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The Social Behavior of Brown Bears at McNeil River, Alaska

Allan L. Egbert

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THE SOCIAL BEHAVIOR OF BROWN BEARS
AT McNEIL RIVER, ALASKA

by

Allan L. Egbert

A dissertation submitted in partial fulfillment
of the requirements for the degree
of
DOCTOR OF PHILOSOPHY
in
Wildlife Ecology

Approved:

Major Professor

Committee Member

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Committee Member

Dean of Graduate Studies

UTAH STATE UNIVERSITY
Logan, Utah
1978
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Allan L. Egbert
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The social behavior of brown bears (Ursus arctos) was studied during the summers of 1972 and 1973 as bears fished for salmon at McNeil River, Alaska. Study objectives were to determine behavioral characteristics of bears in relation to sex and age, changes in social behavior over a 40-day long fishing season, social and environmental parameters correlated with the occurrence of behavior, and to test the hypothesis that brown bears modify social behavior in a feeding aggregation to exploit a resource limited in time and space.

Over one-half of the agonistic interactions consisted of passive deferrals. Encounters that included elements of overt threat were jawing, sparring, charges, and fighting. Jawing was the most prevalent agonistic encounter and generally occurred between individuals of the same sex and age class. Sparring, charges and fights were generally initiated by larger bears against smaller individuals. Females with young were most intolerant. Adult males participated in few encounters that involved overt threat since most bears avoided them. Single adult and adolescent females were neither particularly aggressive nor
especially tolerant. Adolescent males adjusted quickly to McNeil Falls and as a group were unaggressive. Subadults were wary and frequently were the objects of aggression of older bears. Social dominance relationships between bears of the same class were often ambiguous, the exception being adult males. Relationships between bears of different classes were mostly stable; adult males were dominant, followed in order by females with young, single adult females, adolescents, and subadults. However, apparent reversals also were common between single adult females and adolescent males. Nonagonistic encounters occurred only when salmon were exceptionally abundant and usually involved adolescent and subadult bears. Behavioral changes over time included a decline in the frequency of running deferrals, a decline in deferrals in total, and a decline in the frequency of charges. The occurrence of fighting and sparring encounters did not change, but the frequency of jawing increased within each fishing season.

Various factors determined salmon caught by a bear per hour of fishing effort: salmon abundance, water levels, time of day, and fishing location. The time of day a bear could fish and its choice of location depended on its ability to gain and defend a profitable site. Fishing success was directly correlated with social status, but differences in success are probably unimportant in terms of individual fitness except when salmon are relatively scarce. Changes in encounter intensity over time had no detectable effect on fishing success. Salmon abundance, however, resulted in a further reduction of agonistic encounter intensity and an increase in nonagonistic encounters.
Bear social relationships were governed largely by variations in resource abundance. Despite energetic and psychological costs imposed by the bear concentration on individual animals, salmon were evidently sufficiently numerous that these costs were outweighed by returns in protein. Dominance relationships at McNeil Falls did not correspond to predictions of classical dominance theory. This may have been partially attributable to the fact that bears in aggregations derive no benefits from tacit acceptance of subordinate roles; a bear's alternatives were to compete and gain access to food or, if unsuccessful, to try elsewhere. To pose the question if normally solitary bears can adapt behaviorally to efficiently exploit a localized source of food may have been inappropriate. Alternatively, bears can be viewed as occupying and defending areas akin to small territories, with their behavior explicable in terms of energetic costs and benefits based on variations in resource abundance.

(117 pages)
INTRODUCTION

Most studies of mammalian social behavior have been conducted on gregarious species despite the fact that most mammals are solitary for most of the year (Leyhausen, 1965; Geist, 1974; Suthers and Gallant, 1973). Probably the main reason for this disparity is the relative ease of studying gregarious species. Theories on the evolutionary adaptiveness of social behavior and social systems of gregarious species can be critically analyzed, however, only if comparable knowledge is available for less social mammals. The holarctic brown bears (Ursus arctos) are typically solitary. They are subject to few, if any, of the evolutionary pressures (such as protection from predators or enhancement of predation efficiency) that seem to favor formation of social groups (Eisenberg, 1966; Kummer, 1971; Estes, 1974); brown bears have a relatively simple social system based on spacing and mutual or unilateral avoidance that is probably little advanced over that which occurred in ancestral carnivores (Eisenberg, 1966). Social affiliations between brown bears are usually restricted to family groups of a female and her offspring and sibling litter mates that remain together for 1 to 3 years after separation from the female (Stonorov and Stokes, 1972). Males consort with females only during the breeding season (Murie, 1944; Hornocker, 1962; Stonorov and Stokes, 1972).

Like other solitary carnivores, however, brown bears form loose aggregations while feeding on carrion (Craighead and Craighead, 1967; Cole, 1972; Glenn, 1973), in garbage dumps (Hornocker, 1962; Craighead and Craighead, 1967), and on salmon streams (Craighead and Craighead,
Such feeding aggregations are transitory and distinct behaviorally from social groups formed by truly gregarious species. Nevertheless, individuals in such transient aggregations probably face many of the same problems of group living experienced by social carnivores.

An annual gathering of brown bears on a small portion of a salmon stream on the Alaska Peninsula provided the chance to study the social behavior of this little known, generally elusive carnivore. The objectives of the study were to determine the behavioral characteristics of bears in relation to their sex and age, to quantify changes in their social behavior over a 40-day long fishing season, to determine social and environmental factors correlated with the occurrence of different types of social behavior, and to test the hypothesis that brown bears, normally solitary, can adapt behaviorally in a feeding aggregation to exploit a resource limited in time and space.
THE ANNUAL CYCLE

The purpose of this section is to place the McNeil River study in perspective with the full annual cycle of brown bears on the Alaska Peninsula.

Emergence of bears from winter dens presumably depends on weather but varies with sex, age, and reproductive status of the bears. Chronology of hunting kills and den surveys suggest emergence begins in late March and early April and is essentially complete by May (Lentfer et al., 1966, 1967; Lentfer et al., 1968). Males are killed in greater proportionate numbers during spring hunting seasons than in the fall (Lentfer et al., 1966, 1967; Lentfer et al., 1968) which suggests males emerge earlier than females. Females with young seem to emerge latest (Glenn, personal communication).

Bears on Kodiak Island patrol seacoasts for seaweed and carrion after spring emergence (Clark, 1957). Bears on the Peninsula probably do the same; Glenn (1971) observed brown bears around beached marine mammal carcasses in June, 1970, and I made similar sightings while flying with Glenn's research team in June, 1974. Bears in the Black Lake area of the Alaska Peninsula—which supports moose (Alces alces) and caribou (Rangifer tarandus) populations—also seemed quite successful at catching calves and finding dead and dying animals, but the value of ungulates as a source of food in May and June is unknown (Glenn, 1971). Caribou do not occur at McNeil River and moose are rare.

Plant material becomes an important bear food by June and probably constitutes the bulk of bear diets until salmon appear in July (Clark,
Clark found grasses (Calamagrostis, Hordeum, and Elymus) and sedges (Carex spp.) the most important early summer bear foods on Kodiak. Carex lyngbyaei occurring in pure stands around estuaries seemed particularly important at McNeil River; bears grazed Calamagrostis infrequently.

Salmon migrations on the Peninsula begin in May and peak in July and August. Salmon become important for bears by mid-July (Glenn and Miller, 1970; Glenn, 1973). A few streams on the Alaska Peninsula contain salmon into the winter, and bears occur on these streams as late as December (L. H. Miller, personal communication). Rausch (1963) suggested the abundance of high-protein salmon accounted for the greater size of coastal bears in comparison to the grizzlies of the interior.

Berries (mainly Rubus and Vaccinium spp.) ripen by August and September and are fed on for extended periods by bears on Kodiak Island (Clark, 1957). Bears on the Alaska Peninsula move into the foothills during this period, also apparently to feed on berries (L. P. Glenn, personal communication).

Denning occurs in October and November. L. H. Miller (personal communication) observed bears on salmon streams in late December while bears elsewhere had already entered dens. Pregnant females and females with young are apparently the first to enter dens in the fall (L. P. Glenn, personal communication). Most dens are on hillsides between 150 and 450 m elevation (Troyer and Faro, 1975).

Murie (1944) indicated brown bears in the Alaska interior bred throughout May, June, and July. Glenn (1973) recorded most breeding activity between June 20 and July 5 in the Black Lake area of the lower
Peninsula. My observations suggested a peak of mating in mid-July, but this is probably because I saw relatively few bears before this time each year. My earliest record of breeding behavior (not actual mating) was on June 17, 1973, and the latest was on August 7, 1973. A female that gave no indication of being in estrous when first seen in early July, 1973, was accompanied by cubs in 1974, which means she had mated prior to her arrival at McNeil Falls.

Females have produced cubs at 3-1/2 years of age in captivity (Kittrich and Kronberger, 1963) but are typically 5 to 6 years old before they give birth in the wild (Hensel et al., 1969; Glenn, 1973).

Males in the wild can produce viable sperm by 4-1/2 years of age (Erickson et al., 1968). Females have essentially attained full growth by 7 years; males continue to grow until they are 11 or 12 (Glenn, 1973).

Cubs are born while the females are in winter dens, presumably in January (Hensel et al., 1969). Litter sizes typically range from 1 to 3 cubs. Litters of four have occasionally been seen, and Glen (1973) reported one litter of five cubs. Sows at McNeil River generally retain their offspring for at least 1-3/4 years and probably for 2-1/2 years. Most litters are apparently weaned at 1-3/4 years since few captured females accompanied by 2-1/2 year-old offspring still produced milk in Glenn's (1973) study. One sow at McNeil River retained her single cub through the cub's third summer. Glenn (1973) found only 3 of 43 bears 3-1/2 years of age accompanying sows during the June breeding season.
STUDY AREA

In 1967, the Alaska State Legislature established a 5504 ha state game sanctuary encompassing the McNeil River and its tributaries (Figure 1) to preserve the brown bears that annually concentrate at McNeil River Falls (Faro, 1974). Lying about 0.8 km from the river's mouth on Kamishak Bay, McNeil Falls consists of a series of rock slabs jutting from the water that slows the upstream movements of migrating salmon. The area of McNeil Falls is about 30 by 200 m. More than 30 bears have been recorded at one time, and as many as 85 have visited the falls at least once during the 6-week-long salmon migration. Although hunting is prohibited within the sanctuary, five ear-tagged bears captured at McNeil River have been killed outside the boundaries since 1971.

The Alaska Department of Fish and Game (ADF&G) first inventoried brown bears at McNeil River in 1958 (Rausch, 1958) and conducted experimental immobilization and tagging of bears on the area from 1963 to 1972 (Glenn et al., 1976). ADF&G personnel concurrently gathered data on weights, litter sizes, frequency of litter production, and survival of cubs (Glenn and Miller, 1970; Glenn, 1973).

McNeil River lies within the rolling foothills of the Aleutian Range. Most mountains are less than 1,200 m elevation. Upland vegetation is dominated by dense thickets of willow (Salix spp.) and alder (Alnus spp.) with occasional patches of grasses and forbs. Woody vegetation ends at about 300 m above sea level; tundra and alpine plant communities occur at higher elevations and generally end at about 600 m. Tides at McNeil River range from minus 1.7 m mean low tide to 6.5 m during June. The grass and sedge meadows bordering the lower reaches of
Figure 1. McNeil River State Game Sanctuary
Mikfik Creek, the mouth of McNeil River, and McNeil Cove are totally inundated when tides exceed 5 m.

Bears graze extensively on the tidal flats at mid and low tides and seem to prefer the sedges. Other bear foods include mare's tail (Hippurus tetrphyllum) which also grows on the tidal meadows, and, on the uplands, sea coast angelica (Angelica lucida) and a variety of berries (Rubus and Vaccinium spp. and Empetrum nigrum).

Five species of Pacific salmon occur at McNeil River: chum (Oncorhynchus keta), king (O. tschawytscha), silver (O. kisutch), pink (O. gorbuscha), and red (O. nerka). Chum comprise most of the salmon captured by bears at McNeil River. Bears also occasionally capture dolly varden trout (Salvelinus malma).

Starting in 1973, ADF&G regulations limited the number of people present at McNeil Falls at one time to 10 between July 1 and August 15. Access to the falls area is by a prescribed foot trail, and visitors must stay in the immediate vicinity of the small cave near the upper end of the falls. Although the presence of people did not seem to influence the activity of most bears, a few of the older animals, mainly males, rarely crossed to the near side of the river.
METHODS

Data presented here were collected during the fishing season at McNeil Falls in 1972 and 1973. I collected additional information on bear behavior and population composition during July, 1971, while assisting Derek Stonorov in his research and during a brief photographic expedition in July, 1974. My quantitative observations began at McNeil Falls on the day bears started fishing, which was July 15 in 1972 and July 8 in 1973. I ended observations on August 20 in 1972 and on August 15 in 1973. I numbered the days of each fishing season consecutively, with Day 1 being the first day bears fished each season. I generally grouped each fishing season into 5-day periods for analyses.

Bears were observed daily from the cave near the head of the falls. Most observations were made between 0600 and 2200 hours; since the bears were present in greatest numbers during the afternoon, I concentrated my observations in the afternoon (Table 1). In addition, I stayed overnight at McNeil Falls twice in 1972. I supplemented the night observations in 1972 with a 16 mm camera triggered by an intervalometer which exposed four to six frames of film at hourly intervals. A combination of long daylight hours and a fast film emulsion gave a film record spanning 24 hours for a few days in 1972. The camera-intervalometer gave a continuous 11-day record until a bear demolished the set.

I observed the bears with a spotting scope during daylight and a night vision sight at night. Most bear activity was in full view and within 100 m of me.
Table 1. Schedule of observation periods at McNeil Falls

<table>
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<tr>
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Total 187.6 176.3
I have used the words "encounter" and "interaction" interchangeably throughout the text. I considered that an encounter-interaction occurred whenever the behavior of one bear was noticeably altered by the behavior, including actions and movements, of another. A bear "initiated" an interaction by my criteria whenever it caused another bear to respond to its presence. A bear could obviously initiate an encounter by rushing a rival. But, a bear could also "initiate" an encounter by simply moving through an area if by doing so it caused another animal to react in any manner. "Initiate" was used in this sense for two reasons: (1) bears rarely "sought out" other bears in the manner of gregarious species and (2) for consistency; the bear being approached could respond in several ways, but it could not be considered the initiator unless it responded with overt aggression.

Interactions between individual bears were recorded on prepared forms. Identities of the individual animals, location of the encounter, time of day, the distance between the animals at their closest, and the specific actions of each bear were documented as completely as possible. I was sometimes unable to completely record all actions performed in encounters since more than one interaction may have occurred simultaneously; I was aware of other interactions only after they were in progress. I attempted, however, to document all interactions as completely as possible. Co-worker Michael Luque was often able to provide details on such interactions when his research permitted.

A separate record was maintained for each individual bear on the time and route of arrival to and departure from the falls, the amount of time spent actively trying to capture fish, the amount of time expended
at different fishing sites, the location and time for each fish captured, and where each fish was consumed. When possible, I recorded the sex and species of salmon each bear caught.

The individual success of a bear at catching salmon was measured by the number of salmon caught per unit time, with time recorded as (1) the amount of time (hours) the bear was present at McNeil Falls or (2) the amount of time the bear was actively trying to capture salmon. The index given by (2) should reflect a bear's fishing skill, its choice of fishing location, and the time of day it is fishing. The index given by (1) should be influenced by the same factors as in (2) but in addition reflect the bear's ability to gain and hold a fishing location. Unless otherwise stated, I will be referring to the index given by (1).

I have used the term "bear-hour" in the following sections when simple enumeration of the bears would have been misleading. One bear-hour is one bear under observation for one hour.

It was impossible to determine the number of salmon that passed McNeil Falls. To approximate the variation in salmon abundance between 5-day periods and between years, I devised an index whereby I counted the number of salmon that surfaced in a pool approximately 20 m² about 20 m from my observation post for 2 minutes every hour (see Figure 5).

Observations of bears away from McNeil Falls were made opportune except that a schedule of hourly scans was made from a cabin roof 3 m above ground with a spotting scope. These scans were designed to document seasonal and diurnal variations in the number of bears grazing in the sedge meadows. To supplement these observations and to provide general information on annual differences in phenology, I collected 18
stems of Carex lyngbyaei at 5-day intervals along a transect throughout each summer. The stems were measured for length and air dry weight. Analyses for crude protein and crude fiber were subsequently conducted using proximate analysis at the Utah State University Department of Range Science.

Forty-four percent (20) and 37 percent (20) of the bears 2.5 years of age and older observed during 1972 and 1973, respectively, had been previously immobilized and ear tagged for identification by ADF&G biologists. With four exceptions, females of unknown age classed as adult were observed with cubs or yearlings at some point during the study; the size and behavior of the unmarked four indicated they also were fully adult. Only one adult male was ear tagged, but the others all possessed distinctive scars, ear shapes, and claw color that permitted individual identification. Adult males had massive heads and were conspicuously larger than adult females. Known-age adolescent males ranged in age from 4.5 to 8.5 years, and in size from roughly two-thirds as large to slightly larger than adult females. None possessed the scars and massive heads of the much larger adult males. Adolescent females were all of known age, either 4.5 or 5.5 years, and were generally one-half to two-thirds the size of adult females. Bears classed as subadults were 2.5 to 3.5 years of age. Bears of unknown age were classed by size relative to known-aged bears; in many cases I was able to compare my estimates on weights with those of ADF&G biologists experienced in estimating bear weights for immobilization. Adult males were estimated to weigh in excess of 350 kg, adult females 175 kg or more, adolescent males from 150 to 275 kg, adolescent females from 115 to 150 kg, and
subadults 125 kg or less. The sex of unmarked bears was determined by
observation of urination or by sex organs. I will occasionally refer to
subadults and adolescents collectively as "young" bears in the text.

The sex and age composition of the brown bears observed at McNeil
River is given in Table 2. The excess of females was possibly due to
legal restrictions prohibiting hunters from taking females with young
and selective trophy hunting for adult males.
Table 2. Sex and age composition of brown bears observed at McNeil River

<table>
<thead>
<tr>
<th>Sex and age Classification</th>
<th>Year 1971</th>
<th>Year 1972</th>
<th>Year 1973</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males</td>
<td>7</td>
<td>11</td>
<td>7</td>
</tr>
<tr>
<td>Adult females (single)</td>
<td>9</td>
<td>11</td>
<td>11</td>
</tr>
<tr>
<td>Females with cubs or yearlings</td>
<td>12</td>
<td>9</td>
<td>5</td>
</tr>
<tr>
<td>Adolescent males (4.5 to 8.5 years)</td>
<td>7</td>
<td>6</td>
<td>14</td>
</tr>
<tr>
<td>Adolescent females (4.5 to 5.5 years)</td>
<td>2</td>
<td>3</td>
<td>4</td>
</tr>
<tr>
<td>Subadults (2.5 to 3.5 years)</td>
<td>13</td>
<td>3</td>
<td>11</td>
</tr>
<tr>
<td>Cubs (6 to 8 months)</td>
<td>14</td>
<td>9</td>
<td>6</td>
</tr>
<tr>
<td>Yearlings (1.5 to 1.8 years)</td>
<td>6</td>
<td>10*</td>
<td>3</td>
</tr>
<tr>
<td>Unclassified</td>
<td>6</td>
<td>4</td>
<td>3</td>
</tr>
<tr>
<td><strong>Total</strong></td>
<td><strong>76</strong></td>
<td><strong>66</strong></td>
<td><strong>64</strong></td>
</tr>
</tbody>
</table>

*Includes one 2.5-year-old accompanying an adult female
RESULTS

The Pre-fishing Period

Bears at McNeil River grazed *Carex lyngbyaei* almost exclusively during late June and July. At one point in 1972, the 40 ha of sedge meadows bordering the mouth of the McNeil and the lower segment of Mikfik Creek contained 16 grazing brown bears including dependent cubs and yearlings. Bears occasionally cropped the ubiquitous *Calamagrostis canadensis*, but almost always while traveling and not in the sustained manner typical when they grazed sedge. Bear droppings consisted almost exclusively of sedge during this period, the main exception being a few scats that contained red salmon in late June. A small migration of red salmon, 15,000 fish or less, entered Mikfik Creek during mid- and late June but was used by only a few bears.

Plant phenology determined when brown bears began grazing in the tidal sedge meadows. Based on weights of sedge samples collected at 5-day intervals throughout each summer, the growing season of 1973 was 10 to 14 days ahead of 1972 until about late July. Bears started grazing sedge in 1973 at least 2 weeks earlier than in 1972 (Figure 2).

Bears made greater use of sedge about 10 days before maximum vegetative growth (Figure 2). Protein content was comparatively high and crude fiber low while sedge leaves were small and growing rapidly (Table 3). A few bears fed on sedge in mid-June, but the sedge blades were small and apparently profitable for grazing only after the blades had reached a certain size. Protein content decreased and fiber increased as the plants matured, although protein never dropped below 10
Figure 2. Seasonal variation in brown bear use of Carex on Mikfik Meadows
Table 3. Seasonal variation in crude protein (CP) and crude fiber (CF) in *Carex lyngbyaei*. Analyses were conducted using proximate analysis.

<table>
<thead>
<tr>
<th>Collection Date</th>
<th>1972</th>
<th>1973</th>
</tr>
</thead>
<tbody>
<tr>
<td>Collection Date</td>
<td>CP</td>
<td>CF</td>
</tr>
<tr>
<td>June 25</td>
<td>21.8</td>
<td>-</td>
</tr>
<tr>
<td>June 30</td>
<td>27.5</td>
<td>-</td>
</tr>
<tr>
<td>July 5</td>
<td>26.2</td>
<td>-</td>
</tr>
<tr>
<td>July 10</td>
<td>20.5</td>
<td>50.0</td>
</tr>
<tr>
<td>July 15</td>
<td>20.0</td>
<td>53.4</td>
</tr>
<tr>
<td>July 20</td>
<td>16.6</td>
<td>52.4</td>
</tr>
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<td>July 25</td>
<td>15.3</td>
<td>53.3</td>
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<tr>
<td>July 30</td>
<td>13.7</td>
<td>56.7</td>
</tr>
<tr>
<td>August 5</td>
<td>14.6</td>
<td>61.2</td>
</tr>
<tr>
<td>August 11</td>
<td>13.5</td>
<td>63.5</td>
</tr>
<tr>
<td>August 17</td>
<td>13.5</td>
<td>60.1</td>
</tr>
</tbody>
</table>
percent. Crude fiber content continued to increase until late in the collection period.

Bears turned away from sedge after mid-July. There must be some point at which the reduced nutritive quality and lower palatability makes sedge less attractive to bears. Salmon arrived in significant numbers at McNeil River the first week of July each year, but the annual onset of fishing by bears was variable, starting on July 13, 1972, and on July 8, 1973. Bears did not begin fishing until July 25 in 1971. I have no data on plant development nor bear use of sedge for 1971 but it was a very late season. Snow persisted at sea level that year into August whereas snow was gone by mid-July in 1972 and by mid-June in 1973. I doubt that bears preferred sedge to salmon at any time, but I think it possible that bears were more likely to seek out alternative foods once the sedge had reached marginal palatability. Even after the fishing seasons were well underway, however, many bears supplemented their salmon diets with periodic forays to the sedge meadows, especially during the relatively poor salmon season in 1972.

The Fishing Season

The salmon migrations

All five species of Pacific salmon occur in McNeil River. In mid- and late June, a small migration of king salmon moves up the river but are unexploited by bears because their numbers are limited. Water levels are also so high during this period that fishing may be unprofitable. Red and pink salmon appear in very small numbers in July, and a moderate migration of silver salmon begins about the second week of August.
Chum, or dog salmon, constitute the main migration in McNeil River. Chum appear at McNeil Falls during the first week of July and are accompanied by "sea-run" dolly varden trout that prey on salmon eggs. There are no figures available on the size of the chum salmon migration since the McNeil is relatively unimportant commercially.

The chronologies of the salmon migrations during the two years of this study were very different (Figure 3). In 1972, there was no obvious migration peak, salmon numbers being roughly constant from July 23 (day 11) to August 11 (day 30). The arrival of silver salmon in mid-August probably accounted for the modest increase recorded during days 31-35. In contrast, in 1973 chums rapidly increased in numbers between July 8 (day 1) and July 27 (day 20). By August 1, 1973, the bulk of the migration had passed, but chum persisted in considerable numbers into mid-August to be further augmented by the appearance of silvers.

The 1973 chum migration was perhaps three times as great as the 1972 run. Although little is known on the size of the McNeil River salmon migrations in prior years, James Faro's (personal communication) impression was that the runs were slightly below average in 1972 and much above average in 1973.

Seasonal variation in brown bear numbers

As discussed above, the onset of fishing by bears varied annually, most likely a result of annual phenological differences. The first bears to appear at McNeil Falls each summer had generally been present in previous years. In some instances, individual bears had been seen earlier in the summer fishing for red salmon in Mikfik Creek, grazing on
Figure 3. Seasonal variation in salmon abundance at McNeil Falls. The vertical lines indicate the standard error of the mean.
sedge in Mikfik Meadows, or grazing on another tidal area about 14 km southeast. Most were first seen each year, however, when they appeared at the river to fish.

The salmon fishing season of brown bears at McNeil River extended from July into August (Figure 4). The number of individuals at the falls increased to a maximum during days 16 to 20 both summers, but whereas the number of animals gradually declined from days 21-25 in 1972, bears persisted in equal numbers for about 25 days in 1973. Few bears were present during all eight 5-day periods; 7 percent (3 bears) in 1972 and 10 percent (5) in 1973. More animals spent longer periods at the falls in 1973 than in 1972; 36 percent in 1973 versus 24 percent in 1972 were present for six or more 5-day periods. In 1972, 27 percent stayed for 5 days or less compared to 16 percent in 1973. Single adult females and adolescents persisted longest, and adult males and subadults were least likely to be present for extended periods. Adolescent bears generally were the last to cease fishing at the end of the season. Some adult males may have been driven from the falls by growing numbers of people. Other unknown factors were probably also involved, however, since an adult male that appeared thoroughly habituated to humans disappeared for 12 days (days 20 to 32) in 1973.

The gradual cessation of fishing activity in August was due to a number of factors. Clark (1957) found that bears on Kodiak Island switched to berries while salmon were still available; the same was true at McNeil River. Berries (Rubus, Vaccinium, and Empetrum spp.) start ripening in late July, and crowberries (Empetrum nigrum) were first noticed in bear scats on August 9, 1972, and July 21, 1973. Although berries were a ready alternative food when salmon become difficult to
Figure 4. Seasonal variation in numbers of bears observed at McNeil Falls. 1972, 1973
catch with the passing of the main migration body, some bears switched to berries when salmon were still plentiful, apparently for dietary variety. A number of bears alternated between fishing and feeding on berries, but others seemed to concentrate solely on berries. A few bears continued fishing at McNeil Falls long after most bears moved elsewhere; game biologist Nick Steen (personal communication) saw a few bears still fishing (presumably for silver salmon) in late September, 1973, at McNeil Falls.

General fishing activity

Bears fished at about 20 more or less discrete fishing locations scattered throughout the rapids comprising McNeil Falls (Figure 5). Bears used other sites occasionally, but those indicated in Figure 5 accounted for 99.5 percent of the salmon caught. The most productive fishing site in terms of success rate and total fish caught was a slightly nebulous area marked as 1 on the map and located on the north side of the river near the head of the falls. Other lucrative fishing sites in decreasing order of importance were 12, 13, 14, 3, and 8. Sites 1, 2, 3, 8, and 9 marked the channel where the bulk of the salmon passed McNeil Falls. There seemed to be a fairly abrupt drop of the stream bed of between 0.5 to 1.0 m at 1 which made the salmon vulnerable. Bears fishing at this location lunged into the water and pinned fish to the bottom with both forepaws and then grasped their catch in their mouth. Whereas many sites were ephemeral, and bear use varied with changing water levels, the channel adjacent to 1 always carried sufficient flow that salmon attempted to pass through. Fishing sites 16, 19, 18 and 10 were most profitable when water levels were
Figure 5. Fishing locations at McNeil Falls, indicated by numbered sites. The location of the salmon index counting area is indicated by the square with diagonal lines. Main travel routes of salmon are given by arrows.
fairly high. Sites 9, 12, 13, 4, and 5 were most productive at moderate to low water levels. Locations 14 and 3, like 1, yielded salmon at all times except when the river was extremely high or low.

Bears caught about twice as many salmon in 1973 as in 1972, reflecting the great difference in the size of the salmon migrations. In terms of amount of time each bear was present at McNeil Falls, bears caught 1.0 fish per hour in 1972 and 2.1 per hour in 1973. Considering only the amount of time bears spent actively fishing at a fishing site, the rates of success were 1.5 and 3.6 per hour, respectively, in 1972 and 1973. The latter figures are most comparable since the greater number of fish caught in 1973 required proportionately more handling time. However, some bears became glutted on salmon in 1973, and their fishing attempts were half-hearted; adolescent males in particular occasionally did no more than lightly paw salmon struggling over the rocks during the height of the 1973 run.

A number of factors contributed to variations in brown bear fishing success within each season. High water generally meant salmon were harder to catch. Heavy rains during the 21 to 25 day period in 1972 caused a 45 cm rise in water and a corresponding decline in bear fishing success (Figure 6). A sharp drop in fishing success during the 6 to 10 day period in 1972 was probably due to a rapid buildup in bear numbers without a corresponding increase in salmon numbers. Otherwise, fishing success varied little within the 1972 season, reflecting the relative consistency of salmon abundance (see Figure 3).

Salmon were so plentiful in 1973 that water level fluctuations had no detectable impact on bear fishing success. A 60-cm water rise during
Figure 6. Seasonal variation in the rate brown bears captured salmon at McNeil Falls
the 16 to 20 day period caused bears to switch to alternate sites where salmon were still comparatively easy to catch, apparently because the salmon migration peak also occurred at this time (see Figure 3). The sudden drop in success during days 26 to 30 reflected a decline in salmon during the previous 5-day period and a peak of social play activity which detracted from the amount of time actually spent fishing. The low fishing success indicated for the 31 to 35 day period reflected a real decline and is difficult to explain unless related to the large number of bears present that period. Bear numbers dropped sharply during the 36 to 40 day period, and fishing success of those remaining again increased, even though salmon abundance declined sharply.

To estimate the total number of salmon caught each year, the observed number of salmon captured between 0600 and 2200 hours was expanded to cover each 40-day season by an appropriate factor based on the number of bear-hours recorded and the fishing success rate. The estimates were 3,443 salmon caught in 1972 and almost 8,000 in 1973. Since an undetermined but probably significant number of fish was caught between 2200 and 0600, these figures should probably be enlarged by at least 15 percent, giving a total of about 4,000 fish caught in 1972 and 9,200 in 1973. Without estimates of the total salmon migrations, the impact of bear predation on salmon at McNeil River was unknown. At times of low water, however, the rate of attrition was probably fairly high.

The Post-fishing Period

I have little information on brown bear activities following the McNeil River fishing season. James Faro (personal communication) stated
that some McNeil River bears have appeared on salmon streams draining Kulik Lake, roughly 70 km from McNeil Falls, in September. Bears that were ear tagged at McNeil River have been taken by hunters during the fall hunting season (September-October) 15, 35, 40, 43, and 55 km from McNeil Falls.

Brown Bear Social Behavior

A dominant feature of brown bear social behavior prior to the fishing season was a reciprocal wariness that facilitated spacing and discouraged short-range contacts. A bear grazing sedge periodically reared its head and peered about as if to check the locations of other bears sharing the meadow. A bear emerging from the dense alder thickets caused bears on the meadows to pause and take notice. Some bears reared up on their hind legs to get a better view of the newcomer. The new arrival often caused the bears already present to shift locations to maintain dispersion, and some might depart. Although short-range encounters occurred, most encounters on the meadow were settled at long range, at distances of 50 m or more, by one bear simply moving away.

The bear-feeding aggregation caused by the vulnerability of salmon at McNeil Falls gave rise to a social milieu of a different nature. Interactions at McNeil Falls occurred at close range and, although probably not different qualitatively from encounters occurring elsewhere, were frequent and often intense. However, the well known propensity for bears to congregate at locally abundant foods (Storer and Tevis, 1955; Hornocker, 1962; Erickson et al., 1964; Craighead and Craighead, 1967; Rogers et al., 1976) suggests the annual gathering at
McNeil Falls is neither unique nor even unusual. The behavior of brown bears at McNeil Falls is described and analyzed below.

**Communication patterns**

**Facial expressions**

Being solitary much of their lives, bears have been characterized as having a limited signaling repertoire (Lorenz, 1953). Jonkel and Cowan (1971) and Henry and Herrero (1974) challenged the contention that black bears (*U. americanus*) give no indication of aggressive intent prior to attacking. Henry and Herrero identified seven black bear facial expressions that appeared important for social communication and adopted the terminology Van Hooff (1967) developed for primate facial expressions. The facial expressions of brown bears also fit easily in Van Hooff's terminology with a few modifications. The descriptions following are given to convey an impression of brown bear behavioral diversity and to facilitate the narrative on brown bear encounters.

**Relaxed face** (Figure 7a). This expression occurs when a bear's attention is not focused. The ears generally point laterally but are often twitched to the rear. The mouth usually is closed or slackly open. A relaxed face is commonly seen when a bear is walking, resting, grazing, fishing (when the action is slow), and in low-key amicable interactions (see below).

**Relaxed open-mouth face** (Figure 14). The bear's mouth is open and its eyes are alert. Ears shift from being lightly compressed to pointing laterally. Ears also may be briefly cocked to the front. The lower
lip hangs away from the incisors and canines and the nose and the portion of the upper lip covering the front teeth appears to curl upward and back. There is no growling. This expression was observed only during social play.

**Alert face (Figure 7b).** The alert face is distinguished by the cocked, alert ears and wide open eyes. The mouth is closed or opened slightly. It usually occurs when a bear is looking intently at a distant animal. A bear also shows this expression preparatory to pouncing on salmon. The head usually is erect but is lowered if the object of interest is at close range.

**Tense closed-mouth face (Figure 7c).** A bear's ears are laid back but not flattened, and the openings are directed to the side or downward. The mouth is closed. The head is carried in the normal position but might be ducked periodically and there seems to be an effort to avoid eye contact with the opponent. At close quarters the bear may slightly arch its back. This expression occurs when a bear is threatened but does not reciprocate and when it walks at close range past another bear.

**Puckered-lip face (Figure 7d).** This expression in brown bears appears identical to the puckered-lip face of black bears (Henry and Herrero, 1974). The distinguishing feature is a protrusion of the upper lips. The ears are cocked and alert when the other bear is some distance away but laid back and flattened at shorter range or during retreat. Head position varies from erect to lowered. Brown bears show a puckered-lip face at the approach of another bear and preparatory to and during retreat.
Jaw gape face (Figure 7e). The mouth is open and the lower canines are visible. Upper and lower lips hang loosely. A deep rumbling growl accompanies the expression. The ears are rotated to the rear but are not flattened against the head. The eyes are alert and open fairly wide. In some instances the bear slightly arches its back. The head is usually held low. This expression is prevalent during defense of a fishing location or when a bear is attempting to displace another.

Biting face (Figure 7f). This expression is the serious analogue of the relaxed open-mouth face except the ears are flattened against the head and the eyes are opened wide exposing the sclera. Bears switch quickly from the biting face to the jaw gape face and vice versa. The main difference between the two expressions is the upward curl of the nose to expose the upper canines in the biting face. A loud roar accompanies the biting face. It is used in close range conflicts including but not limited to actual biting.

Vocalizations

Brown bear sounds are probably the least ambiguous signals in their communication repertoire. Most sounds are harsh, occurring during conflicts. As with most mammals, some brown bear vocalizations grade together making neat separation impossible. The noise of McNeil Falls often prevented my hearing vocalizations and the following list is undoubtedly incomplete.

Huffing. A common vocalization is a harsh, rasping "huff" given repeatedly at about 2 per second. The sound is apparently produced by explosive exhalations over the vocal cords. The bear's mouth is open
Figure 7. Facial expressions of brown bears. See text for details.
about 20 degrees and its lips flutter as it makes the sound. Huffing was associated with the puckered lip face and seemed to connote a high element of tension. Females with cubs huffed frequently. A female with cubs that charged me roared during the charge but began huffing when she changed course and ran into a thicket. Cubs scrambled about when their mother huffed but whether this was due to the vocalizations or the perceived threat that elicited huffing is uncertain.

Woofing. This sound also has an explosive character but lacks the harsh quality of huffing and is emitted but once. It sounds like pressurized air suddenly being vented. As with huffing, a bear's lips fluttered when sounding a woof. Woofing occurred in conjunction with the alert face and puckered lip face. Bears appeared to woof when startled. An elderly unmarked male that usually fished on the side of the river opposite my observation post topped a small rise about 30 m away late one evening and was moving to the river to fish. Upon spotting me, he recoiled, gave a loud woof, and fled.

Growling. Growls are associated with the jaw gape face and vary from a brief low grrr to a continuous rolling rumble. The sound is harsh and gutteral. Growling occurs when one bear does not tolerate the proximity of another, such as when it is feeding or occupying a fishing site. A bear also growls when it is startled; an adolescent female (Red) growled when bumped by her sibling sister Blue as Blue turned to confront an approaching adolescent male. Bears also growled when pelted with stones during my attempts to dissuade them from passing too near. Bears as young as 2-1/2 years old and probably younger ones as well can give respectable growls.
Roaring. A brown bear's roar is thunderous. With a prevailing or quiet wind, bears at McNeil Falls could be heard roaring from my camp 2 km away. The duration of roars depends on the conflict. A bear charging begins with a deep rumbling growl that builds to a full roar after a few strides and is maintained until the charge ends. Fighting bears roar continuously. Growling and roaring intergrade considerably during less intense interactions. A roar seems little different from a growl except that a roar is much louder to a human and far more intimidating.

Bawling. This sound resembled "waugh!, waugh!..." given repeatedly at one to two per second. Bears bawling were seeking contact. Cubs left stranded on shore as their mothers entered the falls to fish gave this sound. Adults were heard bawling twice. Following a confrontation with another female, Lady Bird became separated from two of her 6-month old cubs. It took a few minutes for her to miss them, but then she began hurrying along their trail bawling as she went. On another occasion, the adult male, Patches, was tending a female in estrous, but became separated when he stopped to fish. After a few minutes, Patches began searching for the female giving "waughs" that sounded identical to those given by cubs and the searching Lady Bird.

Vocalizations given by females and their cubs are probably important but I was never close enough to hear. The offspring immediately react to female vocalizations directed toward other bears, usually by sheltering behind her or by scrambling about.
Agonistic behavior

Scott (1956) defined agonistic behavior as any behavior associated with conflict or fighting, including escape or passivity. Besides obvious overt acts of aggression, interactions which involved one bear skirting or withdrawing from another and a few encounters that consisted only of one or both bears acknowledging the other's presence by changes in facial expressions with shifts in head, ear, and body positions were also treated here as agonistic.

Aggressive interactions

Brown bears employed four easily distinguished forms of aggressive behavior during encounters which represent a continuum ranging from relatively mild threats to conflicts of high intensity. These four patterns were: jawing; sparring; charges; and overt fighting.

Jawing. These encounters consisted of one or both bears exhibiting the jaw gape face but with variations in posture (Figure 7e). A jawing bear held its head down, nose pointed to the ground. The bear's mouth was opened wide as it give a low rumbling growl lasting 1 to 2 seconds. During prolonged encounters, the growl was repeated at intervals of about 2 seconds. A jawing bear's lower canines were visible, but there was not the conspicuous flashing of teeth seen in some other carnivores upon retraction of the lips. The body orientation in jawing encounters was variable; in some cases, the bear advanced slowly toward the opponent and confronted it directly. A bear also jawed from its fishing site, either by turning its body toward the rival or by merely turning its head. Head and body movements were slow and deliberate. Bears
arched their backs slightly during close range encounters. Jawing bears were usually 2 m or less apart, but distances as great as 10 m were recorded.

A bear that approached another fishing, eating, or simply standing or sitting idly could elicit jawing. Bears also jawed to displace a rival or to usurp its catch. A bear approached by another of significantly higher social status might voice a brief growl and depart. In such cases, the approaching animal might not jaw at all. When the rivals were of similar status, jawing encounters were often prolonged, lasting from 5 to 30 seconds before one bear moved away. A bear sometimes slipped into a fishing spot close to another and the two would jaw periodically until one departed with a fish.

Bears had to approach to fairly short range for jawing interactions to occur. Consequently, bears of similar size, where one was likely to at least temporarily resist giving way, had the most frequent jawing interactions (Table 4). However, single adult females were just as likely to jaw with adolescent males as with other females. Females with young had the most frequent jawing interactions and were indiscriminate regarding rivals. In 80 encounters with adult males, females with young jawed in 28 percent. Adult males had the lowest overall frequency of jawing encounters, 11 percent, followed by subadults with 16 percent.

**Sparring.** While sparring, a bear confronted its rival directly squatting on its rear legs with its muzzle extended upward toward the other bear (Figure 8). The forelimbs extended to the ground but bore little weight, apparently freed for striking or fending off the opponent. A sparring bear alternately exhibited the biting face, roaring
Table 4. Percentage of bear encounters at McNeil Falls that included jawing. Figures in parentheses are the number of jawing encounters observed.

<table>
<thead>
<tr>
<th>Encounter initiated by:</th>
<th>Encounter recipient</th>
<th>Same sex and age bear</th>
<th>Different sex and age bear</th>
<th>P&lt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males</td>
<td></td>
<td>18(18)</td>
<td>10(49)</td>
<td>0.05</td>
</tr>
<tr>
<td>Females with young</td>
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<td>33(13)</td>
<td>28(101)</td>
<td>0.50</td>
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<tr>
<td>Single adult females</td>
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<td>23(62)</td>
<td>19(187)</td>
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<tr>
<td>Adolescents¹</td>
<td></td>
<td>28(255)</td>
<td>18(150)</td>
<td>0.005</td>
</tr>
<tr>
<td>Subadults</td>
<td></td>
<td>(0)</td>
<td>16(34)</td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td></td>
<td>26(348)</td>
<td>18(521)</td>
<td>0.005</td>
</tr>
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</table>

¹Includes males and females
loudly or continuously or the jaw gape face with its accompanying monotone growl. When both bears sparred, their mouths almost touched, and one bear might twist its head to about 90 degrees to that of its rival's, giving the impression they were about to lock jaws. Roaring changed suddenly in volume, becoming even louder, when a bear lunged toward its rival or when one or both made sudden head movements as if to hook each other with a lower canine.

Sparring was more intense than jawing and occurred less often. Bears jawed in 20 percent of their encounters but sparred in only 6 percent ($P < 0.001$). A succession of jawing encounters sometimes preceded sparring which probably ensued after the milder threat failed to deter the opponent. Bears that fought usually sparred also at some point during the interaction.

Bears sparred slightly more often with others of the same sex and age, but the pattern was not consistent (Table 5). Adult females sparred with adolescent bears of both sexes almost as frequently as they did among themselves, and females with young sparred in at least 10 percent of their encounters with bears of all groups except adolescent females. In total, females with young sparred in 11 percent of their interactions, including 13 percent with adult males. Single adult females, in contrast, sparred in only 3 percent of their encounters with adult males. Adult males, since most others skirted them, sparred most often among themselves. Subadults, because they themselves avoided others, sparred least often, doing so in only 3 percent of all their agonistic interactions.
Table 5. Percentage of bear encounters that included sparring at McNeil Falls. Figures in parentheses are the number of sparring encounters observed.

<table>
<thead>
<tr>
<th>Encounter initiated by:</th>
<th>Encounter recipient</th>
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<th></th>
<th></th>
<th></th>
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<tr>
<td></td>
<td>Same sex and age bear</td>
<td>Different sex and age bear</td>
<td>p&lt;</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adult males</td>
<td>8 (8)</td>
<td>2 (12)</td>
<td>0.01</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Females with young</td>
<td>19 (8)</td>
<td>12 (44)</td>
<td>0.25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Single adult females</td>
<td>7 (18)</td>
<td>5 (49)</td>
<td>0.25</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adolescents$^1$</td>
<td>6 (53)</td>
<td>5 (46)</td>
<td>0.50</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subadults</td>
<td>(0)</td>
<td>3 (8)</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Total</td>
<td>6 (87)</td>
<td>6 (159)</td>
<td>0.10</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

$^1$Includes males and females
When one bear sparred, its rival typically reciprocated in defense, either by sparring or jawing. In a few cases, the other animal turned quickly and ran. The typical pattern was for one animal to spring toward the other holding its head high and roaring loudly. The rival shifted its weight to its hindquarters and lifted its head to meet the challenge. When a bear fled from a sparring threat, it either escaped or was bitten on the rear. A bear attacked from behind almost invariably turned to face its attacker. As shown below, few bears that stood their ground initially were physically attacked. Both bears sparred in 73 percent of all sparring encounters.

Charges. A brown bear charge was a rush at an opponent. A direct charge was a fast, unequivocal rush with the apparent intent of closing and attacking (Figure 9). A charging bear's eyes were fixed on the other bear, and its ears were erect at the start but flattened against the head after the first few strides. It growled at the onset, but the growl quickly changed into a loud roar as the charge developed. A second type of charge was similar but ended after a few strides and in some cases probably connoted bluffing. These abbreviated rushes usually ended with the receiving bear fleeing or when it stood its ground. A subadult female in 1972 and an adolescent male in 1973 typically ended a short charge by swatting the ground. Bears also growled during short charges but not as loudly as in a direct charge.

A third charge which was uncommon and seen during the early days of the fishing seasons occurred when a bear loped slowly toward an opponent with its head held erect and ears cocked forward. Growling was restrained, and the bear moved stiffly in an exaggerated rocking gait. If
Figure 8. An adult female and an adolescent male sparring

Figure 9. A female with yearlings in the initial stages of a charge
the other bear ran, a chase usually ensued. The charging bear stopped and turned away if its opponent stood firm.

Most charges related to obtaining or defending a fishing location or when an individual distance was violated. An adult female named Lady Bird typically approached her favorite fishing spot at a trot to begin with and if a bear happened to be occupying the location, it often ran when she approached. Lady Bird sometimes made a short rush after the retreating bear before settling in to fish. In a few cases, charges seemed to be a re-direction of aggression, occurring when a bear displaced by a dominant animal soon after crossed paths with a third bear. A bear would also finally charge another after a series of encounters between the two, suggesting that some cumulative effect eventually led to the charge.

Some bears made rushes simply to precipitate a chase. Almost invariably, Red chased a subadult named Long Nose for no apparent purpose. Once, the chase was lengthy, lasting at least 10 minutes. Such chases usually involved adolescent or subadult bears, but an adult male also did the same thing at the start of the season in 1972, seemingly for no reason other than the bears he chased would run from him.

A charge occurred in 9 percent of all agonistic interactions. Females with young were most likely to make charges, doing so in 17 percent of their encounters. Despite being in only 18 percent of all encounters, females with young made 31 percent of the charges. Seventy-four percent of all charges were by adult bears, and of these, 68 percent were at adolescents or subadults. Young animals in turn made few charges themselves and then primarily against other young bears. In
total, adolescents and subadults were the victims of 73 percent of the charges recorded (Table 6).

Fifty-two percent of the charges were hard, fast rushes. Bears that received a direct charge escaped by running away 43 percent of the time, but 33 percent of observed charges culminated with fighting. Eighteen percent led to sparring bouts and 5 percent ended with jawing. Females with young accounted for 44 percent of the direct charges recorded.

Short charges occasionally seemed tentative, suggesting an ambivalence between aggression and flight. Sixty-seven percent of the charges made by adolescent and subadult bears were short rushes. Females with young showed a similar ambivalence in the majority of their charges directed at adult males. A short rush may also have served to test a rival, particularly during the early part of each fishing season when a small individual could often cause a larger bear to flee by making a short rush toward it. A short rush seemed an effective threat with little of the risk of being mauled that other forms of threat entailed.

Other short charges were clearly not tentative but served to allow a bear to retain a fishing spot. As quickly as the bear made the charge and the other bear fled, it immediately returned and resumed fishing.

Fighting. Fighting bears exhibited the biting face and voiced thunderous roars. Fighting animals confronted one another directly. Even when a bear was attacked from behind, it quickly turned to face the aggressor. Whereas sparring bears had their forelimbs extended to the ground, fighting bears shifted their weight completely to the hind-
Table 6. Percentage of bear encounters in which a charge occurred. Figures in parentheses are the number of charges observed.

<table>
<thead>
<tr>
<th>Charges made by:</th>
<th>Type of Charge</th>
<th>Adult males</th>
<th>Females with young</th>
<th>Single adult females</th>
<th>Adolescent males &amp; females</th>
<th>Subadults</th>
<th>Total</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males</td>
<td>Direct</td>
<td>4(4)</td>
<td>0</td>
<td>4(15)</td>
<td>1(2)</td>
<td>0</td>
<td>3(21)</td>
</tr>
<tr>
<td></td>
<td>Short</td>
<td>5(5)</td>
<td>1(1)</td>
<td>3(11)</td>
<td>3(7)</td>
<td>0</td>
<td>3(24)</td>
</tr>
<tr>
<td>Females with young</td>
<td>Direct</td>
<td>2(2)</td>
<td>7(3)</td>
<td>6(14)</td>
<td>17(52)</td>
<td>0</td>
<td>28(22)</td>
</tr>
<tr>
<td></td>
<td>Short</td>
<td>8(6)</td>
<td>7(3)</td>
<td>1(3)</td>
<td>5(16)</td>
<td>0</td>
<td>5(4)</td>
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<td>Direct</td>
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<td>1(2)</td>
<td>2(6)</td>
<td>3(36)</td>
<td>0</td>
<td>9(13)</td>
</tr>
<tr>
<td></td>
<td>Short</td>
<td>1(2)</td>
<td>1(2)</td>
<td>4(11)</td>
<td>4(47)</td>
<td>0</td>
<td>3(4)</td>
</tr>
<tr>
<td>Adolescent males &amp; females</td>
<td>Direct</td>
<td>0</td>
<td>0</td>
<td>1(4)</td>
<td>2(21)</td>
<td>0</td>
<td>3(9)</td>
</tr>
<tr>
<td></td>
<td>Short</td>
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<td>1(2)</td>
<td>1(7)</td>
<td>4(42)</td>
<td>0</td>
<td>4(11)</td>
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<tr>
<td>Subadults</td>
<td>Direct</td>
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<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td></td>
<td>Short</td>
<td>0</td>
<td>0</td>
<td>2(5)</td>
<td>9(1)</td>
<td>0</td>
<td>1(6)</td>
</tr>
</tbody>
</table>
quarters and used the forelegs to clout or fend off the other. Most blows were directed to the chest or shoulders and bites were generally inflicted on the head and neck.

Bears fought rarely at McNeil River. Less than 3 percent of the agonistic encounters included fighting. If encounters involving females with young are excluded, the figure is only 2 percent. Most fights lasted but a few seconds and more than one-third in 1973 consisted only of one or two cuffs. In 75 percent of the fights, only one bear delivered blows or bites with the victim doing no more than trying to fend off its attacker.

A fight frequently ended in an apparent standoff. Once a fight started, a bear ran away only 14 percent of the time. In almost half of the fights, the aggressor was the first to walk away. A bear that stood its ground during an attack generally was less abused than one that fled and was then caught from behind. Unless the rivals were significantly mismatched, a vigorous defense, even when it consisted only of trying to fend off the onslaught, usually ended the attack.

An unusual encounter that illustrates the significance of a defense occurred between a large adult female named Big Momma and a large adolescent male. Big Momma had repeatedly threatened the adolescent male as he tried to occupy a fishing site within 5 m of her. Finally, she lunged at the adolescent and struck him once. The male responded by sparring. Big Momma then turned to resume fishing and the male started to walk in the opposite direction toward a discarded bit of salmon. Big Momma glanced at him from her fishing spot, saw him walking away, and then rushed him silently from behind. As the male lowered his head to
examine the discarded salmon, she landed squarely on his back, knocked him to the ground, and tore at his shoulders and neck. The young male eventually regained his feet and confronted her whereupon she broke off the attack and returned to her fishing location.

As with charges, fights usually occurred between bears of different sex and age (Figures 10 and 11). Adolescents and subadults bore the brunt of the attacks, usually from older and larger bears. Young bears usually did not reciprocate with strikes or bites. Females with offspring were most likely to attack, and while centering their attacks on younger bears, they also fought in 8 percent of their encounters with adult males.

Single adult females fought in less than 2 percent of their encounters. Despite the high frequency of fighting between single adult females and subadults indicated in Figure 10, only 22 encounters in total were recorded. Adult males frequently bore scars on their bodies and occasionally had fresh wounds, but the four fights between adult males I witnessed at McNeil Falls resulted in no apparent injury.

Other agonistic interactions

More than 57 percent of the brown bear interactions observed at McNeil Falls consisted only of a bear passively deferring to another. The most common case consisted of a bear altering its path or withdrawing to avoid conflict. A bear also might find its favored fishing site occupied, and rather than attempt to displace the occupant, the bear would sit down a few m away and wait until the site was vacated. No discernible element of aggression was observed.
Figure 10. Frequency of fighting in bear agonistic encounters at McNeil Falls in 1972. Each solid line is equal to 1 percent of the agonistic encounters between bears of the respective groups and a dashed line indicates less than 1 percent.
Figure 11. Frequency of fighting in bear agonistic encounters at McNeil Falls in 1973. Each solid line is equal to 1 percent of the agonistic encounters between bears of the respective groups and a dashed line indicates less than 1 percent.
Other agonistic encounters consisted of one or both bears acknowledging each other's presence by changes in facial expressions and shifts in body postures but did not lead to deferrals. A bear often interrupted fishing when another walked near and might show an alert or tense closed mouth face until it passed on. In some cases, the bear turned its body to face the passing animal. Such interactions accounted for 8 percent of all agonistic encounters.

Agonistic behavior of bears according to sex and age

**Adult males.** The arrival of an adult male at McNeil Falls usually had a catalytic effect. Bears that had been fishing or feeding in relative calm scrambled wildly out of his way. Besides touching off a small stampede initially, an adult male also caused a successive chain of interactions among bears he displaced as they competed for remaining fishing spots in other parts of the falls. Usually the big males seemed taciturn, outwardly ignoring the other animals. Most walked with a slow, lumbering gait and had a relaxed face as they moved directly to the river to fish. However, should any bear linger, a male might cock his ears and start toward it causing the other to wheel and flee. Often a glance from a big male caused others to move away.

Big males had infrequent encounters that included overt aggression since most bears stayed clear of them. Judging from the reaction of other bears, the appearance alone of big males conveyed significant threat. Only females accompanied by young confronted them consistently, but this too probably stemmed from the concern of females at the males' proximity. Except when Scar Shoulder once trotted after a cub separated
from its mother, apparently to smell it, no adult male showed an interest in cubs.

The scars and battered ears of many adult males belied their apparent lack of aggressiveness. Fighting between males probably occurs regularly during the mating season. In contrast to their usual behavior, males consorting with females in estrous were extremely irascible. Charley Brown, the top ranked male, attached and dislodged another adult male mating with Jeanne. The partially eaten remains of a 2.5 year-old subadult were found July 22, 1973, and an autopsy indicated it had been killed by another bear. At least four adult males were pursuing females in estrous during much of July, and I suspect the subadult was killed by one of these males.

**Females with young.** Brown bear mothers are extremely belligerent, a trait that may have evolved to enable them to protect their offspring from other bears (Herrero, 1972). Females that consistently and successfully defend their offspring from attacks and at the same time remain relatively unscathed may contribute more to subsequent generations than those that do not. I saw no bear threaten cubs, yet the females acted as if each bear posed a danger. They tolerated none near them and if unable to drive the other bear away, they would themselves depart.

However, females reacted differently toward different bears. They were least antagonistic toward single adult females, but they rebuffed adolescents and subadults fiercely. When they encountered large adult males, their behavior often suggested ambivalence between attack and retreat as they first rushed toward the male and then ran back to the
cubs. Usually a female ultimately retreated before an adult male. But cubs frequently scattered, probably because of the female's erratic behavior as much as to the presence of the male, and the encounter was prolonged encounter as the female tried to gather the cubs together, retreat, and simultaneously maintain her vigilance. If the adult male continued to advance without allowing her the opportunity to withdraw, conflict usually resulted.

Also, females with offspring seemed more intolerant of adolescent males than adolescent females and subadults. I suspect this may have been due to the tendency of young males to approach them too closely, perhaps because they did not distinguish females with young from less aggressive single adult females. However, the females may also have perceived males, regardless of age, as a threat to their offspring.

Females with young account for the majority of documented attacks on people (Herrero, 1976). At McNeil River, I was charged by a female with young but once, despite being in contact with them daily. The lone charge was made not at McNeil River but about 10 km away by a female that probably had never seen a human. A lack of such aggressiveness toward humans by females at McNeil Falls suggested that they could learn what posed a threat and what did not and adjusted their behavior accordingly. Consequently, despite the fact that I saw no bear threaten cubs or yearlings, attacks probably occur periodically or the females would not be so universally hostile toward the bears they encounter.

Single adult females. Single females as a group had few distinctive behavioral characteristics. Not nearly as aggressive as females with young, they nevertheless demonstrated little tolerance.
Individuals varied greatly in aggressiveness; Lady Bird and Jeanne were consistently hostile toward adolescents and subadults, whereas Reggie and Red Collar often evidenced little more than passing interest in young animals. "OD" and Hardass were particularly irascible toward subadults. Most females simply walked away from adult males, yet Goldie and Blue Flaps regularly fished within 10 m of a male. Single females occasionally encountered their independent offspring, but with no indication of recognition and it appeared they were as likely to rebuff their own young as any other.

Adolescent males. The social behavior of adolescent males was unique. More than any other group, they adjusted quickly to the crowded conditions at McNeil Falls. Adolescent males persistently approached hostile individuals that others learned to avoid. Young males often reciprocated when threatened but usually briefly and with low intensity. Unlikely to forcefully retaliate when attacked, they would amble away from a rebuff and look for food elsewhere. Unlike most bears, proximity to others did not particularly concern some adolescent males, and they seemed quite willing to fish side by side if the rebuffs were mild. Rarely was such tolerance reciprocated by bears of other age groups, however. The tendency of adolescent males to consistently approach other bears to short range drew numerous threats and relatively frequent attacks. Like most bears, adolescent males harbored considerable respect for adult males and generally stayed away from them.

Brown bear males are capable of producing viable spermatozoa by 4-1/2 years of age (Erickson et al., 1968). However, whereas females attain nearly full growth by 6 to 7 years, males continue to grow until
at least 11 or 12 (Glenn, 1973). The difference in physical development between males and females may also apply to hormonal development and could account for the relatively lower intolerance manifested by the adolescent males. The two oldest adolescent males, Romeo (7 years old) and Zubin (8 years old), were most likely to be intolerant. Dark, a relatively small male 5-1/2 years old in 1973, was frequently hostile toward other adolescents and subadults. Otherwise, aggressiveness employed by the young males was mostly defensive and in response to aggression instigated by others. It should also be noted that young males would ferociously fight for salmon among themselves, and a few consistently tried to steal the catch of adult females and females with young.

Adolescent females. These young females were much like single adult females in their behavior. They were considerably more intolerant than their male counterparts, centering their aggression on adolescent males and subadults and tending to avoid conflicts with adults. As with single adult females, some adolescent females were consistently aggressive and some were timid. I saw but four individuals in this age class, however.

Subadults. Brown bear offspring probably become independent during the spring of their third year when they are 28 to 30 months old (Glenn, 1973). My observations indicate the separation is a gradual process spanning one to two weeks or more and occurs when the mother enters estrous. Adult males attracted to the female probably contribute to and perhaps are the primary cause of the separation. The young bears follow the consorting pair for awhile and may even re-unite with their mother
for brief periods, but the separation is complete by early July. I did not observe a female try to drive her youngster away.

The most consistent attribute of subadults was their extreme wariness. They rarely approached other bears to close range and frequently fled when they were approached. Perhaps because they ran away rather than defend themselves, subadults were charged and attacked fairly often. Subadults obviously could not retaliate as vigorously as larger bears, and an attacker had little to lose when its victim was a subadult. The propensity of subadults to avoid conflict was evidenced by infrequent occurrences of jawing and sparring in their encounters. Their most frequent antagonists were adult females, especially those with offspring, and adolescent females.

Some subadults (and adolescents) continued associating with siblings after becoming independent of the female. Red and Blue remained together until they were 5 years old. This prolonged association may enable them to compete or defend themselves more effectively than they could singly. Subadult siblings acted cooperatively in aggressive interactions in 1971, but such behavior was rare in 1972 and 1973. I doubt that cooperative action would be effective in defense against bears that actually posed a significant danger, although the detection of danger may be enhanced by sibling associations.

**Dominance relationships**

I defined an animal as dominant when it displaced or caused a rival to stop, back up, or alter its direction of movement to avoid or end a confrontation. Interactions that resulted in no clear winner or loser
were termed indecisive. Dominance relationships were examined from two aspects: relationships as a whole between the different sex and age classes of bears and relationships between individuals of the same sex and age.

Relations between bears across sex and age lines have already been intimated. Adult males were unquestionably most dominant, followed in order by females with young, single adult females, adolescents, and finally subadults (Tables 7 and 8). Factors associated with dominance relations between groups were size, size as a function of age in some cases, and aggressiveness. Where bears were much different in size, usually size alone determined status reinforced if necessary by periodic threats. Dominance relations between bears of different sex and age but of similar size were more likely settled on the basis of aggressiveness.

Adult males outweigh adult females by 50 to 100 percent. They could easily prevail over bears of other classes but rarely had opportunity to assert themselves, since they seemed to enjoy a defacto dominance as a consequence of their size advantage alone. Interestingly enough, three single adult females (Goldie, Lady Bird, and Blue Flaps) regularly fished near some adult males without eliciting significant rebuffs.

Females with young owed their high status to aggressiveness. Most of their hostility stemmed from maternal protectiveness, but they also could displace a bear from a preferred fishing site or usurp its catch of salmon. in 1972, a female with a yearling specialized in robbing, sitting aside quietly until another bear caught a salmon and then rushing in to take it away. Female Number 10 appeared
Table 7. Social dominance relationships between classes in 1972. Figures are the percent of encounters that were won.

<table>
<thead>
<tr>
<th>Encounter won by</th>
<th>Adult males</th>
<th>Females with young</th>
<th>Adult females</th>
<th>Adolescent females</th>
<th>Adolescent males</th>
<th>Subadults</th>
<th>Total wins</th>
<th>Percent wins</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males</td>
<td>-</td>
<td>53</td>
<td>93</td>
<td>100</td>
<td>100</td>
<td>100</td>
<td>290</td>
<td>91</td>
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<td>Percent losses</td>
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<td>35</td>
<td>69</td>
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<tr>
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<td>367</td>
<td>531</td>
<td>129</td>
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</table>
Table 8. Social dominance relationships between classes in 1973. Figures are the percent of encounters that were won

<table>
<thead>
<tr>
<th>Encounter won by</th>
<th>Adult males</th>
<th>Females with young</th>
<th>Adult females</th>
<th>Adolescent males</th>
<th>Adolescent females</th>
<th>Subadults</th>
<th>Total wins</th>
<th>Percent wins</th>
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<tr>
<td>Adult males</td>
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<td>93</td>
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<td>17</td>
<td>-</td>
<td>-</td>
<td>32</td>
<td>10</td>
<td></td>
</tr>
</tbody>
</table>

Percent losses 2 14 45 58 72 90
Total losses 7 25 338 514 156 286
with her first litter in 1973 and was unusually timid; she was pro-
tective of her cubs but did not assert herself to displace other bears. Females with young caused adult males to back down in almost half of their encounters in 1972; nearly 40 (24) percent of adult male-female with young encounters were indecisive that year. Stonorov (1972) noted that some females with yearlings gained additional advantage by their offspring's participation during encounters. I did not observe youngsters threatening jointly with their mothers during 1972 and 1973. Rather the offspring usually sought shelter behind their mothers during encounters. On a few occasions, however, I did record some yearlings making threats independently of their mothers.

Single adult females as a group readily gave way to adult males and females with young. They in turn easily dominated adolescent and sub-
adults. Aggressiveness generally determined the status of single adult females. Adolescent males were often as large as and in some cases larger than adult females yet the greater aggressiveness of the females usually made young males defer. Single females conveyed considerable pragmatism in their interactions. They were quite intolerant in 1972 when salmon were in short supply but much less so in 1973 when fish were numerous. Consequently, while winning 90 percent of their decisive interactions with adolescent males in 1972, they won but 62 percent in 1973, apparently because occupancy of a particular fishing site was less important in terms of catching sufficient salmon. Whereas adolescent males were fiercely rebuffed in the former year, single females often passively deferred to them in 1973. Older females, in excess of 11 years among animals of known age, were more dominant than younger
females. A few single adult females, particularly Blue Flaps (a large 22-year-old occasionally supplanted Baldy and Winston, the lowest ranking adult males).

Unless met with moderately vigorous threats, adolescent males showed little inhibition in approaching other bears. They were consistently the least aggressive of all bears, owing their "status" not so much to defense of a fishing site or active displacement of a fishing bear but by the proclivity of other bears to give way before them. When confrontations developed, adolescent males usually lost. The higher ranking of adolescent males in 1973 was due mainly to a decline in intolerance of other bears. Individuals that dominated them in 1972 did not rebuff them as often, or passively deferred more frequently to them in 1973. Unfortunately, I saw few adolescent females, but they seemed less tolerant than adolescent males the same age. Two sibling females, Red and Blue, may have dominated other adolescents and a few single adult females because they often acted in tandem. It appeared, however, that their cooperative efforts were effective mainly against adolescent males and against individuals they also dominated singly.

Subadults as a group were easily dominated by older bears. One exception, Sweet Sue's Cub, had remained with her mother an extra summer (through her third summer) and was unusually large for 3-1/2 years of age. She occasionally caused some adolescent males and the adolescent females to give way. A 3-1/2-year-old male in 1972 was also unusually large, but unlike Sweet Sue's Cub he was easily dominated by other animals. He repeatedly attempted to fish in 1972 but was frequently attacked and eventually left McNeil Falls in mid-season.
Within-class dominance relationships also were associated with differences in size and aggressiveness. Yet because bears of a given sex and roughly similar ages were about the same size, intolerance or the lack thereof was perhaps most important.

Dominance relationships between adult males were linear for the most part. Adult males overall lost but 10 (11 percent) of 88 decisive encounters to males of lower status. Charley Brown, the top-ranked male observed, never lost an encounter. The lone anomalous relationship was between what appeared to be a relatively young male, Winston, and an older male named Scar Shoulder. Whereas Scar Shoulder bore numerous scars, Winston was practically unmarked indicating the latter had only recently reached full maturity. Despite being younger, Winston won four of five encounters. Four encounters between these two occurred on the evening of Day 28; Winston's longer tenure at McNeil Falls (he had been present since Day 3) may have conferred an advantage that would have been reversed with additional subsequent interactions.

Charley Brown was clearly the supreme bear at McNeil River. Although he did not seem significantly larger than other mature males, all seemed to quickly recognize his special status. The only times this male was seen fighting was when he approached other bears from behind apparently without their noticing him. In both cases, he knocked the males down and they then scrambled away. On a separate occasion, he attacked a male mating with a female and that male too fled as soon as he was able to gain his feet.

Despite the fact I saw few fights, the linear, clear-cut nature of the male dominance hierarchy at McNeil Falls suggested relationships were settled by mid-July.
Dominance relationships among adult females were generally ambiguous (Figure 12). Blue Flaps was clearly the dominant female in 1972, but among lower-ranking individuals circular relationships and reversals were common both seasons. A prevalent feature of females was that repeated encounters between the same individuals did not clarify relationships. In 1972, Red Collar (RC) and Reggie (RG) each won 6 encounters over the other. Big Belly (BB) and Jeanne (JN) also seemed evenly matched with Big Belly winning 7 of 13 encounters. Jeanne, in turn, won 5 of 9 encounters with Red Collar. Status positions were considerably different in 1973 with the inclusion of females that had been accompanied by young the previous year and with the demise of Blue Flaps during the spring, 1973, hunting season. Although such relationships indicate instability, individuals became less likely to defer to one another with repeated exposure. In total, subordinate females won a fairly high proportion, 55 of 206 or 26 percent, of their encounters with higher-ranking females.

Status relationships were modified by associations of single adult females. Bears that interacted repeatedly gradually began fishing closer together with the result that another bear that could have displaced them singly avoided them when they were clustered. Reggie probably owed her relatively high status in 1972 to the fact that she often fished near Blue Flaps, even though Blue Flaps won 17 of 21 encounters with her. The absence of Blue Flaps in 1973 may have contributed to Reggie's decline in rank that year.

Females that had borne young in 1972 assumed three of the top four rankings among single adult females in 1973. The fourth female, Jeanne,
Figure 12. Dominance relationships of single adult females at McNeil River, based on 107 encounters in 1972 and 99 encounters in 1973
had produced cubs in 1971 and did so again in 1974 (James Faro, personal communication). Big Belly and Reggie had never produced cubs to my knowledge and another low ranking sow in 1973, Red Collar, had not been seen with offspring since 1968 although she did have cubs in 1974 (James Faro, personal communication). OD regularly produced cubs but she and Spooky were the smallest adult females at McNeil River. Big Momma, whom I observed briefly without young in 1971, also was a high-ranking female when single. These limited observations suggest that females of relatively high rank are most likely to produce cubs. More information is needed before substantive conclusions are possible.

Encounters between females accompanied by young were limited. Outcomes of decisive encounters indicated status relationships were linear, yet 15 of 32 (47 percent) encounters in 1972 were indecisive. Big Momma won a total of eight encounters with Hardass, Goldie, Leland P., and OD without a loss but an additional nine encounters involving Big Momma and these same individuals were indecisive. Only two females with offspring, Big Momma and Spooky, were present for more than a few hours in 1973. Spooky was a small female that produced her first litter in 1973. She was unusual in that she tended to move away from bears rather than provoke a conflict by standing her ground.

Adolescent bears were ranked primarily on the basis of size, although variation was such that generalizations are difficult. The larger and oldest adolescent males were most dominant. As pointed out previously, adolescent males in general were relatively unaggressive, particularly in 1973, when nonagonistic interactions further clouded
rank positions. Woodruff ranked number 3 among nine adolescent males in 1973, but was singularly unaggressive, owing his apparent status to the fact that he seemed to have few inhibitions about walking up to other bears and they would then move elsewhere. The two top-ranking adolescents, Zubin and Romeo, were slightly larger than adult females and their size alone caused others to defer. Romeo and Zubin occasionally were aggressive when smaller males encroached on their fishing areas. Dark was a small adolescent male but was probably most aggressive of all, and his aggressiveness was particularly decisive in 1973 when the abundance of salmon dampened aggressiveness of most other adolescents.

Red and Blue were the only adolescent females observed for significant periods. They ranked third and fourth among a total of nine adolescent males and females in 1972. In some instances, Red and Blue acted in tandem to displace another adolescent. During one occasion early in the 1972 fishing season, Red was fishing at location Number 14 with Blue seated on shore upstream about 4 m away. Dark appeared and approached Red from downstream. When Dark drew to within 6 to 8 m of Red, Red charged, and Dark turned and ran for a few steps but then turned to face Red's rush. Red stopped, but Blue drew alongside Red and together they again charged Dark and attacked, striking and biting him. Dark backed into the river, with Red and Blue now advancing slowly toward him walking abreast with their heads lowered. Dark wheeled and swam to the other side of the river. Two other adolescent females, one a full sister to Red and Blue, ranked at the bottom of the adolescent hierarchy, suggesting the joint participation of Red and Blue enhanced their status. Red and Blue also interacted with other bears.
independently and seemed generally as successful as when they were together. Even if true, however, the psychological advantage of acting in unison may have contributed to their success as individuals.

Encounters between subadults were so limited (a total of 11) that no rank associations were feasible.

Nonagonistic behavior

Although agonistic behavior predominated at McNeil Falls, bears also interacted without hostility in amicable interactions (Ewer, 1968) and social play. Additional nonagonistic encounters involved individuals in family groups and males consorting with females in breeding condition.

Amicable and play interactions

Amicable interactions consisted of bears nosing one another about the head and neck, rubbing heads together, and other gentle body contacts in nonhostile contexts (Figure 13). Play bouts were vigorous, consisting of mock fighting (Figure 14). A playing bear had a relaxed open mouth face. A common feature of play consisted of one bear clasping with its teeth the hair on the head or neck of its partner and tugging vigorously. Bears at play also lunged at one another as if sparring and shoved their partners with their forelegs. In contrast to real battle, playing bears were silent except for labored breathing and an occasional snort.
Figure 13. An amicable interaction between adolescent males

Figure 14. Adolescent males playing
Amicable encounters and social play are probably not distinct behaviorally. Usually both were initiated in the same manner, and mock fights were sometimes preceded by amicable rubbing and nuzzling. A bear typically initiated a nonagonistic contact by slowly walking toward a potential partner with an alert face. One indication of nonaggressive intent was the great mobility of the approaching bears' ears; the ears were alternately and repeatedly cocked to the front and then flicked to the side or slightly to the rear. A bear sometimes shook its head as it approached a play partner. Other nonagonistic interactions began spontaneously between two animals standing side by side. Bears were silent as they initiated interactions, and an absence of growling was apparently requisite to sustain the encounter. One bear abruptly broke off a play bout when its partner voiced a low growl when cuffed too roughly.

I saw no play bouts in 1972 and only six amicable interactions. Four amicable contacts involved Dark, an adolescent male, and Patchbutt, a relatively large subadult male; another occurred between Dark and his brother Light (Dark and Light became separated between August, 1971, and June, 1972); and one interaction was between Red and Blue, the sibling adolescent females. The amicable contact between Red and Blue occurred following a brief separation (a few hours) when Blue walked to meet Red; upon meeting, they reciprocally rubbed heads and necks for about 30 seconds. Amicable interactions between the others were brief, lasting only a few moments.

Nonagonistic interactions were common in 1973 (Figures 15 and 16). Adolescent bears were most likely to have amicable and play interactions. Of 14 different adolescent males, 10 engaged in nonhostile
Figure 15. The occurrence of "amicable" brown bear interactions in 1973 expressed as a percent of the total number of amicable and agonistic encounters. Each solid line equals 1 percent of the encounters and a dashed line indicates less than 1 percent. Numbers in parentheses are the number of amicable interactions observed.
Figure 16. Frequency of social play bouts in 1973 expressed as a percent of the total number of play and agonistic encounters. Each solid line indicates 1 percent of the encounters. Numbers in parentheses are the number of play bouts observed.
encounters at a rate of 0.4 per hour, and the two eldest adolescent males, aged 7 and 8 years, had regular friendly contacts.

Seven-year-old Zubin, who weighed an estimated 300 kg, played repeatedly with 4-year-old Woodruff who was roughly two-thirds Zubin's size. Most play bouts occurred among the smaller 4- to 5-year old males that weighed 175 to 225 kg. Neither adult males nor adult females played, and they had infrequent amicable encounters.

Cubs and yearlings played rarely and briefly at McNeil Falls and never engaged in sustained social play. A cub once played with a piece of wood for about 4 minutes. Another cub appeared to playfully paw at an object floating in a pool near shore. Cubs played among themselves and with their mothers on Mikfik Meadows.

The nonagonistic behavior of adolescents sometimes provided anecdotal evidence that bears could recognize one another as individuals. As described above, Blue apparently recognized her sibling sister Red at roughly 60 m and began walking toward her with the alert face. Patchbutt seemed to identify his frequent play partner Light when the latter topped a ridge 80 m distant; Patchbutt immediately left his fishing site to meet him whereupon they rubbed heads briefly before Light moved into the river to fish.

Brown bears played only in a relaxed atmosphere. Cubs and yearlings were continually distracted by the coming and going of other bears at McNeil Falls and usually huddled against their mothers for security. Adolescents and subadults played at McNeil Falls during the 1973 season only when salmon were so abundant that competition was occasionally nonexistent. Freedom from hunger due to the salmon glut
created the relaxed environment requisite for social play. The prevalence of play dropped sharply during days 31 to 35 where salmon were again in relatively short supply.

Play in carnivores consists of actions also used seriously, e.g., capture of prey, manipulation, fighting, and escape (Ewer, 1968). Play is held to have functional survival else it would not occur so commonly (Schaller, 1972). As Henry and Herrero (1974) reported for black bears, brown bear play consisted mostly of mock battles. Males played more than females. Although my data are lacking because I saw few adolescent females, Masatomi (1964) also found males most playful among his captive group of young Japanese brown bears. Without dismissing other possible functions of play, including expenditure of excess energy (Schaller, 1972), the emphasis on mock battle and the fact that animals nearing full maturity played regularly suggested play in bears may relate to adult dominance relationships. By playing, adolescent males might assess their prowess without risk. Unfortunately, only four adolescent females were present in 1973 while adolescent males were common. It is possible that young females might have played as often as males if a comparable number of peers had been available. Whatever its function, social play between bears nearing full maturity seemed striking in a species noted for its solitary tendencies.

Mother-young relationships

Brown bear mothers are extremely solicitous of their offspring, especially when the cubs are roughly 5 to 10 months old. A female apparently views everything as a threat to her young and will defend
them against all comers. The proximity of other bears caused families
to behave quite differently at McNeil Falls in comparison to what
occurred as the females grazed on the sedge meadows. Whereas cubs
rough-housed among themselves and with their mothers on the meadows,
they did not do so at McNeil Falls. Also, cubs on the meadows often
moved 20 to 30 m from their mothers and yearlings ranged even further.
Cubs usually huddled tightly against their mothers at the falls and
never ventured more than a few feet away.

However, cubs were occasionally left stranded when a female forded
a portion of the falls to reach a fishing site. Most remained huddled
together on the bank and bawled until their mother returned. A female
frequently was 20 m or more from her cubs. One female, Big Momma, left
her cubs sitting a few m from my observation post twice rather than have
them follow her down to the river. The means she used to make them stay
are unknown. Unlike cubs left stranded at the edge of the river, Big
Momma's cubs did not bawl when she left them, although they watched her
intently as she fished 30 to 35 m away. Unless frightened by a passing
bear, her cubs remained where Big Momma left them until she returned.

Some cubs left stranded would attempt to follow their mothers after
a few moments. Most were swept downstream where they eventually washed
ashore. A female would run after her cubs and eventually gather them
back together. One of Big Momma's cubs attempted to follow but was also
cought by the current; rather than run along the shore, however, Big
Momma dived into the water and with one paw gathered the cub to her
chest and carried it to quiet water.
Despite the close association between a female and offspring, cubs occasionally had difficulty recognizing their mothers. Litters became mixed fairly often and females suckled cubs besides their own at least twice. Big Momma was once followed by her three cubs and two belonging to Lady Bird. Big Momma nosed the strange cubs but did not try to drive them away. Subsequently Big Momma and Lady Bird were followed by three cubs each, but I do not know if each retained her own. On one of the occasions Big Momma parked her cubs, the cubs fled from her upon her return. As she slowly walked toward them, the cubs stood on their rear legs, showed a puckered-lip face and then ran. Eventually, the cubs cautiously approached and nosed her on the head and neck; she then walked on and the cubs fell in behind.

Brown bear females made no special effort to share their salmon catches with their offspring. Cubs consumed only what they could wrestle from their mothers and siblings. Mothers usually tolerated the competitiveness of their offspring unless they tore the bulk of the fish away which the females usually reappropriated quickly. On one occasion, Hardass clouted her yearling when he pulled her catch away.

Courtship behavior

A male typically initiated courtship by approaching an estrous female at a slow deliberate walk. With ears cocked toward the female, the male held his head slightly higher than normal until within 1 to 2 m. At that point, he stretched his head toward her and repeatedly flicked his ears from erect to a relaxed lateral position. The female faced the
male, lifting her head to meet his. The male usually nosed the female on her head and neck which the female sometimes reciprocated. The entire sequence resembled the amicable encounters commonly seen between adolescents.

Females dictated the course of courtship activities (Figure 17). Mating sometimes occurred within seconds of the males' first approach. On a few occasions, the males briefly nosed and rubbed against the females only to have them walk on showing no further interest. It was common, however, for females to persistently walk or run away when a male drew near, and the females actively rebuffed the males with threats on a few occasions. Females seemed never to completely shed their fear of adult males and were likely to flee when approached. No estrous female ran at the approach of an adolescent male. To be successful in mating, adult males perhaps must tend females for a period to mitigate female wariness.

A typical courtship sequence involved a 6-year-old female and the adult male Patches. The female ran from Patches initially but as he followed slowly she settled into a fast walk, intermittently stopping to face him until he was within a few m. Patches followed always at a slow walk, stretching his head out to her. After repeating this sequence for 13 minutes, the female allowed Patches to nuzzle her. They reciprocally nosed each other for about 10 seconds before Patches moved to her hindquarters and mounted.

Another instance involved a female that repeatedly resisted the advances of Patches. The female was seated when Patches first approached, in this case, walking fast. She saw him when he was still
Figure 17. Generalized patterns and sequencing of brown bear breeding behavior based on 29 male solicitations of unattended estrous females.
50 m away. She ran for about 30 m, turned to face him, and then quickly walked on as Patches followed with his head raised and mouth slightly agape. The female circled and resumed fishing. Patches approached again, this time slowly, shifting his ears, and holding his head elevated. This time she allowed him to nose her on the neck but then rebuffed him with sparring, causing Patches to draw back and turn his head to the side. He again nosed her neck whereupon she turned and walked away. Six minutes later she moved back to her fishing site only to again run when Patches immediately moved toward her. She returned to fish 2 minutes later and Patches resumed his deliberate advance. This time she rushed him with a roar, stopping just short of contact. Patches give a brief growl, backed up a step, lowered his hindquarters to a squat, and turned his head to the side. The female turned and resumed fishing leaving Patches seated about 8 m behind her. This general pattern was repeated over the next 4 hours with the female attempting to fish during the intervals between the advances of the male. The female periodically turned her head toward the seated male as she fished, lowering her head and flattening her ears when doing so. Patches usually turned his head to the side when she looked at him. Despite her threats, the female could not dissuade Patches and eventually she left the falls with Patches following.

Temporal Changes in Brown Bear Social Behavior

A recurrent hypothesis regarding animal social organizations is that once individuals in a group are sorted out on the basis of dominance, the resultant increase in stability leads to higher group
efficiency (Wilson, 1975). Changes over time in the frequency and form of brown bear agonistic interactions at McNeil Falls should be reflected in how successful bears were at catching salmon. Changes in the frequency of occurrence of agonistic encounters, and some of the factors causing such changes are the topics of this section. Unless otherwise stated, data were analyzed by grouping observations into eight 5-day periods of each fishing season.

**Frequency of agonistic encounters**

In 1972, agonistic encounter rates increased gradually in small increments from the first through the sixth 5-day period (0.44, 1.52, 1.49, 1.59, 1.81, and 2.37 encounters per bear hour) only to decline during days 31 to 35 and 36 to 40. The same pattern did not appear in 1973 except possibly during the first three 5-day periods (0.89, 1.70, and 2.02 encounters per bear hour). I am uncertain whether this trend was behaviorally significant or a coincidental artifact. If real, however, it indicates bears became increasingly likely to approach one another after some period of experience. The decline in encounter rate during the later stages of the fishing seasons could be due to a decline in responsiveness to one another's approach or presence. Some data given below indicate this to be a reasonable possibility. Despite this variation, there was a highly significant ($P < 0.01$) positive linear correlation between bear hours (which in trend was nearly identical to absolute numbers of bears) and the number of agonistic encounters recorded during each 5-day period indicating no appreciable change in encounter rate with time. These statistics indicated 92 percent of the
variation in the number of encounters was attributable simply to the number of bear-hours (which reflected the number of bears present).

I had anticipated that individual bears would learn to avoid confronting dominant bears based on their experiences during interactions. If so, individuals of a given sex and age would gradually have proportionately more encounters among themselves and less with bears of other sex and age groups. To arrive at an estimate of the number of encounters bears of each sex and age class should have among themselves and with individuals of other classes, I summed the number of encounters initiated by each bear class and then apportioned the total encounters among the classes on the basis of the number of bear-hours each class was present. For example, assume bears of Class A initiated 100 encounters and that bears belonged to Classes A, B, and C were present a total of 200 bear-hours. Bears belonging to Class A were present during this period for 80 bear-hours (40 percent of the total bear-hours), bears of Class B were present 100 bear-hours (50 percent), and bears of Class C were present 20 hours (10 percent). Bears of Class A would be expected to have 40 encounters (100 encounters x 0.4) with other Class A bears, 50 (100 x 0.5) with Class B and 10 (100 x 0.1) with Class C. The main assumption involved in arriving at the expected number of encounters in this manner was bears were evenly distributed by time and place with an equal likelihood of encountering any bear. As shown later, this assumption clearly was erroneous, but should show in relative fashion if the ratio of the observed number to expected number of encounters between classes varied over time.
There was no evidence that experience had an effect on deciding which animals were likely to participate in encounters. Although in all cases the ratio of observed to the expected number of encounters initiated by bears of each class against bears of other classes was significantly different \((P < .01)\), the ratios were no different between the first half versus the last half of the seasons. In general, adult bears had more encounters than expected with other adults and fewer than expected with adolescents and subadults. Likewise, adolescents and subadults were most likely to interact among themselves and to initiate fewer encounters than expected with adults. This pattern persisted throughout each season.

Interactions were most often initiated by the more dominant individuals. Adult males, for example, initiated 68 percent (229) of 335 encounters with single adult females. Adult females in turn initiated but 53 percent (459) of 861 encounters with adolescent males. The greater an animal's relative dominance, the greater the proportion of its total encounters that it initiated. Agonistic interaction rates and the proportion initiated for each sex and age class are given in Table 9.

Frequency of behavior patterns

A number of bears, particularly adolescents and subadults were exceptionally wary during the first days of the fishing seasons. Bears periodically interrupted fishing to stand upright and gaze to their rear as if anticipating the approach of other bears. Twice in 1972 and once in 1973, both bears fled the other simultaneously. Some bears would run
Table 9. Bear interaction rates and percent initiated by sex and age group

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<th>Classification</th>
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<th>Rate (per hour) 1972</th>
<th>Percent initiated 1972</th>
<th>No. of encounters 1973</th>
<th>Rate (per hour) 1973</th>
<th>Percent initiated 1973</th>
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<td>1202</td>
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<td>Females with young</td>
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<td>3.8</td>
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<td>236</td>
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<td>29</td>
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<tr>
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<td>Adolescent females</td>
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<tr>
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<td>2.4</td>
<td>34</td>
<td>387</td>
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</tr>
</tbody>
</table>
away when another bear appeared on the opposite side of the river. Such behavior waned rapidly, however, and the balance of temporal changes in behavior were more subtle after the initial 5-day period.

Long-range avoidance of one another, presumably adaptive under normal conditions when bears are widely dispersed, became an inappropriate time- and energy-consuming diversion for bears at McNeil Falls. Consequently, subordinate bears became increasingly disposed to walk away from dominant animals as opposed to running (Figure 18). Figure 18 also shows that bears became less likely to defer at all as the seasons progressed, and illustrates the increasing ambiguity in dominance relationships among these animals. Bears that were clearly dominant were not tested by subordinate animals, but relationships between many bears that interacted repeatedly were never firmly established in the sense of traditional dominance-subordinance.

The occurrence of charges by bears likewise declined with time and mirrored the changes in frequency and form of deferrals (Figure 19). Unfortunately, I do not know if the frequency of charges declined because bears were less likely to run away or if bears were less likely to flee because their rivals made fewer charges. I suspect that both factors are involved. There was a consistent tendency for bears to approach one another even more closely with time within each season, implying an increasing boldness or at least a decline in wariness. Like most carnivores, bears chased anything that ran away. An adolescent female chased me as I trotted across a sedge meadow, apparently because she perceived that I was running from her. Since fleeing could elicit chasing, bears that grew less likely with time to run away at McNeil
Figure 18. Seasonal variation in the pattern and occurrence of deferrals by bears during agonistic encounters.
Figure 19. Seasonal variation in the pattern and occurrence of charges during agonistic encounters.
Falls were less likely to be chased (or charged). In 1972, short, abbreviated charges became relatively more prevalent as the season progressed. A bear that left its fishing site to make a protracted, hard charge not only lost fishing time, but might also lose its fishing site if it were claimed by another bear with similar rank. A short, abbreviated rush would usually turn rivals away as effectively as a full charge.

In 1973, however, there was little seasonal variation in the frequency or form of charges made by bears. Phenologically, the spring and early summer of 1973 were about two weeks advanced over 1972. Bears feeding in the sedge meadows prior to fishing in 1973 seemed less antagonistic than in the year previous, so perhaps bears were less hungry and therefore less competitive from the very onset of fishing in 1973.

The occurrence of jawing in agonistic encounters gradually increased with successive 5-day periods (Figure 20). For jawing to occur, bears had to approach one another to fairly close range, and the tendency for bears to approach more closely over time probably explains much of the seasonal variation in jawing frequency. In both years, there was a significant negative relationship between the average minimum distance between bears during encounters per 5-day period and the occurrence of jawing threats ($r = -0.70$, $F = 5.69$ in 1972; $r = -0.82$, $F = 5.99$ in 1973).

However, there was not a corresponding increase in sparring (Figure 20) or fighting over time, even though sparring and fighting, like jawing required close contact. Fighting and sparring occurred at
Figure 20. Seasonal variation in the occurrence of jawing and sparring during agonistic encounters.
consistently low rates throughout both seasons. Consequently, fighting and sparring can be viewed as growing less prevalent over time since the opportunities for such behavior to occur presumably increased as it did for jawing. Bears gradually replaced intense forms of aggression with a less intense form. So-called subordinate bears grew less wary with experience and -- although stopping short of provoking sparring threats or attacks -- perhaps elicited jawing threats later each season when earlier they did not approach closely enough to elicit any threat at all.

Altogether, such modifications in the form and frequency of agonistic behavior are even more striking when one considers that the representation of bears at McNeil Falls was constantly changing. New arrivals at McNeil Falls apparently took cues from established individuals and adjusted to the proximity of many conspecifics quickly.

There was little direct evidence that social pressures forced some bears either to stay away or to prematurely leave McNeil Falls. I suspect a subadult male that was repeatedly attacked in 1972 may have been driven away, but adolescents in general and some subadults persisted as long as individuals of any sex and age class despite their low status. Probably the greatest social tension was experienced by females with young cubs (especially novice mothers), reflected in their extreme and generally unwavering aggressiveness. Stonorov and Stokes (1972) suggested such females generally stayed away from the falls because the concern for their offspring outweighed the resource gained. While probably true in some cases, some females with offspring were among the most persistent residents at the falls, particularly in 1972. At some
point, the tradeoff between food obtained in relation to social pressure likely favors some bears departing, but such was not clearly demonstrated during this study.

Other considerations that influenced the frequency and pattern of brown bear interactions at the falls are treated in the next section on bear behavior and fishing success.

Bears Behavior and the Salmon Fishery

The annual salmon migrations, general fishing activity by bears and some factors that influenced fishing success, and a description of McNeil Falls proper were summarized previously as a prologue to the section on bear social behavior. Bears gathered at McNeil Falls only because salmon were vulnerable there and their behavior, with minor exceptions, can be linked directly to their attempts and success at procuring food.

Determinants of fishing success

Several interrelated factors determined a bear's fishing success, success measured here by the number of salmon caught per hour the bear was present at McNeil Falls. Salmon numbers and their vulnerability to fishing bears varied according to time of season (already discussed), time of day, and with fishing location. A bear's social rank determined its ability to gain and hold a choice fishing location. Rank further may have determined the time of day a bear fished, and, although the evidence is equivocal, the length of time it stayed at McNeil Falls
during each fishing season. An additional factor is fishing skill, of which I can say little. When fish were scarce, skill was probably a significant factor but became less important as fish abundance increased. Michael Luque (1977) has treated some aspects of skill in his discussion of brown bear fishing techniques.

Diurnal patterns of bear fishing success

The diurnal movements of salmon varied considerably (Figure 21). I am uncertain that the salmon surfacing in the count pool was related directly to the number that attempted to scale the falls where they were most readily captured by bears. Studies by the Commercial Fisheries Division of the Alaska Department of Fish and Game on the Yukon River and its tributaries showed few chum salmon moved through counting weirs between 0600 and 1600 hours. Movement through weirs gradually increased after 1600 until evening when an abrupt increase occurred starting about 1900 hours (Mauney, 1977). Trasky (1974) found 81 percent of the chum salmon in the Anvik River moved upstream between 1300 and 0700 hours. I too saw chums moving over the falls in large numbers after midnight during my overnight observations in 1972. They continued to move upstream well into daylight, but movement slowed when bears began arriving to fish around 0700 hours.

Bear numbers at McNeil Falls increased steadily from early morning until about 2100 hours (Figure 22). Nighttime activity appeared
Figure 21. Hourly variation in salmon abundance at McNeil Falls based on 2-minute counts conducted on the hour of salmon surfacing in a pool. The vertical lines indicate the standard error of the mean.
Figure 22. Hourly variations in bear numbers and the number of salmon caught per bear-hour at McNeil Falls. The vertical lines indicate the standard error of the mean.
limited; no more than three bears were present at once between midnight and 0600 hours during my two overnight observations in 1972. Time-lapse film records taken between July 21 to 31 (days 9 to 19), 1972, show a pattern of bear activity similar to Figure 22. Of twelve legible film sequences obtained between 2300 and 0400 hours, none revealed bears. Film records also showed a preponderance of large bears between 0500 and 0600 and again between 2100 and 2200.

Much of the hourly variation in the occurrence of bears at McNeil Falls was probably related to salmon availability since bear numbers paralleled changes in fishing success. Bears caught few salmon during the morning and mid-day, being more successful in the afternoon and evening (Figure 22). Hour to hour differences in fishing success were shared equally by all ages indicating the variation in success resulted from changes in salmon availability.

Salmon at McNeil Falls seemed to accumulate in pools below the rapids during the day, the fishing bears apparently causing them to hesitate before attempting to scale the rapids. By afternoon and evening, the concentration of salmon in the pools may have pressured some to move upstream. The large schools would probably have made the fish less aware of the bears. I believed that salmon attempted to scale the falls in schools in 1972 since four or five bears would suddenly catch fish within seconds of one another after standing idly for 30 minutes or more; an en masse movement may have been another means of avoiding predators and might also account for their hesitation in scaling the falls during early and mid-day when their numbers were few. Trasky (personal communication) suggests that chum are the wariest
salmon with the diurnal timing of their movements related to avoidance of predators. The abrupt drop in upstream movement shortly after bears appeared in the morning indicated that chum salmon were indeed wary of the bears.

Choice of fishing location

The importance of fishing locations depended on the size of the salmon migration. When salmon were limited, as in 1972, a bear's choice of location and its ability to gain and hold that site had an important bearing on its rate of fishing success. When salmon were abundant, as in 1973, fish were vulnerable at more locations and in some cases a bear's rate of fishing success seemed mostly a function of handling time. The relative importance of specific fishing locations varied slightly between years, presumably also a reflection of the differences in salmon abundance. Considering the 10 most important fishing sites, ranked by multiplying the number of salmon caught by the number of bear-hours expended, two sites (5 and 6) ranked 8 and 9 in 1972 were replaced in the top ten by two other sites (9 and 10) in 1973. In terms of bear-use of fishing sites, the average bear expended a minimum of 75 percent of its fishing time at 3.7 sites in 1972 compared to 4.2 sites in 1973.

Regardless of age and sex, bears tended to concentrate their fishing efforts at a few sites. The highest ranking adult males spent 75 percent or more of their fishing effort at the least number of locations, an average per bear of 2.8 (range 2 to 6). Other bears averaged from 3.6 sites (females with young) to 4.4 (single adult
females). Adolescent bears checked out slightly more locations (17.3) than other bears but nevertheless spent a minimum of 75 percent of their effort at an average of 4.3 fishing sites (range 2 to 7). OD, a single adult female in 1973, tested the most locations, 25.

In 1972, bears spent 86 percent of their actual fishing effort at the 10 best fishing sites. The proportion of time expended at these sites was directly related to social rank: adult males, 96%; females with young, 88%; single adult females, 86%; adolescents, 84%; and subadults, 81%. A similar pattern held in 1973, except that bears spent a smaller proportion of their time, 76%, at the 10 best locations.

The importance of social rank

A bear's ability to gain and hold a profitable fishing location ultimately determined its fishing success. Consequently, fishing success, in terms of fish caught per bear-hour, was directly related to social status (Table 10). As already pointed out, subordinate bears had considerable access to the best fishing locations. But apart from having ready access to the best sites, dominant animals concentrated their fishing efforts during the afternoon and evening when salmon were caught at the fastest rate (Figure 23). Subadults, adolescents, and, to a lesser extent, single adult females were present at McNeil Falls during the less profitable fishing periods of morning and mid-day, in addition to the lucrative evening hours, which dampened their fishing success rate. Furthermore, subordinate animals, while having ready access to good fishing sites early in the day, were likely to be excluded from those sites with the arrival of adult males and females with
Table 10. Number of salmon captured and capture rate by bears at McNeil Falls

<table>
<thead>
<tr>
<th></th>
<th>1972 Number observed captures</th>
<th>Number caught per hour</th>
<th>Estimated total catch*</th>
<th>1973 Number observed captures</th>
<th>Number caught per hour</th>
<th>Estimated total catch*</th>
</tr>
</thead>
<tbody>
<tr>
<td>Adult males</td>
<td>238</td>
<td>1.9</td>
<td>514</td>
<td>190</td>
<td>2.9</td>
<td>635</td>
</tr>
<tr>
<td>Adult females (single)</td>
<td>338</td>
<td>1.0</td>
<td>960</td>
<td>762</td>
<td>2.2</td>
<td>2,376</td>
</tr>
<tr>
<td>Females with young</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Adolescents males</td>
<td>190</td>
<td>1.3</td>
<td>483</td>
<td>192</td>
<td>3.4</td>
<td>532</td>
</tr>
<tr>
<td>Adolescents females</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Subadults</td>
<td>231</td>
<td>0.8</td>
<td>733</td>
<td>1,128</td>
<td>2.2</td>
<td>3,528</td>
</tr>
<tr>
<td></td>
<td>184</td>
<td>0.8</td>
<td>537</td>
<td>226</td>
<td>1.9</td>
<td>657</td>
</tr>
<tr>
<td></td>
<td>77</td>
<td>1.0</td>
<td>215</td>
<td>75</td>
<td>0.6</td>
<td>250</td>
</tr>
<tr>
<td>Total</td>
<td>1,258</td>
<td>1.0</td>
<td>3,442</td>
<td>2,573</td>
<td>2.1</td>
<td>7,978</td>
</tr>
</tbody>
</table>

*Estimated total number of salmon captured between 0600 and 2200 during the 40-day fishing season.
Figure 23. Percent of time bears spent at McNeil Falls during different periods of the day. Percent bear-hours for each sex and age group were adjusted according to the number of hours of observation made during each 4-hour period. Figures in parentheses are the number of bear hours.
young. Adult males, in fact, would cause most other bears to depart the falls when four or more were present at once.

The significance of fishing success

The biological significance of the differences in fishing success is difficult to evaluate. In years of salmon abundance, it is tempting to suggest that differences are inconsequential in terms of survival. Subadults, besides catching 0.6 fish per bear-hour in 1973, scavenged an equivalent of 0.4 fish per hour. Further, there is no a priori reason to assume that because it takes low-ranking bears longer to capture a given number of fish that their survival or fitness is significantly impaired. The capacity of bears to utilize alternate foods may in part buffer a scarcity of salmon. Finally, it should be noted that bears other than adult males and females with young generally caught more total fish because they fished for longer periods. Patchbutt, a low-ranking adolescent male, was the record-holder by catching 246 in 78 hours in 1973; at that rate, he probably caught in excess of 800 salmon at an average weight of 3 kg apiece during the course of the 1973 season.

The availability of protein-rich salmon may be quite important to adult females. Female physiological status presumably affects vigor of their newborn cubs (possibly even whether implantation occurs) and milk production during the prolonged nursing period. Females of cub-producing age may well be under continual pressure to increase food intake. Females that were accompanied by yearlings in 1972 and present as single adults in 1973 outranked and outfished these adult females that were
either nonproductive or which produced cubs infrequently. Goldie, OD, Hardass, and Lady Bird caught 343 salmon in 137 bear-hours (2.5 per hour) while Reggie, Red Collar, Jeanne, and Big Belly caught 407 fish in 211 bear-hours (1.9 per hour). Only one female, Spooky, appeared at McNeil Falls with cubs in 1973 after the poor salmon migration of 1972; at least two additional females were potential cub producers. In 1974, after the large migration of 1973, many females appeared with new cubs, including Red Collar last seen with young in 1968, and litters of three and four cubs were common (James Faro, personal communication). Substantive conclusions are inappropriate with a short-term study such as this, but the relationship between access to and abundance of salmon in relation to brown bear productivity merits further examination.

The relevance of the McNeil River fishery is undoubtedly related to the proximity of other salmon streams in the area. Although I am probably not aware of all streams, the Little Kamishak River roughly 10 km southwest of McNeil River is fairly important to commercial fishermen and perhaps to bears as well. Bears from McNeil River have been repeatedly observed fishing streams draining Kulik Lake about 70 km north-east of McNeil. I suspect a long-term study that considers all facets of brown bear ecology would be necessary before definitive statements regarding the importance of McNeil River and salmon in general to brown bears on the Alaska Peninsula are possible.

**Fishing success and bear social behavior**

Despite the steady decline in encounter intensity over time, there was no demonstrable improvement in bear fishing success as a result.
This is best shown by examining bear fishing success starting with day 11 and continuing through day 35 in 1972 (see Figure 6). Fishing success during these consecutive five 5-day periods was 1.1, 1.3, 1.0, 1.3, and 1.3 fish caught per bear-hour, respectively. Bear behavior during agonistic interactions was undergoing considerable modification in the meantime. In 1973, fishing success improved as salmon increased for about the first 20 days; fish by then were so abundant that variation in success as a consequence of behavior was impossible to detect. Although the number of fish apparently plummeted during days 21 to 25, sufficient salmon remained such that the decline had no measurable impact on bear fishing success until days 26 to 30 (compare Figures 3 and 6).

Another way of examining the extent to which moderation of encounter intensity over time might have affected fishing efficiency is to compare in successive periods total bear-hours spent at the falls with the amount of time spent actively fishing. The less time devoted to agonistic interactions should be reflected in a greater proportion of time spent fishing. Regardless of sex and age, bears spent a greater proportion of time actively fishing at the start and at the end of the seasons and the least time during mid-season. This occurred because there were fewer bears at the start and finish, and these had less contested access to fishing sites. During mid-season, when many bears were present, some inevitably were excluded from fishing sites altogether or sat by and waited for a favored site to be vacated. Even though agonistic encounters declined in intensity, the effect on fishing success was masked by the greater number of bears present contesting for a limited number of fishing locations.
Salmon abundance had a striking impact on bear social behavior.

Salmon abundance data and bear fishing success indicate little variation in salmon numbers throughout the 1972 season. Salmon were in short supply at all times, and competition between bears was keen. In 1973, however, fish were numerous practically from day 1. All elements of agonistic behavior were less prevalent than in 1972 (Table 11). Social play bouts and amicable encounters were common after days 16 to 20. Bears often stood side by side fishing at the same fishing site in 1973 with no outward sign of intolerance, and passive sharing of fish by unrelated animals was also common. Bears tried to steal fish others had caught more often in 1973 (231 attempts) than in 1972 (185 attempts), but more than twice as many salmon were caught in 1973. For every 100 fish caught, 15 steals were attempted in 1972 compared to 9 attempted steals per 100 caught in 1973. During days 21 to 30 in 1973, bears either shared their catch or relinquished it without reacting when others approached as they ate. Although impossible to quantify, many bears seemed to become so gluttoned with salmon in 1973 they were lethargic, which probably contributed to lessened hostility.

Variations in salmon abundance within the 1973 season affected bear behavior. The rate of salmon captured by bears dropped from 2.1 per bear-hour during days 26 to 30 to 1.0 per hour during days 31 to 35. Bears immediately became more aggressive. Nonagonistic encounters were halved in frequency. The abrupt decline in success resulted in the greatest number of fish-stealing attempts documented in a single 5-day period.
Table 11. Occurrence (percent) of aggression in bear agonistic encounters. Figures in parentheses are the number of observations of the indicated action.

<table>
<thead>
<tr>
<th>Form of behavior</th>
<th>1972</th>
<th>1973</th>
<th>P &lt;</th>
</tr>
</thead>
<tbody>
<tr>
<td>Jawing</td>
<td>25 (532)</td>
<td>16 (338)</td>
<td>0.001</td>
</tr>
<tr>
<td>Sparring</td>
<td>7 (157)</td>
<td>4 (84)</td>
<td>0.005</td>
</tr>
<tr>
<td>Charges</td>
<td>12 (258)</td>
<td>6 (139)</td>
<td>0.001</td>
</tr>
<tr>
<td>Fighting</td>
<td>4 (78)</td>
<td>2 (44)</td>
<td>0.005</td>
</tr>
</tbody>
</table>
Greater efficiency in catching salmon as a result of an implied increase in the stability of the bear social order was not apparent. However, it was clear that the reverse was true, that is, fishing success had a profound affect on bear social behavior. Satiation and a lack of competition created such tranquil conditions that professional wildlife photographers in attendance bemoaned the lack of action. As soon as salmon were in short supply, however, aggression abruptly increased.
A primary objective of this study was to determine how animals that are normally solitary adjusted to grouped conditions to exploit a localized, abundant source of food. One indication of such an adjustment would be a decrease in strife and improved efficiency in obtaining the resource. I found no indication that bears became more efficient at capturing salmon over time at McNeil River. Such may have occurred but was masked by variations in salmon abundance and the number of bears in attendance. Bears clearly were able to devote more time to fishing when few bears were present, with the greatest proportion of fishing time occurring at the beginning and end of the fishing seasons.

The occurrence of strife between bears decreased with time, but in subtle ways. Sparring bouts and fighting were rare always, with no variation by period. Bears moderated agonistic behavior by walking away from rivals as opposed to running. There was also an increasing tendency to not defer at all except when the interacting bears were significantly different in size or aggressiveness. My data also show that bears approached one another to closer distances in successive 5-day periods. Bears were forced closer together as the number of bears increased, so the progressively closer approaches during the first one-third of each season may have been an artifact. However, interacting bears continued to approach more closely after numbers had stabilized and even started to decline. The least intense form of overt threat -- jawing -- gradually increased in frequency paralleling the closer proximity of bears. I interpreted this as further evidence of
growing tolerance since sparring and fighting did not show similar increases. It should be emphasized that the greatest changes in social behavior occurred among adolescents and subadults. Adults were neither as wary initially nor did they accommodate to the same extent over time as young bears.

A number of behavioral ecologists have advanced the thesis that gregarious species have a greater array of social signals than solitary forms (Kleiman, 1967; Fox, 1970; Schaller, 1972), the idea being that signals reduce physical strife in the group. Kleiman and Eisenberg (1973) suggested that encounter context, identity of individuals, and resolving efficiency of signal receivers may be as important as signal variety and complexity. Brown bears clearly are capable of signaling intent, but this is supplemented by their perception of all strange bears as threats until proven otherwise. A large adult male like Charley Brown spawns terror, in part because of his size and perhaps also because he made infrequent visits to McNeil Falls and the residents had not had a reasonable opportunity to assess him.

Schenkel (1966) found that strife among African lions (Panthera leo) was inversely related to food availability. Kleiman and Eisenberg (1973) interpreted increased strife with less food among lions as meaning that communicatory mechanisms designed to minimize aggression within a pride worked only when food supplies were adequate. The degree to which brown bears adjusted behaviorally was likewise limited by the extent they were forced to compete for salmon. Strife among bears, as with the social lions, was strongly related to food availability, but excessive rather than merely adequate food may be necessary to reduce
aggression among bears. The transient nature of lessened strife in 1973 was indicated by an abrupt increase in bear aggressiveness when salmon were suddenly less abundant during days 31 to 35.

Food abundance was not the only factor moderating bear agonistic behavior, however. In 1972, bear behavior seemed governed largely by pragmatism. A bear rarely pressed an attack if its opponent stood its ground. All presented a vigorous defense if cornered or overtaken. A tactic employed by subadults and adolescents was to beat a retreat to a hillcrest and then turn to face their antagonists with the advantage of height. Young bears received the brunt of attacks, usually from larger bears. Young animals were most likely to run away when confronted, which usually invited pursuit, and they were also less able to present a strong defense against adults. Bears of equal size fought rarely, perhaps because each could inflict unacceptable damage to the other regardless of the "winner." Schaller (1972) noted that lions also concentrated their attacks on smaller victims.

The unusual concentration of brown bears at McNeil River presumably imposes costs in terms of psychological stress which bears must weigh in relation to the return in protein. At some point of declining salmon abundance, stress will cause some individuals to leave. A greater number of bears persisted for longer periods in 1973 than in 1972, because the returns in food were greater in 1973 and also because food surpluses contributed to reduced aggressiveness. Bears I considered most susceptible to social pressure, females with young and subadults, gave no clear indication that the proximity of other bears caused their exclusion from the falls or shortened their tenure there. Few subadults
were present in 1972, but this may have been due to a low representation in the population at large. Females with young were present mainly during mid-season, indicating they avoided the area when food returns were low, but this was generally true of bears in general.

Rogers (1976) noted that captive black bears provided ad lib food developed more rapidly and produced cubs earlier than wild bears even though the captives were housed with other bears that dominated them. Rausch (1961) also found that well-fed captives developed more rapidly than wild bears in Alaska. Rogers et al. (1976) reported that black bear females with access to garbage, where they were in frequent contact with other bears, had larger litters than females dependent on natural foods. In black bears, social stress appears minor in relation to nutritional considerations. My data and intuition suggest brown bears are no different from blacks in their tolerance of social stress, an indication of the great flexibility of bear social systems to allow exploitation of short-term but abundant sources of food.

However, there is considerable evidence that social factors have a direct impact of bear populations. Kemp (1976) found that removal (by shooting) of adult male black bears in 1971 and 1972 was followed by an increase in the total bear population from 80 to 175 by 1973. Selective removal of adult male brown bears by sport hunters on the Alaska Peninsula may have accounted for the growing brown bear population during the last 15 years. It is unknown if these population responses stem from a reduction in directly induced mortality or due to improved survival among younger cohorts as a result of decreased dispersal. Reports of cannibalism among brown and polar (U. maritimus) bears are
common, however (Troyer and Hensel, 1962; also see discussion on Bear Behavior, pages 243-254 in Bears - Their Biology and Management, IUCN Publications new series 23, 1972).

Social factors may also affect family units. Females retain their offspring for 2-1/2 years on the Alaska Peninsula. Roughly 1/3 of the females observed in Yellowstone National Park separated from their young after 1-1/2 years (Craighead and Craighead, 1967). An important difference may be the longer growing seasons in southerly regions that allow cubs to gain significantly more weight during their first summer. However, the lush environment of coastal Alaska may offset the brief growing season somewhat, and the longer retention of young may be related to population density. Precise figures are lacking, but bear density on the Alaska Peninsula is among the highest in North America. The advantages of prolonged protection afforded offspring by their mothers on the Peninsula may lead to greater overall fitness of the females than would the production of young every two rather than every three years.

The high population density on the Alaska Peninsula may also contribute to the prolonged association of siblings after they leave the females. There was no direct evidence that sibling associations materially benefited the animals at McNeil Falls. Such an association may, however, enhance detection of danger from other bears. Siblings also huddled together during times of stress as if physical contact provided psychological comfort.

Social relationships among bears at McNeil Falls did not fit easily into classical ideas regarding dominance hierarchies. With the excep-
tion of adult males, dominance relationships among many animals were ambivalent. Etkin (1964) suggested that partial or relative dominance, in contrast to absolute dominance that is typical of gregarious species, results when animals can not recognize one another as individuals. According to Etkin, partial dominance would have little effect as an organizing principle and probably would not lead to a diminution of conflict. I am satisfied that bears can recognize one another as individuals, although the evidence is anecdotal. Barash (1974) has shown that solitary raccoons (Procyon lotor) and red foxes (Vulpes fulva) can distinguish neighbors from strangers. Although individuals of a gregarious species may derive significant benefits despite low status (DeVore and Washburn, 1960; Altmann, 1962), no such advantage is conferred to an individual in a feeding aggregation. If the animal can not compete, then it obtains less food. Bears gave little indication of a tacit acceptance of status when competing for salmon except when differences in size and aggressiveness of rivals clearly made deferral appropriate.

Dominance relationships among brown bears may be more complex than my observations at McNeil Falls indicate. Subadults, besides being most easily intimidated, were also likely to harass another bear once they discovered they could do so. Subadults were observed following and periodically chasing others for no apparent reason. Such behavior was also observed among some adolescent females. Young bears were most likely to attempt harassment of people, whether by refusing to give ground, by following, or with bluff charges. It was an important point among our field personnel to never permit a younger bear to "dominate"
them lest we would be continually harassed by that animal from then on. These young bears apparently tested whatever they encountered, and presumably the consequences of such interactions had a bearing on their adult relations. Dominance relations among adults may be less ambivalent when the bears are normally distributed and a rich source of food is not a motivating factor.

Considering the ambiguity of bear social relationships at McNeil Falls, and the difficulty of meshing such relationships with traditional concepts of dominance hierarchies, the question of improved efficiency in capturing salmon as a result of stable relationships and lessened strife may be inappropriate. Dominance relationships between individuals were not resolved with repeated encounters as classical dominance theory predicted, and in fact reversals become more prevalent over time. There was no indication a reduction in agonistic encounter intensity bore any relationship to bear fishing success.

Carpenter and MacMillen (1976) proposed a model that indicated the social organization of a species (their example was nectarivorous birds) will vary with food abundance. Their model predicts that territoriality will occur when the costs (energy expenditure, risk of injury or predation) of maintaining a feeding territory are less than the resultant increase in food availability. When the costs of territoriality equal or exceed net returns in profitability, such as when food is scarce, territorial defense should cease. Conversely, if food is not limiting (i.e., is very abundant), territoriality should also cease since no additional energy gain is conferred.
To adapt Carpenter and MacMillen's model to the brown bear aggregation at McNeil Falls, the 20 fishing locations can be considered defensible areas akin to territories. My data are inadequate to evaluate the model from an energetic standpoint except by inference. However, bear behavioral changes should also be explicable based on the correlates of energetic profitability.

The model prediction that bears will actively defend fishing locations at an intermediate level of salmon abundance and be less likely to do so as salmon abundance increases is fully consonant with the data. Agonistic interactions were much more intense and frequent during the relatively poor salmon year of 1972 as opposed to 1973. In 1973, it was common for an individual to give up a fishing location without a contest. For example, single adult females "lost" 38 percent of their encounters with adolescent males in 1973, since a female would often simply vacate a location as an adolescent male moved in. In 1972, however, these same females were likely to defend a site, losing only 10 percent of their interactions with young males. As pointed out previously, an adolescent male, regardless of size, was no match for an adult female, and the young males' apparent rise in status relative to single adult females in 1973 mainly stemmed from the latter's tendency to passively defer to them. Even so, some individuals fished side by side at the same location, neither defending the site. Salmon were sometimes so numerous in 1973 that any of several locations yielded an excess of salmon (judging by the amount of fish discarded), making defense (or usurpation) of any one location unnecessary. In 1972, salmon were accessible only at a few locations and may have made defense
of such areas profitable on average for an occupying individual. An indication of the relative value between years of the best fishing locations is reflected in the proportion of time bears spent fishing at the 10 most productive locations, 86 percent in 1972 versus 76 percent in 1973. Reversals in apparent dominance relationships could be explained by changes in motivation to defend a site based on degree of satiation; a bear that has eaten may be less inclined to defend a fishing spot against an individual of similar rank that is hungry.

I cannot examine the model's prediction that bears will cease defending fishing locations when salmon are exceedingly rare. However, I have pointed out that more bears stayed for longer periods in 1973 as opposed to 1972, which suggests that the costs of defending (or usurping) sites exceeded net gains quicker during the earlier year.

Carpenter and MacMillen's model does not explain the decline in agonistic encounter intensity with time. However, in retrospect, it appears that bears may have habituated to the simple proximity of one another independently of any decline in actual competition for fishing locations. The presence of other bears becomes relevant to a fishing individual only if it was required to defend its fishing location. Whether or not defense of a site was appropriate depended on food abundance.
LITERATURE CITED


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