bears were observed near a dead Greenland right whale (*Balaena mysticetus*) located at 79°55′N, 29°49′E on 2 August 1980 (Andersen, 1981; Christiansen, 1981). Females with COYs were not present; however, females with yearlings were in the area, but not at the carcass where the density of bears was greatest. No aggressive behaviour was observed, even though eight adult polar bears were feeding literally shoulder-to-shoulder. Females with COYs may have perceived the larger bears as threats to the cubs and avoided the area.

Kongsoya, a small island in the Svalbard archipelago, was inhabited by approximately 50 polar bears and surrounded by open ocean in early August 1980 (Taylor, pers. obs.). A 10-km strip of remaining shorefast ice provided a substrate for the polar bears to hunt seals. The highest concentrations of polar bears (25–30) were found on or in close proximity to the shorefast ice, which was dotted with 20 or more seal kill sites. One female with a yearling was observed near, but not on, the shorefast ice. One female with two COYs was observed on a nearby mountainside, and another female with two COYs was observed hiding under a rock outcropping about 2 km from the shorefast ice.

Cannibalism as the Primary Vector of Trichinella *Propagation in Polar Bears*

While the frequency of cannibalism among polar bears is unknown, observed levels of *Trichinella* larvae in polar bear populations across the circumpolar basin suggest that cannibalism is not rare. Table 2 summarizes available information on the occurrence of *Trichinella* larvae in wild polar bears. Madsen (1961), Rausch (1970), Rogers (1975), and Rogers and Rogers (1976) proposed cannibalism as a primary vector of infection for bears. Infanticide is not suggested as an important vector of *Trichinella* infection since cubs are nourished primarily by nursing and only secondarily by carnivory.

TABLE 2. Observations of *Trichinella* larvae in free-ranging polar bears

Location	Number Examined	Number (%) Infected	Source
Alaska	17	9 (53)	Rausch *et al.* (1956)
Alaska	104	57 (55)	Fay (1960)
Chukchi and Beaufort Seas	292	188 (64)	Lentfer (1976)
Southampton I., N.W.T.	3	2 (66)	Brown *et al.* (1948)
Greenland	16	6 (39)	Thorborg *et al.* (1948)
Greenland	112	31 (26)	Roth (1950)
Greenland	231	56 (24)	Madsen (1961)
Svalbard	7	7 (100)	Brown *et al.* (1949)
Svalbard	8	7 (88)	Connell (1949)
Svalbard	342	112 (33)	Larsen and Kjos-Hanssen (1983)
Franz Josef Land	4	4 (100)	Ozeretskoyskaya *et al.* (1969)
Greenland and Barents Sea	278	163 (59)	Thorshaug and Rosted (1956)
N.E. Siberia	19	1 (5)	Ovsjukova (1965)
Total	1333	519 (38.9)	Average

Pinnipeds, particularly ringed seals, are the main prey item of polar bears (DeMaster and Stirling, 1981). These seals feed on cold-blooded invertebrates and fishes, which cannot host *Trichinella* larvae (Madsen, 1961). Roth (1950), Rausch *et al.* (1956), and Madsen (1961) found evidence of *Trichinella* infection in $< 1\%$ of ringed and bearded seals examined. Lentfer (1976) suggested that occasional ingestion of an infected seal could be a sufficient vector for the observed levels of infestation and proportion of bears infected.

To examine the potential effectiveness of a seal vector, we assume that an adult polar bear catches and kills 50 seals in one year. Of those seals perhaps 15 are pups killed in birth lairs; they cannot have accumulated any *Trichinella* larvae. Of the 35 adult or subadult seals killed, many will be incompletely consumed. Stirling and McEwan (1975) and Eley (1979) noted that bears often eat only the blubber of the seals they catch, leaving the organs and muscles. Assume that 25 of the seals are completely consumed; if 1% of those seals are infected with *Trichinella*, then a polar bear will eat, on average, an infected seal once every four years.

The life cycle of *Trichinella* larvae may be completed inside a single host. Each ingested cyst will produce about 300 larvae, which encyst primarily in the skeletal muscle of the host (Zimmerman, 1971). Lentfer (1976) reported that the mean number of cysts$\cdot g^{-1}$ of masseter muscle of infected Alaskan polar bears was 4.15. Assuming (from research on domestic pigs) that 40% of total weight is skeletal muscle, and that the density of cysts in masseter tissue is 2.5 times the average for skeletal muscle taken as a whole (Zimmerman and Schwartz, 1961; Olsen *et al.*, 1964), a 300-kg polar bear would have to ingest 664 cysts to achieve 4.15 larvae$\cdot g^{-1}$ masseter tissue. The few ringed and bearded seals that were infected showed only trace levels of infestation (Roth, 1950; Rausch *et al.*, 1956; Madsen, 1961). Larsen and Kjos-Hanssen (1983) also indicated that the arctic strain of *Trichinella* is relatively non-infectious; thus every ingested cyst will not necessarily cause infection.

If we allow 300 cysts per infected seal (i.e., assume that the seal ingested one cyst, which subsequently produced 300 larvae, which then encysted in the seal's muscle tissue) and assume that all cysts are ingested by the bear and that each ingested cyst produces an infection, a 300-kg polar bear would have to eat 2.21 infected seals to achieve the observed (Lentfer, 1976) mean level of infestation (Table 3). Our calculations suggest that a polar bear would take about nine years to consume 2.21 infected seals (Table 3). Employing equivalent assumptions, a polar bear would have to consume only 400 g of skeletal muscle from another polar bear infected at 4.15 larvae$\cdot g^{-1}$ masseter muscle to achieve the same level of infestation. We suggest that cannibalism could be an important if not the primary vector of *Trichinella* propagation in polar bears.

TABLE 3. Calculation procedures to determine average time taken for a polar bear to become infested with *Trichinella* from eating seals

4.15 cysts/g massiter tissue = mean infestation rate (Lentfer, 1976)
$\frac{\text{4.15 cysts/g massiter tissue}}{\text{2.5 massiter to skeletal ratio}}$ = 1.66 cysts /g skeletal tissue
$\text{300000.0 g/bear} \cdot \frac{\text{0.40 g skeletal tissue}}{\text{1.0 g total weight}} = \frac{\text{120000.0 g skeletal tissue}}{\text{bear}}$
$\frac{\text{120000.0 g skeletal tissue}}{\text{bear}} \cdot \frac{\text{1.66 cysts}}{\text{g skeletal tissue}} = \frac{\text{199200.0 cysts}}{\text{bear}}$
$\frac{\text{199200.0 cysts/bear}}{\text{300.0 cysts produced/cyst injested}}$ = 664.0 cysts ingested/bear to produce the observed level of infection
$\frac{\text{664.0 cysts ingested/bear}}{\text{300.0 cysts/seal}}$ = 2.21 seals ingested/bear
$\frac{\text{2.21 seals ingested/bear}}{\text{0.25 infected seals ingested/year}}$ = 8.84 years to reach observed mean level of infestation

The very high levels of *Trichinella* observed in some bears (Lentfer, 1976) probably resulted mainly from cannibalism.

Additional evidence is available from the levels of *Trichinella* infection in indigenous human populations along the arctic coast. Ringed and bearded seals, sometimes consumed raw, are staples in the diet of coastal Inuit. These people did not suffer high levels of *Trichinella* infection unless they had eaten uncooked polar bear meat (Williams, 1946; Lentfer, 1976). Larsen and Kjos-Hanssen (1983) recount the decline of *Trichinella* infection of Svalbard arctic foxes following the moratorium on polar bear hunting in Svalbard. They suggest that the decline in *Trichinella* in arctic foxes resulted from elimination of polar bear carrion as a food item for foxes.

Born *et al.* (1982) found that one walrus from the Thule area was infected with 50 *Trichinella* larvae·g^{-1} muscle tissue. Only 40 g of this walrus would have to be ingested to achieve the mean level of infestation found by Lentfer (1976). However, only 2 out of 126 west Greenland walruses tested were infected with *Trichinella* (Born *et al.*, 1982). This low level of infection was typical of all walrus populations tested except the Svalbard population (Born *et al.*, 1982; Thorshaug and Rosted, 1956). About 10% of the Svalbard walrus population were infected with *Trichinella* during the period of set-gun and sport harvest. Born *et al.* (1982) and Larsen and Kjos-Hanssen (1983) suggested polar bear carcasses as a vector for *Trichinella* infection of walrus.

The likelihood that walruses could serve as a major *Trichinella* vector for polar bears in Canada (as suggested by Manning, 1960) appears low because in Canada the walrus is not a primary food item of polar bears (Killiaan and Stirling, 1978; Uspenskii, 1977). Walruses are relatively uncommon in Canada and Svalbard but seasonally abundant in the Chukchi Sea (Mansfield, 1958; Fay, 1982; Larsen and Kjos-Hanssen, 1983). Walruses may be a more common prey item and *Trichinella* vector for polar bears in the Chukchi Sea.

DISCUSSION

Social interactions have been proposed as a form of population regulation in other bear populations (Stokes, 1970; Kemp, 1972, 1976; Beecham, 1980; Ruff and Kemp, 1980; McCullough, 1981; Young and Ruff, 1982; Stringham, 1983). Jonkel and Cowan (1971), Beecham (1980), and Rogers (1975) documented conspecific predation and cannibalism in black bears. Troyer and Hensel (1962) and Pearson (1975) noted several instances in which brown bears were killed and eaten by other brown bears. The strongest evidence for population regulation by intraspecific aggression in bears was from an experimental removal of adult male black bears from an unharvested population in northern Alberta (Kemp, 1972, 1976; Ruff and Kemp, 1980; Young and Ruff, 1982). This study showed an initial increase in population size due to immigration and retention of subadult animals, followed by a gradual population decline. The decline resulted from maturation of male bears and increased egress of subadult animals, presumably because of aggressive behaviour by mature males toward subadults.

Polar bears do not defend territories (DeMaster and Stirling, 1981). Population regulation by aggressive exclusion of subdominant polar bears from quality seal hunting areas may occur; but data on such interactions are not available. Mortality of cubs could serve as a regulating mechanism provided infanticide occurred with sufficient frequency. Larsen and Kjos-Hanssen (1983) suggested that the low rates of polar bear cub survival observed on Svalbard (Larsen, 1985a,b) may be a result of infanticide.

Another motivation for infanticide was suggested by observations of a radio-collared Alaskan female polar bear whose yearling cubs were killed by a large male bear. Because the female was radio-collared, MT was able to observe her intermittently over the period 11–20 April 1980. The female was accompanied, in turn, by three different males. Although copulation was not observed, wounds on the males suggested that they had been fighting for or with the female. After her recovery from immobilizing drugs, the female's behaviour was qualitatively similar to that of other breeding females when accompanied by males. Wounds on the female, which occurred after the deaths of her cubs, suggested that she had been forced to copulate with the accompanying males. The interest shown by the males in a female that had been recently lactating suggests that receptivity and ovulation can be induced by repeated copulation, relief of stimulation from suckling, or precopulatory behaviour (Bunnell and Tait, 1981). During the breeding season, killing cubs may provide a male with a reproductive opportunity as well as a nutritional reward. This phenomenon has been observed in other carnivores, in primates, and in rodents (Sherman, 1981; Packer and Pusey, 1984).

The high frequency of *Trichinella* infestation in polar bear populations and the widespread observations of cannibalism suggest that cannibalism is not an uncommon phenomenon in polar bear biology. Carcasses of polar bears of any age class are probably scavenged opportunistically.

The frequency of intraspecific killing is less apparent. Social

behaviour suggests that intraspecific killing is usually not a threat to healthy adult polar bears (Latour, 1980, 1981; Stirling, 1974). Social behaviour of family groups appears to be related to the age of the cubs. Cubs > 1 year old and subadults are probably able to resist attacks by being more agile and faster than larger, heavier adult male bears (Stirling, 1974). This advantage appears to be augmented by active maternal defense in most situations. Victims of intraspecific predation appear to be predominately COYs and sick, starved, or drugged individuals.

Although infanticide may be minimized in some areas by spatial segregation of family groups from other adult bears, existing data are insufficient to determine the vulnerability of healthy family groups. Previous studies in Canada (Latour, 1980, 1981; Stirling, 1974; Stirling and Latour, 1978) and Svalbard (Hansson and Thomassen, 1982) did not suggest that cubs were particularly vulnerable. Other studies in Svalbard indicated high rates of cub mortality at least partly attributed to intraspecific attacks (Lønø, 1970; Larsen, 1985a). A second, unsettled issue is what effect either vulnerability or the perception of vulnerability has on polar bear social behaviour. Does the threat of infanticide lead to spatial stratification of family groups from other adult bears, particularly during the spring and early summer of the cubs' first year? The instances of infanticide observed for this remote and relatively solitary species suggest that social behaviour may play a more important role in polar bear ecology than was previously suspected.

ACKNOWLEDGEMENTS

Funding for this work was provided by the University of British Columbia, Norsk Polarinstitutt, and Northwest Territories Wildlife Service. Thanks to Jack Lentfer, Dennis Andriashak, Paul Latour, John Lee, and the weather station personnel and set-gun hunters of Svalbard for providing us with their observations. E. Born, T. Bray, F. Bunnell, H. Cleator, M. Ramsay, D. Seip, D. Shackleton, S. Sheldon, and I. Stirling reviewed the manuscript and contributed greatly to its organization and content. Our additional thanks to C.R. Upton and two anonymous referees for their constructive and thorough review. Particular thanks to Pat Mills for her secretarial and editorial assistance. Support was provided by Michigan Agriculture Experiment Station Journal Article No. 11788.

REFERENCES

ANDERSEN, O.N. 1981. Photograph in: Cousteau, J. The ocean. National Geographic Magazine 160:781-832.

BEECHAM, J. 1980. Some population characteristics of two black bear populations in Idaho. In: Martinka, C.J., ed. Bears — Their Biology and Management. IUCN New Series 3:201-205.

BELIKOV, S.E., and KUPRIJANOV, A.G. 1977. Behavior of the polar bear on Wrangel Island. In: The Polar Bear and its Conservation in the Soviet Arctic: Collection of Scientific Papers. Moscow: Central Laboratory for Nature Conservation. 40-55.

BORN, E.W., CLAUSEN, B., and HENRIKSEN, S.A. 1982. *Trichinella spiralis* in walruses from the Thule district, North Greenland, and possible routes of transmission. Zeitschrift fur Saugetierkunde 47(4):246-251.

BROWN, M., CRANK, B., DESINNER, F., GREER, J.E., GIBBONS, J.E., and KNUITUNEN-EKBAUM, E. 1948. Intestinal parasites of Eskimos on Southampton Island, Northwest Territories. Canadian Journal of Public Health 39:451-454.

_____. 1949. A note on trichinosis in animals of the Canadian Northwest Territories. Canadian Journal of Public Health 40:20-21.

BUNNELL, F.L., and TAIT, D.E.N. 1981. Population dynamics of bears — Implications. In: Fowler, C.W., ed. Dynamics of large mammal populations. New York: John Wiley and Sons, Inc. 75-98.

CHRISTIANSEN, B.O. 1981. Isbjørntreff sydvest for Kvitøya pa Spitsbergen. Fauna 34(3):129-130.

CONNELL, F.H. 1949. Trichinosis in the Arctic: a review. Arctic 2:98-107.

DEMASTER, D.P., and STIRLING, I. 1981. *Ursus maritimus*. Mammalian Species, American Society of Mammalogists 145:1-8.

ELEY, T.J. 1979. An analysis of polar bear predation on ice pinniped populations of Alaska. (Unpubl. report to and available at the Alaskan Department of Fish and Game, 1300 College Road, Fairbanks, Alaska 99701.)

FAY, F.H. 1960. Carnivorous walrus and some arctic zoonoses. Arctic 13:111-122.

_____. 1982. Ecology and Biology of the Pacific Walrus *Odobenus rosmarus divergens* (Illiger). North American Fauna 7:1-279.

HANSSON, R., and THOMASSEN, J. 1982. Isbjørnbinner med unger i Bogen hiområde, Kongsøya, Svalbard — en etologisk grunnstudie. [Behaviour of female polar bears with cubs of the year in Bogen denning area, Kongsoya, Svalbard.] Norsk Polarinstitutt Rapportserie 12. 140 p. (Mimeo.) In Norwegian.

HARRINGTON, C.R. 1963. Polar bear study. South Hampton Island, Northwest Territories, 1962. Canadian Wildlife Service Report. 57 p.

JONKEL, C.J. 1970. The behavior of captured North American bears with comments on bear management and research. BioScience 20:1145-1147.

_____ and COWAN, I. 1971. The black bear in the spruce-fir forest. Wildlife Monographs 27. 57 p.

KEMP, G.A. 1972. Black bear population dynamics at Cold Lake, Alberta, 1968-70. In: Herrero, S., ed. Bears — Their Biology and Management. IUCN Publications, New Series 23:26-31.

_____. 1976. The dynamics and regulation of black bear (*Ursus americanus*) populations in Northern Alberta. In: Pelton, M.R., Lentfer, J.W., and Folk, G.W., eds. Bears — Their Biology and Management. IUCN Publications New Series 40:191-197.

KILLIAAN, H.P.L., and STIRLING, I. 1978. Observations on overwintering walruses in the Eastern Canadian High Arctic. Journal of Mammalogy 59:197-200.

LARSEN, T. 1985a. Abundance, range and population biology of the polar bear (*Ursus maritimus*) in the Svalbard area. Unpubl. Ph.D. thesis. Norsk Polarinstitutt, Postbooks 158, 1330 Oslo, Lufthaun, Norway. 247 p.

_____. 1985b. Polar bear denning and cub production in Svalbard, Norway. Journal of Wildlife Management 49(2):320-326.

_____ and KJOS-HANSSEN, B. 1983. *Trichinella* sp. in polar bear from Svalbard, related to age and hide length. Polar Research 1(1):89-97.

LATOUR, P. 1980. Social behavior of polar bears (*Ursus maritimus* Phipps) concentrated on land during the ice-free season of Hudson Bay. Unpubl. M.A. thesis, Department of Zoology, University of Alberta, Edmonton, Alberta. 78 p.

_____. 1981. Spatial relationships and behaviour of polar bears (*Ursus maritimus* Phipps) concentrated on land during the ice-free season of Hudson Bay. Canadian Journal of Zoology 59:1763-1774.

LENTFER, J.W. 1976. Environmental contaminants and parasites in polar bears. Federal Aid to Wildlife Restoration Report, 5.5.R. 22 p.

LØNØ, O. 1970. The polar bear in the Svalbard area. Norsk Polarinstitutt Skrifter No. 129. 115 p.

MADSEN, H. 1961. The distribution of *Trichinella spiralis* in sledge dogs and wild mammals in Greenland under a global aspect. Meddelelser om Gronland 159:1-124.

MANNING, T.H. 1960. Comments on "Carnivorous Walrus and some Arctic Zoonoses". Arctic 14:76-77.

MANSFIELD, A.W. 1958. The biology of the Atlantic Walrus *Obodenus rosmarus rosmarus* (Linnaeus in the eastern Canadian Arctic. Ph.D. thesis, McGill University, Montreal. 344 p.

McCULLOUGH, D.R. 1981. Population dynamics of the Yellowstone grizzly bear. In: Fowler, C.W., and Smith, T.D., eds. Dynamics of Large Mammal Populations. New York: John Wiley and Sons. 173-196.

NANSEN, F. 1897. Farthest North. London: MacMillan and Company Ltd. Vol. 2:254-256.

OLSEN, B.S., VILLELLA, J.B., and GOLD, S.E. 1964. Distribution of *Trichinella spiralis* in muscles of experimentally infected swine. Journal of Parasitology 50:489-495.

ØRITSLAND, N.A., and LAVIGNE, D.M. 1976. Radiative surface temperatures of an exercising polar bear. Comparative Biochemistry and Physiology. 53A:327-330.

OVSJUKOVA, N.I. 1965. Rasprostranenie trihinelleza sredi zhivotnykh Chukotskogo Poluostrova. Materialy Nauchas Konfernc VOG 2:178-182. As cited in: Rogers, L.L., and Rogers, S.M. 1976. Parasites of bears: review. In: Pelton, M.R., Lentfer, J.W., and Folk, G.E., eds. Bears — Their Biology and Management. IUCN Publications New Series 40:411-430.

OZERETSKOYSKAYA, N., ROMANOVA, V., and BRONSTEIN, A. 1969. Trichinellosis from polar bear meat in the Soviet Arctic. The Polar Bear and Its Conservation in the Soviet Arctic: A Collection of Scientific Papers. Central Laboratory for Nature Conservation, Ministry of Agriculture of the U.S.S.R. Leningrad: Hydrometeorological Publishing House. As cited in: Lentfer. 1976. Environmental contaminants and parasites in polar bears. Federal Aid to Wildlife Restoration Report, S.S.R. 22 p.

PACKER, L., and PUSEY, A.E. 1984. Infanticide in carnivores. In: Infanticide in Animals and Man. Hausfater, G., and Blaffer-Hrdy, S., eds. New York: Aldine, Hawthorne. 31-42.

PAROVSHCHIKOV, V. Ja. 1964. A study of the population of the polar bear of Frans Joseph Land. Acta Sociologia Zoologica Bohemoslov 28(2):167-177.

PEARSON, A.M. 1975. The northern interior grizzly bear *Ursus arctos* L. Canadian Wildlife Service Report Serial 34. 86 p.

RAUSCH, R.L. 1970. Trichinosis in the Arctic. In: Gould, S.E., ed. Trichinosis in Man and Animals. Springfield, Ill.: C.C. Thomas. 349-373.

_____, BABERO, B.B., RAUSCH, R.V., AND SCHILLER, E.L. 1956. Studies in the helminth fauna of Alaska. 27. The occurrence of larvae of *Trichinella spiralis* in Alaskan mammals. Journal of Parasitology 42:259-271.

ROGERS, L.L. 1975. Parasites of black bears of the Lake Superior Region. Journal of Wildlife Diseases 11:189-192.

_____ and ROGERS, S.M. 1976. Parasites of bears: a review. In: Pelton, M.R., Lentfer, J.W., and Folk, G.E., eds. Bears — Their Biology and Management. IUCN Publications New Series 40:411-430.

ROTH, H. 1950. Nouvelles experiences sur la trichinose avec considerations speciales sur son existance dans les regions arctiques. Bulletin Officiel International Epizoology 34:197-220.

RUFF, R.L., and KEMP, G.A. 1980. Population dynamics of black bears in boreal forests of Alberta, 1968-77. Fifth International Conference on Bear Research and Management. Abstract:6.

SHERMAN, P.W. 1981. Reproductive competition and infanticide in Belding's ground squirrels and other animals. In: Alexander, R.D., and Tinkle, D.W., eds. Natural Selection and Social Behavior. New York: Chiron Press. 311-331.

STIRLING, I. 1974. Midsummer observation on the behaviour of wild polar bears. Canadian Journal of Zoology 52:1191-1198.

_____, JONKEL, C., SMITH, P., ROBERTSON, P., and CROSS, D. 1977. The ecology of the polar bear along the western coast of Hudson Bay. Canadian Wildlife Service Occasional Papers 33:1-69.

STIRLING, I., and LATOUR, P. 1978. Comparative hunting abilities of polar bear cubs of different ages. Canadian Journal of Zoology 56:1768-1772.

STIRLING, I., and McEWAN, E.H. 1975. The caloric value of whole ringed seals in relation to polar bear ecology and hunting behaviour. Canadian Journal of Zoology 53:1021-1027.

STOKES, A.W. 1970. An ethologist's views on managing grizzly bears. BioScience 20(21):1154-1157.

STRINGHAM, S.F. 1983. Roles of adult males in grizzly bear population biology. International Conference on Bear Research and Management 5:140-151.

THORBORG, N.B., TULINIUS, S., and ROTH, H. 1948. Trichinosis in Greenland. Acta Pathologica 25:778-794.

THORSHAUG, K., and ROSTED, A. 1956. Researches into the prevalence of *Trichinosis* in animals in arctic and antarctic waters. Nordisk Veterinaermedicin 8:115-129.

TROYER, W.A., and HENSEL, R.J. 1962. Cannibalism in brown bear. Animal Behavior 10:231.

USPENSKII, S.M. 1977. The polar bear. Nauka — Man and the Environment Series. Moscow. (English translation by Canadian Wildlife Service, 1978.) 107 p.

_____ and KISTCHINSKII, A.A. 1972. New data on the winter ecology of the polar bear (*U. Maritimus*) on Wrangel Island. In: Herrero, S., ed. Bears — Their Biology and Management. IUCN Publications New Series 23:181-197.

WILLIAMS, R. 1946. Bears and trichinosis. Alaska's Health 4:5-6.

YOUNG, B.F., and RUFF, R.L. 1982. Population dynamics and movements of black bears in east central Alberta. The Journal of Wildlife Management 46(4):845-860.

ZIMMERMAN, W.J. 1971. Trichinosis. In: Davis, J.W., and Anderson, R.L., eds. Parasitic Diseases of Wild Animals. Ames, Iowa: Iowa State University Press. 127-139.

_____ and SCHWARTZ, L.H. 1961. Distribution of *Trichinella spiralis* larvae in tissues of swine. Proceedings of the Iowa Academy of Sciences 68:553-557.