

**Paper 4**

## **The Social Behaviour of Brown Bears on an Alaskan Salmon Stream**

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### **INTRODUCTION**

Adult brown bears *Ursus arctos* are typically solitary. Subject to few, if any, of the evolutionary pressures (e.g. interspecific predation, food procurement) that favour formation of social groups (Eisenberg 1966; Kummer 1971; Estes 1974), brown bears retain a simple social system that is probably little advanced over that of primitive carnivores (Eisenberg 1966). Social affiliations between brown bears are restricted to family groups of a female and offspring and sibling litter mates that remain together for 1 to 3 years after separation from the female (Stonorov & Stokes 1972). Brief male-female consort relationships occur during the breeding season (Murie 1944; Hornocker 1962; Stonorov 1972).

Like other solitary carnivores, however, brown bears form loose aggregations to feed on carrion (Craighead & Craighead 1967; Cole 1972; Glenn 1973), in garbage dumps (Hornocker 1962; Craighead & Craighead 1967), and on salmon streams (Stonorov & Stokes 1972). Though feeding aggregations are transient and clearly distinct from social groups formed by truly gregarious species, many of the associated behavioural contingencies are similar.

A gathering of brown bears on a small portion of a salmon stream provided the chance to study the social behaviour of this little-known, elusive carnivore. The objectives of the study were to learn the behavioural characteristics of various brown bear sex and age classes, to quantitatively describe the dynamics of their social behaviour over a 40-day summer fishing season, and to determine social and environmental factors correlated with the frequency of different types of behaviour. We further hoped to make inferences about the overall social system of brown bears and to determine the way in which brown bear behaviour parallels or differs from the behaviour of gregarious carnivores. Some of our preliminary results are presented here.

### **STUDY AREA AND METHODS**

Stonorov & Stokes (1972) have previously described McNeil River State Game Sanctuary. The sanctuary is situated near the base of the Alaska Peninsula immediately north of Katmai National Monument. A series of rock slabs jut from the water about 0.8 km from the McNeil's mouth to form McNeil Falls. The width of the river is about 30 m at this point, and the rapids forming McNeil Falls extend for about 130 m. The falls impede the upstream movements of migrating salmon, mostly *Oncorhynchus keta*, and the bears gather during July and August to feed on the vulnerable fish. During the peak of the salmon migration, thirty or more bears may be present at one time; as many as 85 different bears have visited McNeil Falls in a single summer (Rausch 1958).

Data presented here were collected during the summers of 1972 and 1973.

Bears were observed daily from an observation post 8 m from the edge of the river near the upper terminus of McNeil Falls. Observation schedules were apportioned according to bear diurnal activity patterns. Most bears seemed unaffected by our presence, although large adult males avoided the falls when more than three or four people were present; a limited number of other bears would not cross to the near side of the river.

We defined an interaction (=encounter) as occurring when one or more bears responded overtly to the presence of another. We recorded all interactions observed. Records on each bear were kept on its time of arrival and departure from the falls, amount of time spent actively fishing, location of fishing effort, the time each salmon was caught, its behaviour during encounters, and the identity and responses of bears it encountered.

Individual bears were identified by ear tags, distinctive scars, claw color and other distinguishing features. Thirty-seven percent of the bears observed had been captured by biologists of the Alaska Department of Fish and Game and were of known age. Bears of unknown age were classified by their size relative to known-age animals. The sex of untagged bears was determined by the direct observation of sexual organs, urination patterns or by the presence of young.

### **POPULATION COMPOSITION**

The composition of the bear population at McNeil Falls for 1971 to 1973 is listed in Table 1. Fully-mature adult males were characterized by massive bone structure and conspicuously large size (350 kg or more) in relation to adult females. Bears classed as adult females were of known age or had, with four exceptions, been observed with cubs or yearlings; the size and behaviour of the other four indicated they also were fully mature. Subadults were 2½ or 3½ years of age, ranging in estimated size from 75 to 120 kg. Males and females are technically sexually mature by 4½ years of age (Erickson *et al.* 1968; Glenn 1973), but females continue to grow for 2 to 3 additional years and males may not attain full size before age 10 or 11 (Glenn 1973). For this reason, males from 4½ to 8½ years of age and females 4½ to 5½ were classified separately as adolescents.

### **SEASONAL AND DIURNAL BROWN BEAR ACTIVITY PATTERNS**

The seasonal abundance of brown bears at McNeil Falls for the 1972 and 1973 seasons is shown in Fig. 1. Salmon were observed at McNeil Falls during the first week of July each year, but the arrival of bears was variable, ranging from 8 July 1973 to 25 July 1971 (Stonorov 1972, unpublished report).

The reasons for the disparate arrival times for bears are not clear. It may be related to water levels at the falls, with high water making the salmon less accessible and delaying the onset of fishing. Bears also graze sedge extensively during June and into July, but only until the plants mature and presumably become less palatable. Phenologically 'late' years, as 1971, delay sedge growth. In 'early' years the sedge matures at a faster rate (early July in 1972 and 1973), perhaps forcing bears to turn elsewhere earlier for alternative sources of food.

Bears that were present in previous years were generally the first to arrive at McNeil Falls each fishing season. Sixty-one percent arrived during the

TABLE 1. POPULATION COMPOSITION OF McNEIL RIVER BROWN BEARS, 1971 to 1973

	Males	Females	Females with young	Number of cubs	Number of yearlings	Subadults <sup>e</sup> (2.5 to 3.5 yrs)	Unclassed (125 kg)	Total
1971	7 <sup>a</sup>	9 <sup>c</sup>	12	14	6	13	6	76
	7 <sup>b</sup>	2 <sup>d</sup>	12	14	6	13	6	
1972	11 <sup>a</sup>	11 <sup>c</sup>	9	9	9	3	4	66
	7 <sup>b</sup>	3 <sup>d</sup>	9	9	9	3	4	
1973	7 <sup>a</sup>	11 <sup>c</sup>	5	6	3	10	5	66
	14 <sup>b</sup>	5 <sup>d</sup>	5	6	3	10	5	
Mean	17.7	13.7	8.7	9.7	6.0	8.7	5.0	69.5
percent	26	20	12	14	9	12	7	100

<sup>a</sup>Adult males, 350 kg or more.

<sup>b</sup>Adolescent males 4.5 to 8.5 years old, less than 275 kg.

<sup>c</sup>Adult females, 175 kg or more.

<sup>d</sup>Adolescent females 4.5 to 5.5 years old, less than 140 kg.

<sup>e</sup>Both sexes, 2.5 to 3.5 years old, 75 to 125 kg.

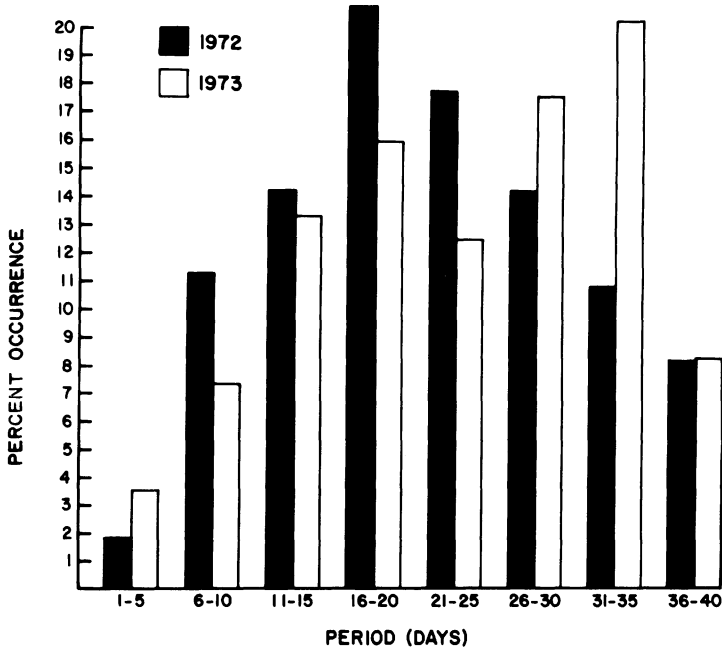


Fig. 1 Seasonal abundance of brown bears at McNeil Falls, 1972 and 1973. Days are numbered consecutively from the first day (Day 1) bears were fishing each year.

first 15 days following the onset of fishing. Twenty-seven percent were present for 30 days or more, 47 percent were present for at least half the season, and about 9 percent stayed for 5 days or less. In general, adult females and adolescent males and females persisted the longest.

Bears were active at McNeil Falls at all hours of the day. The level of activity was lowest during the early and mid-morning hours, steadily increased to a peak at 1800 to 1900 hours, and then declined again. Activity dropped sharply between 2200 and 2300 hours. No more than three bears were present at once from midnight to 0600 hours during our two overnight observations in 1972 (Days 11 and 28). These data were corroborated by time-lapse photographic records obtained during the first 13 days bears were fishing in 1972.

#### **FREQUENCY AND FORM OF BROWN BEAR ENCOUNTERS**

Brown bear interactions consisted of behavioural components variably and unpredictably sequenced. For purposes of analysis, we have simplified interactions into seven generalized forms: (1) head-low threat (low intensity); (2) head-high threat (high intensity); (3) charges; (4) contact or fighting; (5) approach-avoid; and (6 & 7) two forms of non-agonistic interactions (see below). Charges, threat, and fighting often occurred in combinations during a single encounter. Fighting, for example, was usually associated with threat, but since threat and charges did not always culminate in fighting, we arbitrarily treated each separately here. The characterizations omit for the most part the subtle aspects of brown bear social behaviour concerning head and body positions, facial expressions, and sequencing of behavioural components.

*Head-low Threat* involved variable body orientations toward the opponent. The head was held below the horizontal line of the body, ears were laid back flat against the head, and low monotone roaring accompanied a slowly opening and closing mouth. Distances separating interacting bears were generally less than 4 m.

*Head-high Threat* occurred at close range. One or, most often, both bears extended their heads diagonally upward toward the opponent. Their mouths were continuously open giving the impression they were about to interlock jaws. Body orientations were frontal. Body weight was shifted to the hind-quarters, presumably to free the forelimbs for striking or fending off the opponent. Loud roaring was continuous, changing in volume and amplitude with sudden head movements. Bears were typically less than 0.2 m apart.

*Charges* occurred in a variety of forms. 'Direct' charges were hard, fast rushes at an opponent. The charging animal's gaze was fixed on the receiving bear, and its head was held slightly below normal. The ears were erect initially and oriented toward the other bear but were laid back flat as it closed or when the receiving bear began to flee. Low growls at the start of the rush gradually increased in volume to a loud roar. 'Short' charges appeared identical to the initial phases of direct charges except that the rushes were terminated after three or four strides. A third form, seeming to involve a combination of threat and avoidance (ambivalence), was characterized by a series of exaggerated rocking and hopping movements toward an opponent.

*Contact* consisted of striking an opponent with one or both forepaws occasionally coupled with biting. Striking was oriented to the opponent's chest and shoulder region, and most biting was directed to the head and neck.

The most common agonistic interaction consisted of a simple avoidance of an in situ bear or the withdrawal of one animal at another's approach. Head and ear positions were variable. Direct gazes at an opponent were generally associated with lowered heads and erect ears, but as avoiding bears moved away or circled, heads were raised slightly, and the ears were alternately erect, compressed, or at various intermediate positions.

Non-agonistic encounters were classified into two broad categories. Brief interactions in which two or more bears pawed, mouthed, rubbed, or otherwise lightly contacted each other in the head and neck regions and which involved no elements of agonistic behaviour, were termed 'amicable' after Ewer (1968). Prolonged interactions involving mock fighting and, more rarely, sexual mounting, were labelled 'play'. Exaggerated head movements, restrained striking and biting, and a lack of loud growling distinguished play from serious fighting.

The balance of bear encounters consisted of little more than glances toward each other accompanied usually by slight shifts in body orientation, alternately erect or lowered ears, and an occasional lowering of the head. In some instances bears moved past each other at close range (2 m or less) without either making an observable response.

The occurrence of the above forms of social behaviour varied with the sex, age and size, and reproductive status of bears (Table 2). In general, combat and both forms of threat were most likely to occur in interactions between bears of roughly similar social status and within the same sex and age class. Overt fighting was usually momentary, and we never directly observed the infliction of serious wounds.

The low frequency of aggressive behaviour recorded for interactions that involved large adult males is misleading. They were widely avoided by bears

TABLE 2. PERCENT OCCURRENCE OF SIX BEHAVIOUR CATEGORIES IN BROWN BEAR SOCIAL INTERACTIONS AT McNEIL FALLS, 1972-73.

	Head-low threat		Head-high threat		Charge		Contact		Play		'Amicable'	
	1972	1973	1972	1973	1972	1973	1972	1973	1972	1973	1972	1973
Adult males	11.5	4.2	5.6	1.1	6.3	2.9	2.2	1.1	0.0	0.0	0.0	0.0
Adult females	22.8	16.4	8.0	3.8	7.0	4.0	3.0	1.3	0.0	0.0	0.0	1.5
Females with young	36.1	27.0	13.6	6.5	17.2	13.5	6.2	5.7	0.0	0.0	0.0	0.0
Adolescent males	20.8	12.6	6.7	3.4	2.7	1.3	4.6	0.9	0.0	7.3	0.0	9.0
Adolescent females	29.2	13.8	7.8	2.5	4.0	2.5	4.6	1.0	0.0	5.4	0.0	6.9
Subadults	0.0	0.9	4.2	0.5	0.0	0.0	0.0	0.5	0.0	0.9	0.0	2.8
Mean	23.4	13.2	8.0	3.3	6.6	2.8	4.0	1.3	0.0	4.0	0.0	5.4

of other sex and age classes, and four or more present at once caused most other bears to leave the area of the falls. Males were most active at McNeil Falls in late evening, and the abrupt drop in activity of bears between 2200 and 2300 hours seemed to correspond with their arrival. Though overt aggression between males was rarely observed, most of them bore scars and battered ears. Males were much more irascible toward other bears, and especially other males, when they were consorting with or trailing females in oestrus. The alpha male, Number 22, attacked and dislodged a subordinate male copulating with a female in 1973. Fresh and partially-eaten remains of a 2½-year-old subadult were found on 22 July 1973, and autopsy showed it had been killed by another bear (James Faro pers. comm.); this occurred at a time when at least four large males were variously consorting with five oestrous females.

Females with young (cubs or yearlings or, in one instance, a 2½-year-old) were highly intolerant of other bears and were the only individuals to consistently challenge adult males. Forty-two percent (10 of 24) of the head-high threat and 50 percent (5 of 10) of the overt fighting interactions that large males engaged in were with females accompanied by young. Unless the males pressed them, the females usually retreated, but often they seemed ambivalent, repeatedly rushing toward the males and then running away. Females with young were most tolerant of single adult females, but they were particularly irascible toward adolescent males and, to a lesser extent, adolescent females. On three occasions their yearlings independently rushed an adolescent male and two subadults.

As Hornocker (1962) reported, single adult females were more tolerant of other bears than were females with young. Yet tolerance varied greatly between different individuals; females that were highly aggressive when single were especially so when they had cubs or yearlings. Older females, in excess of 10 to 12 years of age, seemed more aggressive than younger females, but the differences could have been due merely to individual variation. Excluding those in oestrus, single females were generally wary of adult males, but their responses to them varied. Two aggressive females regularly fished side-by-side with a few of the large males. In 1972, a 22-year-old female regularly approached and occasionally supplanted two of the lower-ranking males.

Adolescent males, ranging in age from 4½ to 8½ years, were the least aggressive of all sex and age groups. Two males (4½ and 5½ years old, respectively) were never seen initiating an aggressive encounter. These animals would slide in beside other bears without attempting to displace them by threats. An indication of the overall tolerance of adolescent males for one another occurred in 1973, when two males walking side by side approached an oestrous female and 'tested' her simultaneously. Seventeen percent (70 of 411) of the intra-class interactions between adolescent males and 11 percent (17 of 154) of the interactions between adolescent males and adolescent females were non-agonistic in 1973. Adolescent males initiated fewer charges than any sex and age group other than subadults. The two oldest adolescent males, each 8½ in 1973, were the most aggressive of the class.

The behaviour of adolescent females was not appreciably different from single adult females. They were less tolerant of other bears than were adolescent males. As with the other sex and age classes, there were wide differences in aggressiveness between individuals. Two 4½-year-olds seemed extremely timid and were little different behaviourally from subadults. Two sibling females, still associating closely and travelling as a unit at 5½ years of age, were moderately aggressive, particularly toward adolescent males. Adolescent females were distinguished, however, by participating in a relatively high

frequency of non-agonistic encounters in 1973, though not to the same extent as adolescent males. None of the adolescent females to our knowledge had ever been in breeding condition.

Subadults were in few encounters involving overt aggression mainly because they usually gave other bears wide berth. Subadults were occasionally chased by some adolescents and other subadults, but it is doubtful that these posed a serious threat. Their wariness for other bears in general, however, coupled with the mortality record described above, indicate that other bears on occasion do pose a serious threat to subadults. In general, subadults patrolled the periphery of McNeil Falls scavenging for salmon scraps; occasionally during morning and midday they occupied fishing sites when few other bears were present. One 3½-year-old female was unusually large, and behaviourally she resembled an adolescent female rather than a typical subadult.

Overall levels of aggression were considerably lower in 1973 compared to 1972 (Table 2). There were fewer females with young during the 1973 season, with only two staying at the falls for a significant period. More important, however, was the much larger salmon run of 1973. Index figures and the average number of salmon bears caught per hour (1.04 in 1972, 2.06 in 1973) indicated roughly twice as many fish entered McNeil River in 1973. Consequently, there was less competition for lucrative fishing sites since almost any spot in the falls would yield salmon. Moreover, the bears were simply less aggressive, at times to the point of appearing lethargic. Whereas in 1972 it was extremely rare to see an animal not react agonistically to the close approach of another, it was commonplace in 1973. Altogether there was an approximate twofold decrease in the proportion of interactions that involved elements of aggression from one year to the next.

Also associated with the abundance of salmon in 1973 was a higher incidence of non-agonistic encounters, especially among and within the adolescent and subadult classes (Table 2 and Fig. 2). Fully-mature adult males and females



Fig. 2 Adolescent brown bear males (4.5 and 5.5 years old) playing, McNeil Falls, 1973.



that had produced cubs at least once were not observed playing; single adult females engaged in a limited number of 'amicable' encounters, usually with adolescent males.

### BEHAVIOURAL CHANGES WITHIN EACH FISHING SEASON

The social behaviour of brown bears during the first days of each fishing season appeared no different qualitatively from encounters observed in other contexts (e.g. as bears grazed in tidal sedge meadows). Interactions usually were limited to long-range avoidance, and bears generally seemed extremely wary, even to the extent that two interacting animals might flee each other simultaneously. Indiscriminate avoidance and flight were most characteristic of subadults and adolescents. Adult females initially ran from adolescent males, however, and on one occasion a fully-mature adult male fled from a much smaller adolescent male. Overt fighting, never common, was seldom observed during this period since bears did not often approach one another to short range.

The tendency of young bears to flee indiscriminately often seemed to invite pursuit. Many so-called 'charges' developed only after one of the animals had begun running. Other chases were initiated when animals made brief, tentative rushes (characterized by a few exaggerated hops, elevated heads and erect ears, and a slightly gaping mouth) toward potential rivals; the receiving animals usually fled and chases ensued. If chases were prolonged, fleeing bears eventually turned to face the pursuers. Pursued animals tended to stop on a crest or promontory to confront the pursuers. The latter stopped 1 to 2 metres short, and most soon backed away. Striking and biting in these circumstances were initiated by bears that had been chased.

The rate of agonistic encounters did not vary from period to period. Bears moving to and from fishing locations invariably precipitated encounters with others already occupying sites. Many encounters were the result of direct competition for specific fishing locations. Thus, the number of agonistic interactions was strongly correlated with the number of bears present in successive 5-day periods ( $R^2=0.92$  for 1972, 0.92 for 1973). Encounter rates during the first 5 days, however, were the lowest recorded for each year (0.44 per hour in 1972, 0.80 in 1973). The few bears present at the start of the fishing season avoided one another by dispersing widely over the falls. Encounter rates in subsequent periods varied from 1.49 to 2.37 per hour.

The frequency of different forms of brown bear interactions changed with successive 5-day periods, corroborating the results of Stonorov and Stokes (1972). Fleeing and chasing declined rapidly during the first 10 days. All bears, including some of the small subadults, began gradually reciprocating threats. Subordinate animals continued to defer to larger bears but did so to an increasing extent by walking away rather than running. Bears also progressively approached one another to closer range (Table 3), culminating with some individuals standing 2 m or less apart mid-way through the 40-day season. These animals were generally similar in size and, by definition (see below), roughly equal in social status. Bears in the youngest sex and age classes showed the most dramatic changes in behaviour. More subtle behavioural changes, mainly in the form of tolerance to the proximity of others, occurred in older sex and age classes. Females with young remained highly intolerant at all times, however, and most bears continued to give the large adult males wide berth.

TABLE 3. SEASONAL CHANGES IN MINIMUM DISTANCES (M) BETWEEN BEARS DURING SOCIAL INTERACTIONS AT McNEIL FALLS, 1972-73. DATA ARE EXPRESSED AS THE MEAN PLUS OR MINUS STANDARD ERROR. THE NUMBER OF OBSERVATIONS FOR EACH 5-DAY PERIOD ARE IN PARENTHESES.

Period (days)	1972	1973
1-5	13.8 ± 2.7 (14)	9.7 ± 0.6 (49)
6-10	8.0 ± 0.3 (267)	7.4 ± 0.3 (209)
11-15	5.8 ± 0.2 (264)	7.2 ± 0.2 (384)
16-20	5.3 ± 0.2 (296)	6.1 ± 0.2 (304)
21-25	5.8 ± 0.2 (424)	5.0 ± 0.2 (235)
26-30	5.1 ± 0.2 (388)	5.1 ± 0.2 (333)
31-35	5.0 ± 0.3 (207)	3.8 ± 0.1 (384)
36-40	6.0 ± 0.5 (64)	5.7 ± 0.3 (127)

While the frequency of head-low threat ('jawing', Stonorov and Stokes 1972) increased as the season progressed, the occurrence of head-high threat and fighting did not vary significantly from period to period (Figs. 3 & 4). The rise in mild threats was correlated directly with the tendency of bears to approach one another to shorter range; by so doing, the opportunities for head-low threats, and presumably for other forms of aggression as well, were enhanced.

That the more intense forms of aggression did not increase correspondingly suggested that (1) bears had habituated to the proximity of one another and (2) individuals learned to avoid approaching too closely bears likely to respond to them aggressively. 'Dominant' bears were much more likely to initiate encounters with subordinates than vice versa.

Tolerance among bears also varied within seasons in relation to fishing success much as it did between years. This relationship was most apparent during the last 15 days of the 1973 season. The number of salmon bears caught per hour decreased from an average of 2.1 during days 26 to 30 to 1.0 during days 31 to 35. Threat and striking and biting concomitantly increased during days 31 to 35 (Figs. 3 & 4), and the rate of non-agonistic interactions (amicable and play) between bears declined 74 percent. In the following period (days 36 to 40), salmon abundance again increased, and fishing success averaged 1.6 caught per hour. Threat and fighting declined sharply and non-agonistic encounters rose 70 percent.

### **SOCIAL DOMINANCE RELATIONSHIPS**

Not all agonistic interactions between bears gave clear indications of relative social status. For consistency, a bear was considered dominant when (1) the bear it encountered moved off by backing up, walking away or running away,

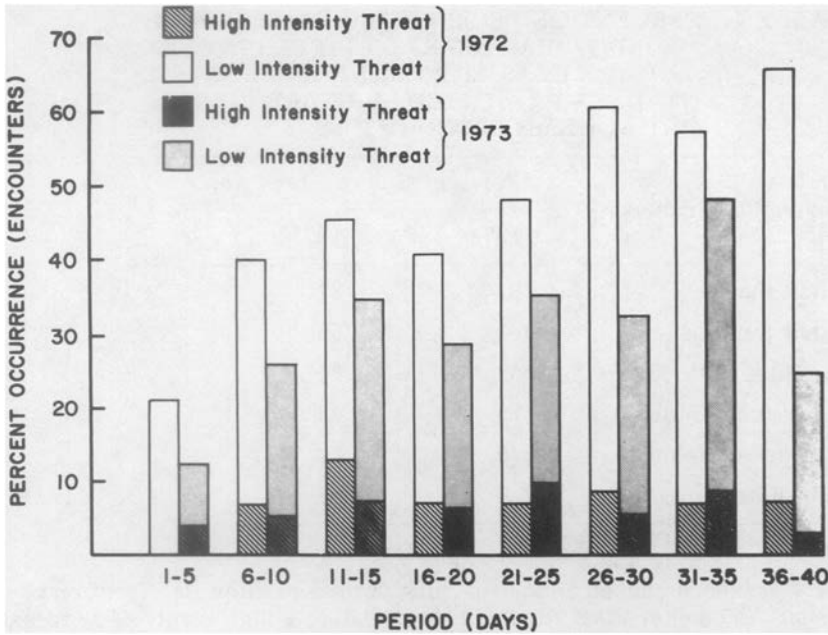


Fig. 3 Changes in the occurrence of two forms of threat in brown bear interactions over the 40-day fishing season at McNeil Falls, 1972 and 1973.

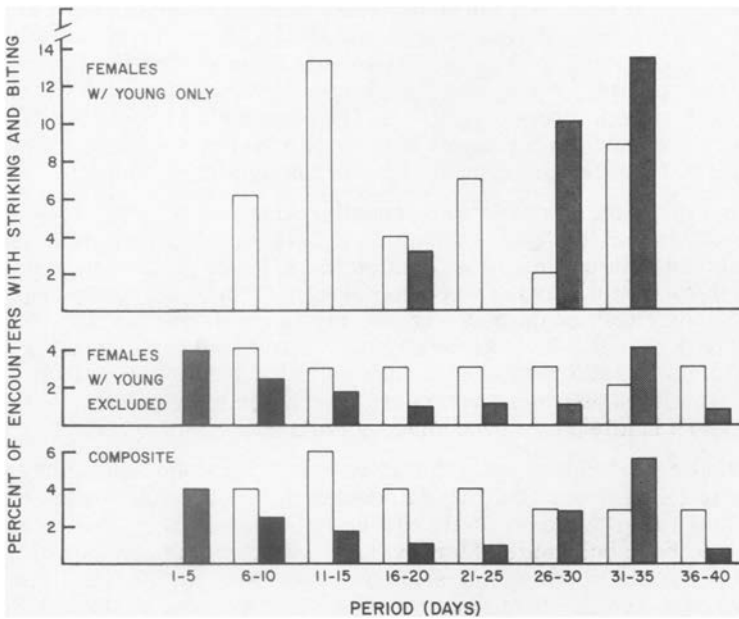


Fig. 4 Changes in the occurrence of contact (striking and biting) in brown bear interactions over the 40-day fishing season at McNeil Falls, 1972 and 1973.

TABLE 4. PERCENT OF DECISIVE ENCOUNTERS WON BY INDIVIDUAL BEARS OF DIFFERENT SEX AND AGE CLASSES AT McNEIL FALLS, 1972-73. DATA PRESENTED HERE ARE FOR INTRA-CLASS INTERACTIONS.

Sex and age class	Percent of encounters won	
	1972	1973
Adult males	91	97
Adult females	63	55
Females with young	82	84
Adolescent males	15	42
Adolescent females	30	27
Subadults	0	2

or (2) its presence caused an approaching animal to alter its direction of movement. Encounters that involved comparatively high levels of aggression, such as charges or striking and biting, were occasionally indecisive by these criteria but probably served to establish status relations between the two in subsequent encounters. A bear charged by another might defend itself in that instance but would later defer. The outcomes of decisive encounters between bears of different classes are shown in Table 4. Large adult males were unequivocally the most dominant animals. Most of their losses (19 of 35) were to females with young. Females with offspring deferred consistently only to large males, losing 34 of 53 encounters to them during the two years. Females with young were occasionally supplanted by single females (31 of 152). Adolescents of both sexes were generally subordinate to single females, but some of the older adolescent males and the two sibling females, acting in concert, occasionally were dominant over low-ranking single females.

Status relationships within classes were equally variable. Only the top-ranked male (Number 22) never 'lost' an encounter. A 22-year-old single female won 46 of 53 encounters with other single females in 1972. Reversals and triangular relationships within classes were common, and dominance between individuals in many cases could be assigned only in a relative fashion. Patterns of relative dominance have generally been attributed to an inability by interacting animals to recognize one another as individuals (Etkin 1964). Though likely true in cases where two bears interacted infrequently, there is no doubt that bears can learn to recognize individuals.

Hornocker (1962) reported that male grizzlies 'vied' for dominance, suggesting dominance in itself was a goal among adult males. The alpha male (Number 22) at McNeil River, however, seemed firmly entrenched and was never challenged by another adult male. Moreover, he was consistently intolerant of the general presence of other males. In one case, Number 22 left a fishing location to approach another large male that had just arrived at McNeil Falls and was standing about 40 m distant. Number 22 approached slowly, his lowered head held vertical to the ground, with his eyes and erect ears oriented in the other's direction. After closing to about 10 m, he charged and attacked, striking and biting the other male on the head and neck until it withdrew

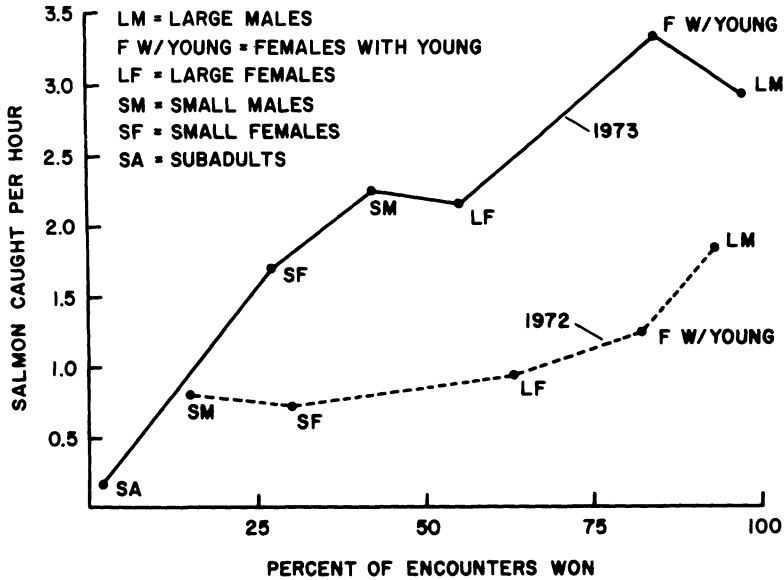


Fig. 5 Relationship between brown bear social dominance (percentage of decisive encounters won) and the rate of fishing success, McNeil Falls, 1972 and 1973.

running. On a separate occasion, the alpha male walked up to another adult male from behind and first knocked it to the ground and then into the river.

Lower-ranking males were considerably less aggressive toward one another, except that all were highly aggressive when associating with females in oestrus. Status relationships among five adult males, excluding Number 22, were triangular in 1972 but were linear in 1973. Male social rank in the latter year was, however, based on a total of only 19 encounters.

Status relationships among bears of different classes varied between years. Adolescent males 'won' 15 percent of their decisive encounters in 1972 but 42 percent in 1973. Whereas other animals (mainly single adult females and adolescent females) that engaged young males in 1972, generally reacted to them aggressively, the same animals a year later were more likely to defer. Consequently, adolescent males won a greater proportion of their encounters the latter year because other bears were simply less aggressive.

The main consequence of social status was that it determined when and where an individual bear could fish, and, in large measure, its rate of fishing success (Fig. 5). The impact of high social status on fishing success rates was most evident in 1972, when only a limited number of locations consistently yielded salmon. Socially-subordinate animals were largely excluded from these sites. Status was less a factor in 1973, because the abundant salmon could be taken at fishing sites that had, at best, been marginally productive the previous year.

For reasons presently unknown, all bears, regardless of age or status, captured salmon at a faster rate during mid-afternoon and evening. Whereas adolescent bears and subadults were present in roughly equal numbers throughout the day (0600 to 2200), bears in the adult sex and age classes, the most dominant animals, were most active during the most lucrative afternoon and evening period (1500-2200). Consequently, while subordinate bears occasionally

occupied profitable fishing locations during morning and mid-day, they were generally excluded from these sites by mid-afternoon.

### THE SOCIAL BEHAVIOUR OF A SOLITARY CARNIVORE

Recent comparative studies on the social behaviour of some species of Canidae indicate solitary forms have a smaller, less complex array of close-contact visual social signals than the gregarious species (Kleiman 1967; Fox 1970). These results suggested social species have evolved communication repertoires to minimize aggression among group members by the substitution of ritualized behaviour for actual fighting. Brown bears seem to fit this pattern in that being solitary they do not have a wide assortment of visual signals in comparison to other carnivores. 'Submission' postures, for example, are lacking; the nearest analogous behaviour in brown bears is similar (perhaps homologous) to the 'defensive threat' Leyhausen (1956) described for felids. Bears further lack the dramatic forms of 'weapons threat' (Geist 1971) typical of many other carnivore species (e.g. retraction of the lips to expose the canines). The small tail of bears precludes its value as a signaling device (Stonorov & Stokes 1972).

Yet despite retaining conservative patterns of social behaviour, most bears accommodated easily to conspecific proximity at McNeil Falls. The greatest changes in behaviour occurred among adolescents and sub-adults. Adults of both sexes were neither as wary at the onset of the fishing season nor did they habituate to the same extent as younger animals. Whereas non-agonistic relationships actually developed and persisted between some adolescent males, the behaviour of adults changed only by degree in that they tolerated closer proximity, with neither a concomitant increase in high-intensity threats nor actual fighting. Low-intensity aggression (head-low threats) by all bears gradually increased as distances declined and reflected an increasing unwillingness on the part of interacting bears to give way. Bears became progressively less likely to initiate encounters with animals that were appreciably higher in social status; in 1973, adolescent males initiated only 23 percent (24 of 103) of their encounters with the highly aggressive and more dominant females with young. While there was no group integration and coordination typical of social carnivores, and while individual relationships were flexible, the sum of these factors resulted in formation of a social organization that was relatively stable. The presumed relationship between the social organization of a species and complexity and quantity of close-contact social signals has been questioned by Kleiman & Eisenberg (1973). They suggest that information value of signals may be as important or more so than complexity or number, and that the context of an interaction may carry considerable information as well.

Intensity of brown bear aggression was strongly related to salmon abundance. Formation of a stable brown bear social system did not result in a more efficient exploitation of salmon, but rather salmon abundance determined in large part the degree of social stability. A decline in salmon numbers was reflected by an immediate increase in intolerance among the bears. There is evidence that lions (*Panthera leo*), a gregarious species, also show significant increases in aggression when food becomes scarce (Schaller 1972; Kleiman & Eisenberg 1973).

There is growing evidence that killing and cannibalism may be common among bears (Larsen *et al.* 1972). Bears responsible in eye-witness accounts

are generally described as large or are known to be adult males. The wariness most bears retain for large males at McNeil River indicates they are perceived as a serious threat. Bears in the young age classes and sows with young are most wary of males, but even oestrous females reflect this pattern, seeming more receptive to sexually-mature, but relatively small, adolescent males than to the big adults. Regulation of black bear populations is related to mortality in young age classes that is induced by adult males (Kemp, this volume, Paper 17). Circumstantial evidence suggests the same may be true for brown bears.

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