INTERSPECIFIC AND INTRASPECIFIC SOCIAL INTERACTIONS AMONG BROWN BEARS AND WOLVES IN AN ENCLOSURE

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Abstract: We investigated bear–bear, wolf–wolf, and bear–wolf interactions in a 2-ha enclosure, which was occupied by 13 brown bears (*Ursus arctos*) and a wolf (*Canis lupus*) pack. The hierarchy of bears and wolves was determined by behavioral observation and rank order analysis. All behavioral interactions between bears and wolves were systematically videotaped for 1 month and analyzed. Bears and wolves had a hierarchical organization similar to that found in nature, although we found a relatively low position in the rank order of blind bears. Social interactions between wolves appeared to be very serious at times. Bear–wolf interactions were mostly playful, but were sometimes agonistic. Young bears were more often victims of wolf harassment than other bears and were sometimes seriously bitten. However, no deaths were recorded, contrary to descriptions from natural bear–wolf interactions. We concluded that bears and wolves could be kept safely together in a single enclosure with apparently few consequences. Interactions we observed were comparable to interactions between bears and wolves under natural conditions and concerned mainly competition over food or a den (wolf or bear). The size of the food (large prey carcasses in the wild vs. chicken in the enclosure) probably plays a role in the severity and the eventual solution of the bear–wolf conflict.

Ursus 13:85–93 (2002)

Key words: bear–wolf interactions, brown bear, *Canis lupus*, enclosure, *Ursus arctos*, wolf

Bear research in enclosures has advantages and disadvantages over bear research in natural conditions. Disadvantages include the very small area, compared with natural home ranges, and the absence of escape possibilities. These factors can increase social stress even in animals kept in larger enclosures. Advantages of relatively large enclosures lie in the possibilities of intensive research concerning animal behavior, welfare, and health.

Bear behavior varies considerably among individuals (Fagen and Fagen 1996, Koene 1998). This can be demonstrated to the public in a bear enclosure and can be used to illustrate the individual distinctiveness and personality of bears (Fagen and Fagen 1996), together with their cognitive abilities. Thus, enclosures are important in public education. Furthermore, behavioral and veterinary research in enclosures can add to knowledge acquired in nature, as for example, testing radiotelemetry equipment in relation to activity. Also, the study of behavioral changes relative to environmental conditions can be related to the welfare of the animals; for example, a decrease in stereotypic behavior or an increase in play behavior may indicate a better relationship between a bear and its environment or increased well being (Koene 1998). In this paper we present an analysis of social interactions between brown bears and wolves, coexisting in the Bear Forest enclosure in the Ouwehand Zoo in Rhenen, the Netherlands.

We addressed the following questions in this paper: (1) How are bears and wolves socially organized in the 'Bear Forest' enclosure of the Ouwehand Zoo, in Rhenen, the Netherlands? (2) Do bears and wolves interact? (3) How does the behavior of bears and wolves in the enclosure compare to free-ranging animals? and (4) What are the management implications for similar situations in captivity?

STUDY AREA

Bear Forest, a refuge for bears, was created in the Ouwehand Zoo in Rhenen, the Netherlands, in 1993 by the International Bear Foundation (Koene 1998). The 2-ha area is enclosed by a 3.5-m high double fence (3 m apart) electrified on top with a 1-m electric fence inside the double fence. The area is bisected into northern and southern sections by a public walkway through the enclosure. Tunnels under the walkway connect the northern and southern sections. The refuge houses former zoo bears, circus bears, Turkish dancing bears, and bears from Bosnia relocated because of the war. In 1994, 3 wolves from Belgium and Germany were moved to the Bear Forest in Rhenen along with 7 wolves from the Ouwehand Zoo. Since then interspecific and intraspecific behavioral interactions among bears and wolves have been noted, but not systematically investigated.

Thirteen European brown bears (6 male:7 female) of different ages (range 3–23 years) resided in the enclosure (Table 1). Three of the bears were blind due to previous mistreatment. Years of birth were known for all bears except the blind bears and a veterinarian estimated their approximate age in 1993. We designated 3 age classes: young (0–4 years), adult (5–10 years) and old (>10 years of age). Bears were individually recognized by their posture, color, and facial details.

In addition to the 13 bears, 7 wolves lived in the enclosure at the time of observation (Table 1). Each wolf was distinguished by facial and body characteristics. All male animals except Cazar were castrated and all females were sterilized. The bears and wolves lived outdoors all year round; the bears had unimpeded access to 8 dens, while the wolves dug their own den. Normally the bears and wolves were fed 3 times daily at irregular hours. During the first feeding, only dog pellets were given. The second and third feeding consisted mainly of apples, bread, cabbage, and carrots for the bears and rats, chicken, ducks, fishes, or offal for the wolves. There were 2 feeding places, and the caretakers distributed the food from the walkway.

METHODS

Bear–bear Interactions

We observed bears at feeding times during 13–21 May 1997. Observations began 0.5 hr before and ended 1.5 hr after food was offered. We (2 observers) recorded agonistic encounters, which we defined as any situation where ≥2 bears interacted with each other in such a way as to disrupt their ongoing patterns of moving or feeding (Stonorov and Stokes 1972). A bear was labeled dominant (DOM) when it approached, charged, and maintained a frontal orientation to another bear. A bear was labeled subordinate (SUB) when it ran or walked away, backed up, and had a lateral orientation to another bear. We calculated 2 measures of rank order. The DS (dominance–subordinate) rank order was based on reordering the dominance–subordinate matrix (Martin and Bateson 1993) using the MatMan program (De Vries 1994). The DV-rank order was based on the individual dominance value (DV; Lehner 1996) of each animal (No. DOM encounters/total [No. DOM + No. SUB] encounters).

Table 1. Brown bears and wolves residing in the Bear Forest, Ouwehand Zoo, Rhenen, the Netherlands, for a behavioral study conducted in 1997.

Species	Name	Label	Sex	Age(yr)[a]	Age class
Bear	Battir	Ba	M	23	old
	Geert	Ge	M	22	old
	Koröglû	Ko	M	>10[b]	old
	Mackenzie	Mk	M	7	adult
	Bora	Bo	M	5-10[b]	adult
	Axel	Ax	M	4	young
	Nelly	Ne	F	23	old
	Fiona	Fi	F	5-10[b]	adult
	Mascha	Ma	F	8	adult
	Niki	Ni	F	5	adult
	Tory	To	F	4	young
	Wolke	Wo	F	4	young
	Bjorna	Bj	F	3	young
Wolf	Cazar	Ca	M	7	adult
	Traan	Tr	M	4	adult
	Streep	St	M	4	adult
	Poot	Po	M	4	adult
	Brenda	Br	F	4	adult
	Noeska	No	F	4	adult
	Sylvia	Sv	F	4	adult

[a] Wolves were not categorized by age class.
[b] Blind bear; age estimated by a veterinarian.

Wolf–wolf Interactions

We observed wolves during 3–28 February 1997. We normally observed from 0800–1700, Monday–Friday, using a Latin square design. Total observation time was 144 hrs. We collected data by behavior sampling (Martin and Bateson 1993) on a portable recorder with The Observer software (Noldus 1991). We distinguished 22 behavioral elements that occurred during social interactions based on the wolf sociogram from Zimen (1982). Actor, behavior, and receiver were recorded on tape. Active submission appeared to be the best indication of rank order according to our analysis and Van Hooff and Wensing (1987). Thus, we based rank order only on this behavioral element. Active submission is a behavioral complex in which the actor actively seeks contact with a recipient by approaching it in a crouched manner with curved back and bent legs, the tail curled down, often wagging, with ears folded back. From this position, the animal tries to contact the recipient by licking its nose (Van Hooff and Wensing 1987, Derix 1994). When constituent elements occurred separately, we recorded them as separate categories. We also calculated the same 2 measures of rank order for the wolves.

Bear–wolf Interactions

We observed bear–wolf interactions on 3–21 February 1997 around the feeding hours (1000–1400), when most interactions occurred (Koene 1998). We videotaped interactions when (1) a bear or wolf approached a member of the other species, or (2) bears or wolves started running without an apparent obvious trigger.

We recorded the following data from the videotaped sequences: date, time, and context (bear den, wolf den, food, unknown). Concerning the approach, we recorded the approacher (bear or wolf); name; sex and age of first, second, and third wolf and first, second, and third bear; distance from which approach started; behavior of approacher (approach, attack, bite, etc.); whether the approacher stopped or passed; and distance when the

approacher stopped or passed the approached. Concerning the short distance interaction, we recorded the number of bears and wolves participating in the interaction; actor (bear or wolf), behavior of the actor (same as approacher behavior); recipient (bear or wolf); behavior of the recipient (bear, wolf, unknown); distance between the participants of the interaction; and loser (bear or wolf). We collected some data from interactions in the wild for the same variables and compared the enclosure data with data from the wild. Data were analyzed with SAS 6.01 (1990).

RESULTS

Bear–bear Interactions

As a rule, agonistic interactions between bears occurred as soon as the caretaker offered food to the bears. Some animals gained access to the center of the feeding spot with the highest food concentration. Others had to wait or were even forced to stay entirely away from the place where all the food was thrown. As bears gradually left the feeding spot, the number of encounters decreased rapidly with time after feeding. Most encounters were without physical contact and occurred as follows: a dominant bear would appear and subordinate bears would back up or even run or walk away, turning the head away from the opponent; ears of both bears were back. If the subordinate bear did not back away, the dominant would usually charge it. In a charge the dominant bear ran, frontally oriented, directly toward the other with ears back and mouth slightly open. It was possible to distinguish the dominant and subordinate bears in most encounters. We recorded 419 agonistic encounters between the bears and determined the DS-rank order of the 13 bears (Table 2).

The DS-rank order yielded the following dominance hierarchy: (1) old males were highest in rank, followed by an adult male, (2) next an old female followed by an adult female, the oldest blind male, and the last adult female, and (3) finally the younger male and females, the old blind female, and the adult blind male.

Although the hierarchy did not differ between feeding spots, the amount of agonistic behavior of some individual bears differed significantly for the different feeding spots. For example, Geert, highest in DS-rank, was involved in more aggressive interactions with other bears at the place he occupied most than at other feeding places. Battir, second in DS-rank, was less involved in aggressive encounters in the home range of Geert.

Not all bears were present at all feeding places. For example, 1 adult blind male (Koröglû) did not walk through the tunnels and did not eat when food was offered at the other side of the tunnel. The old blind female sometimes continued her stereotypic behavior and did not eat.

Based on the dominance value, a somewhat different rank order was found (Table 2). Four groups could be distinguished based on the dominance-value: (1) Geert and Battir (DV 0.97 and 0.92, respectively), (2) Koröglû (blind), Mascha, Nelly, and Mackenzie (DV = 0.50–0.69), (3) Niki, Bora, and Fiona (both blind) and Axel (DV=0.14–0.41) and (4) Wolke, Bjorna, and Tory (DV = 0.01–0.05).

Wolf–wolf Interactions

The behavioral element associated with most observations of the total (415 of 1,491) was active submission. Brenda was the only female that copulated with Cazar; she was the alpha female. Noeska was the most active wolf in the pack, with 46% of the total submissive behaviors, of which 57% were directed toward Brenda and 39%

Table 2. Rank ordered dominant (DOM: rows) – subordinate (SUB: columns) matrix of 13 brown bears based upon agonistic interactions won and lost over food for a 1997 behavioral study in a 2-ha enclosure at Ouwehand Zoo, Rhenen, the Netherlands. A dash indicates that no encounters were observed between this pair of animals.

Label of dominant animal	Ge	Ba	Mk	Ne	Ma	Ko[a]	Ni	Ax	Fi[a]	Bo[a]	To	Wo	Bj	Total DOM	Age	DS–rank	DV	DV–rank
Ge		3	14	4	9	1	22	1	–	–	3	5	7	69	old	1	0.97	1
Ba	2		19	24	30	2	25	4	3	5	11	9	3	137	old	2	0.92	2
Mk	0	2		1	0	1	0	2	–	1	10	9	11	37	adult	3	0.50	6
Ne	0	1	1		2	1	–	2	–	3	5	10	11	36	old	4	0.55	5
Ma	0	4	1	0		–	2	8	1	3	17	14	16	66	adult	5	0.61	4
Ko[a]	0	0	1	–	–		0	2	–	–	4	1	3	11	old	6	0.69	3
Ni	0	2	1	0	0	0		3	2	2	16	4	5	35	adult	7	0.41	7
Ax	0	0	0	–	0	0	0		2	0	–	–	2	4	young	8	0.14	10
Fi[a]	–	0	–	0	0	–	1	0		1	–	–	–	2	old	9	0.20	9
Bo[a]	–	0	0	0	0	–	0	2	0		2	2	2	8	adult	10	0.33	8
To	0	0	0	0	0	0	0	–	–	1		–	–	1	young	11	0.01	13
Wo	0	0	0	0	0	0	1	–	–	0	–		2	3	young	12	0.05	11
Bj	0	0	0	0	1	0	0	0	–	0	–	0		1	young	13	0.02	12
Total SUB	2	12	37	29	42	5	51	24	8	16	68	54	62	419				

[a] Blind bear

toward Cazar. But she was also very aggressive to Sylvia. The majority of all dominant behaviors were directed toward Sylvia. The dominance–subordinate matrix based on active submission (Table 3) ranked the wolves (dominant to subordinate) as Cazar, Brenda, Poot, Traan, Streep, Noeska, and Sylvia.

We found a DV–rank order (Table 3) different from the DS–matrix for the males Poot and Traan. We distinguished 3 groups based on the dominance-value: (1) Cazar and Brenda (DV = 1.00 and 0.96, respectively), (2) Traan, Poot, and Streep (DV= 0.19–0.43), (3) Noeska and Sylvia (DV 0.07 and 0.00, respectively).

Bear–wolf Interactions

We recorded 19.5 hours of video including 79 bear–wolf interactions. The context of these interactions in the enclosure were as follows: interactions over food 19%, near wolf den 8%, near bear den 5%, and unknown 68%. In 70% of the interactions, only 1 bear was involved; 8% involved 2 bears, 3% involved 3 bears, and 1%, 4 bears. In 57% of the interactions only 1 wolf was involved; in 14%, 2 wolves; in 4%, 3 wolves; in 8%, 4 wolves; and in 18% >4 wolves. In 28%, the bears were the actors (initiating the interaction), and in 72% the wolves were the actors. Bears retreated in 23% of the encounters, wolves in 77% (Table 4).

When approaching another animal, bears and wolves stopped or passed in the expected frequency ($\chi^2 = 0.01$, $P = 0.92$). The animal that approached was usually also the actor in the interaction ($\chi^2 = 63.94$, $P = 0.001$). Wolves initiated more interactions than bears ($\chi^2 = 15.51$, $P = 0.001$), and wolves retreated more often than bears, as expected ($\chi^2 = 0.41$, $P = 0.52$).

Bear and wolf behavior during interactions was rather comparable (Table 5). Bears and wolves did not differ in behavior elements as approacher ($\chi^2 = 4.83$, 9 df, $P = 0.78$) or as an actor ($\chi^2 = 9.82$, 9 df, $P = 0.28$). As recipient, however, wolves avoided bears more often than expected ($\chi^2 = 21.52$, 9 df, $P = 0.011$).

Most bears that interacted with wolves were young bears (Table 6); Bjorna, a 3-year old female, accounted for 47% of all bear–wolf interactions. There was a significant relationship between DV-rank order and number of interactions ($r_s = 0.60$, $P = 0.039$, $n = 13$); the relationship was stronger in sighted bears ($r_s = 0.81$, $P = 0.016$, $n = 10$). In most cases the wolf or wolves involved in the interactions could not be identified (87%). Traan (9%) and Poot (3%), the subordinate males, were involved in most identified (recognized individuals) interactions, and Brenda, the alpha female, only once (1%).

Table 3. Rank ordered dominant (DOM: rows) – subordinate (SUB: columns) matrix of 7 adult wolves based on the behavioral element active submission for a 1997 behavioral study in a 2-ha enclosure at Ouwehand Zoo, Rhenen, the Netherlands.

Label of dominant animal	Ca	Br	Po	Tr	St	No	Sy	Total DOM	Age	DS–rank	DV	DV–rank
Ca		4	17	5	25	100	9	160	adult	1	1.00	1
Br	0		2	2	4	133	73	214	adult	2	0.96	2
Po	0	2		1	1	5	0	9	adult	3	0.32	4
Tr	0	2	0		0	2	2	6	adult	4	0.43	3
St	0	1	0	0		3	3	7	adult	5	0.19	5
No	0	0	0	0	0		19	19	adult	6	0.07	6
Sy	0	0	0	0	0	0		0	adult	7	0.00	7
Total SUB	0	9	19	8	30	243	106	415				

Table 4. Pathway representation of bear–wolf interactions[a] for a 1997 behavioral study of 13 brown bears and 7 wolves in a 2-ha enclosure at Ouwehand Zoo, Rhenen, the Netherlands.

Approacher	Pass or stop	Actor	Bear retreat	Wolf retreat
Bear	pass	bear	2	5
Bear	stop	bear	2	10
Bear	pass	wolf	0	0
Bear	stop	wolf	0	0
Wolf	pass	bear	0	1
Wolf	stop	bear	0	2
Wolf	pass	wolf	9	11
Wolf	stop	wolf	5	32
Total			18	61

[a] Protocol was started when a subject approached a subject of the other species after which the action of the approacher could be either stops or passes. The actor in the interaction could be either the approacher or the approached animal. Frequency of withdrawing by brown bears and wolves is presented dependent on the type of approacher, the action of the approacher near the approached (pass or stop), and the type of actor in the interaction.

Table 5. Behavioral elements shown by brown bears and wolves as approacher (app), actor (act), and recipient (rec), expressed as percentage of total number of interactions. Data from a 1997 behavioral study of 13 brown bears and 7 wolves in a 2-ha enclosure at Ouwehand Zoo, Rhenen, the Netherlands.

	Approacher		Actor		Recipient	
Behavior	bear	wolf	bear	wolf	bear	wolf
Approach	63	70	41	39	0	5
Attack	16	7	14	16	4	5
Bite	5	7	5	11	0	5
Chase	0	2	14	2	0	0
Defend	0	0	0	0	33	23
Look at	11	5	9	14	23	9
Avoid	0	0	0	0	2	27
Flee	0	0	0	0	21	18
Rob food	0	2	0	4	0	0
Sniff	0	2	0	2	2	0
Threat	0	5	5	11	9	0
Threat bite	5	2	14	4	7	9
Total number of interactions	19	60	22	57	57	22

DISCUSSION

Bear–bear Interactions

All bear species are primarily solitary in the wild, and individuals avoid each other if possible (Brown 1993). Bears that do associate are typically a mother and her cubs, siblings that recently left their mother, or male and female during the breeding season (Brown 1993). The best known example of a social grouping is when bears congregate temporarily on places where good food is abundant, such as garbage dumps and salmon (*Oncorhynchus* spp.) streams (Stonorov and Stokes 1972, Egbert and Stokes 1976). In this situation, bears develop a stable social structure to use resources as efficiently as possible without spending too much time fighting. Their repertoire of threatening behaviors enables them to keep distance without showing overt aggression. The Bear Forest, with its high food availability, compares well to the brown bears in Alaska studied by Stonorov and Stokes (1972). Weber (1988) reported that 252 of 478 (52%) bear–bear encounters at natural feeding places in Romania were aggressive. Unfortunately, no rank order was presented. Weber (1988) found the same repertoire in his bears as Stonorov and Stokes (1972) found, except for the behavior "jawing", which was not recorded in the Romanian bears.

We provoked agonistic interactions among the bears in the Bear Forest by offering all the food for a meal in one place instead of scattered around. The dominance hierarchy we found was based on the dominance–subordinate matrix and on the dominance value of each individual. Blind bears were ranked lower than expected on the basis of their age and sex. However, based on dominance-value, the blind female Fiona was the only one with a lower rank than expected based on her age and sex. Despite their handicap, the blind bears still dominated younger bears in the Bear Forest.

Literature on social structure in brown bears revealed the existence of temporary hierarchies in groups of bears on rich feeding places (Stonorov and Stokes 1972, Weber 1988). Large adult males were highest in rank, followed by females with cubs, adult males, and other females. Finally young bears deferred to all the other bears (Brown 1993). The hierarchy found in the Bear Forest was very similar to that in the wild under favorable food conditions. Furthermore, as in nature, agonistic interactions without physical contact were used to maintain this hierarchy, with strong bear–bear tolerance (Colmenares and Rivero 1983).

Wolf–wolf Interactions

Whereas in bears social grouping is an exception, in wolves it is expected. Therefore, dominance relationships are well established. It is nearly impossible to observe social relationships of a wolf pack in the wilderness, because wolves have home ranges between 50–1,000 km^2. As a result, nearly all studies of social relationships of wolves have been conducted on captive packs in large enclosures. The enclosure in Zimen's study (1982) of wolf pack sociogram was 6 ha. Mech (1970) used Isle Royale as a natural enclosure with an area of 54,400 ha. Van Hooff and Wensing (1987) described pack structure under captive conditions in a small enclosure (0.3 ha) and concluded that: (1) there are different rank orders for females and males, especially for the higher ranking members, (2) the sexual rank order is mainly structured according to age, with older animals generally dominant over younger animals; (3) the rank differences are larger in the higher ranks and lower between the lower ranking wolves; and (4) there is no cross-sex dominance relationship, as long as the wolves have the same rank level in their sexual rank order; if the rank levels are different and there are significant age differences, there are cross-sex dominance

Table 6. Brown bear–wolf interactions in relation to bear dominance in descending order, for a 1997 behavioral study of 13 brown bears and 7 wolves in a 2-ha enclosure at Ouwehand Zoo, Rhenen, the Netherlands.

Bear	Sex	Age	DS–rank	DV–rank	IA (No.)	IA (%)
Bj	female	young	13	12	39	49.4
Wo	female	young	12	11	4	5.0
To	female	young	11	13	4	5.0
Mk	male	adult	3	6	12	15.2
Ax	male	young	8	10	9	11.4
Ge	male	old	1	1	8	10.1
Ni	female	adult	7	7	1	1.3
Ma	female	adult	5	4	1	1.3
Ne	female	old	4	5	1	1.3
Ba	male	old	2	2	0	0
Ko[a]	male	old	6	3	0	0
Bo[a]	male	adult	10	8	0	0
Fi[a]	female	old	9	9	0	0
					79	100%

[a] Blind bear

relationships. The wolf dominance hierarchy is thus best described as a pyramid with the alpha male and female at the highest position, followed by the beta male and sometimes the beta female, then adult subordinate females and males.

In the Rhenen wolf pack, there were 4 especially active wolves: Cazar, Brenda, Noeska, and Sylvia. Cazar showed no submissive behavior, much dominant behavior, and was apparently the alpha male of the pack. He was also the only intact male in the pack (with testicles and thus hormonal activity). Cazar was the only wolf observed copulating with a female (Brenda, the alpha female). There was a clear linear hierarchy within the females of the pack: Brenda, Noeska, and Sylvia. The relationships among the wolves were sometimes very aggressive and led to injuries, especially for Sylvia, the lowest in rank.

Only 6% of all interactions occurred in the non-alpha males Traan, Streep, and Poot. It was difficult to rank these wolves based on a small number of interactions. Poot and Streep showed more submissive behaviors than Traan; Traan could be the beta male and the others the adult subdominants. This agrees with the dominance rank from the dominance-value (DV). On the other hand, Landau's index of linearity (Lehner 1996) for the pack was 0.77, indicating no clear linear hierarchy (a linearity index of 0.9 is considered as indicative of a linear hierarchy).

Comparison of our results with the hierarchy of a free-ranging wolf pack is difficult. In the Rhenen wolf pack, the social interactions seemed to be more aggressive and more concentrated on only some individuals than in a free-ranging wolf pack. Mech (1999) emphasized that free-living wolf packs are family groups in which dominance displays are uncommon except during competition for food. He suggested that active submission is primarily a food-begging gesture and not primarily an indicator of a dominance relationship. At the beginning of each breeding season, Brenda, the alpha female, severely injured Sylvia by biting her in the back near the tail, causing deep open wounds. In the wild, biting will not occur because low ranked females leave the group before the breeding season (Mech 1999). In captivity there is no possibility to leave the area and to avoid the alpha female. We speculate that in the wild, Sylvia probably would have left the pack to avoid being attacked by Brenda and Noeska. Traan, Streep, and Poot would have been more socially active if they had retained their natural hormonal level. No sexually related behavior was observed in these 3 animals. Although the hierarchy appeared to be somewhat normal for wolves, it seemed to be restricted by the non-intact males and the restrictions of the enclosure.

Bear–wolf interactions

Magoun (1976) observed bears and wolves near a carcass simultaneously in the wild, and during 173 5-min periods she recorded 39 aggressive acts by the bears toward wolves and only 1 aggressive act by a wolf toward a bear. Unfortunately, the behavior is not described in detail; most aggressive acts of bears involved a short lunge or swipe, although sometimes a bear chased a wolf. Murie (1981) also described wolves as the losers in bear–wolf interactions, but others observed the opposite (see Mech 1970, Brown 1993). In Nelchina Basin, brown bears contested wolves in 13.1% of 130 observations of wolves on kills (Ballard 1982; Table 7).

A more recent description of interactions showed that wolves attack bears fiercely, especially when bears are near the wolves' den (Kehoe 1995). Wolves mainly initiated the bear–wolf interactions in the Bear Forest. Wolves also retreated the most from interactions and were therefore the probable losers. The interactions were sometimes related to fights concerning the bear den, wolf den, or food. However, most interactions (68%) were still of an unknown origin. Bears and wolves showed approach behavior as actors and defensive or flee behavior as recipients.

The wolves did not often harass the blind bears. Only one video showed interactions between Bora and wolves and Koröglû and wolves. The first confrontation between the blind bears and the wolves was described earlier, "all blind bears were at least once attacked by the group of wolves, but the bears did not react and the attack stopped" (Koene 1998: 582). A possible explanation is that the interactions were mostly play motivated and that the blind bears reacted inadequately to the wolf behavioral initiative.

Comparison between the bear–wolf interactions in the enclosure and interactions in the wild is rather complicated. Bears do not normally conflict with wolves. Wolves cannot win an aggressive encounter with an adult bear. Still wolves often kill bears, but only when the bear is rather young, ill, or trapped in the den. In North America, cases of bears as victims of wolves have been reported, but also the reverse is found. We made an attempt to evaluate bear–wolf interactions as reported in the available literature (Table 7).

Based on the data collected in the Bear Forest and the data extracted from the literature (Table 8), we made some general comparisons. Contrary to expectation, interactions in the Bear Forest were more of unknown origin than in the wild ($\chi^2 = 37.14$, 4 df, $P = 0.001$). Wolves and bears in the Bear Forest began interactions in the same proportion as in the wild ($\chi^2 = 1.31$, $P = 0.25$). Losers of the interactions in the wild were wolves in fewer cases than expected ($\chi^2 = 47.24$, 3 df, $P = 0.001$), but wolves were more often the losers in the Bear Forest.

Conditions of the Bear Forest may explain these dis-

Table 7. Literature review of bear–wolf interactions recorded in the wild.

Actor	Behavior	Loser	Bears (No.)	Wolves (No.)	Bear species	Source
wolf	chase	bear	1	5	brown	Mills 1919
bear	kill	wolf	1	5	brown	Mills 1919
bear	attack	unknown	4	5	brown	Murie 1944
wolf	attack	unknown	4	5	brown	Murie 1944
wolf	attack	bear	1	5	brown	Murie 1944
bear	approach	unknown	3	2	brown	Murie 1944
bear	eat	unknown	1	1	brown	Lent 1964
wolf	eat	unknown	1	1	brown	Lent 1964
wolf	eat	bear	1	5	brown	Pulliainen 1965
bear	kill	wolf	1	4	black	Joslin 1966
bear	attack	unknown	1	5	black	Rutter and Pimlot 1968
wolf	kill	bear	1	5	black	Rutter and Pimlot 1968
wolf	kill	bear	1	5	brown	trapper (in Mech) 1970
bear	kill	wolf	?	1	brown	Ballard 1980
bear	attack	wolf	1	5	brown	Herning (in Murie) 1981
bear	attack	wolf	4	5	brown	Murie 1981
bear	attack	wolf	4	5	brown	Murie 1981
bear	attack	none	1	1	brown	Murie 1981
bear	attack	none	1	1	brown	Murie 1981
bear	attack	wolf	3	1	brown	Murie 1981
wolf	attack	bear	1	12	brown	Murie 1981
bear	chase	wolf	1	1	black	Rogers and Mech 1981
bear	chase	wolf	>3	1	black	Rogers and Mech 1981
bear	chase	wolf	1	1	black	Rogers and Mech 1981
wolf	eat	bear	>3	9	black	Rogers and Mech 1981
bear	chase	wolf	4	2	brown	Ballard 1982
wolf	chase	bear	4	2	brown	Ballard 1982
bear	displace?	wolf	1	1	brown	Ballard 1982
wolf	chase?	bear	2	3	brown	Ballard 1982
wolf	displace	unknown	1	4	brown	Ballard 1982
wolf	kill	bear	1	2	brown	Ballard 1982
wolf	displace	unknown	1	1	brown	Ballard 1982
wolf	displace	unknown	1	3	brown	Ballard 1982
wolf	displace	unknown	1	4	brown	Ballard 1982
wolf	kill	bear	?	1	black	Horejsi et al. 1984
wolf	eat	bear	3	2	polar	Ramsay and Stirling 1984
bear	eat	wolf	1	4	brown	Hornbeck and Horejsi 1986
wolf	kill	bear	1	10?	black	Paquet and Carbyn 1986
wolf	kill	bear	1	2	black	Paquet and Carbyn 1986
wolf	kill	bear	1	5	black	Paquet and Carbyn 1986
bear	approach	unknown	3	1	brown	Hayes and Mossop 1987
bear	kill	wolf	1	3	brown	Hayes and Baer 1992
wolf	attack	unknown	1	3	black	Gehring 1993
wolf	attack	unknown	1	1	black	Veitch et al. 1993
wolf	attack	unknown	2	5	brown	Kehoe 1995
wolf	approach	bear+cubs	3	1	brown	Koene[a] 1995
wolf	chase	bear	1	2	brown	Follmann[b] 1997
wolf	attack	wolf	4	1	brown	James[b] 1997
wolf	stand	unknown	1	1	brown	Mago[b] 1997
bear	chase	unknown	1	1	brown	Reynolds[b] 1997
wolf	chase	unknown	1	1	brown	Reynolds[b] 1997
wolf	attack	bear	1	1	brown	Stephenson[b] 1997

[a] Koene, personal observation. During the excursion of the Tenth IBA (International Bear Association) conference in Fairbanks, Alaska, 1995, a wolf coming from a long distance encountered a grizzly bear mother with 2 cubs. The cubs were directed higher up hill, while the mother stood on her hind legs. The wolf stopped and made a half circle around the bear and her cubs and continued on its way. Immediately thereafter, the cubs ran toward the mother (as if they had been called) and the mother bear suckled them for a short while (as if to calm them). They then continued their foraging behavior.

[b] Data from northwestern Brooks Range near the Kokolik River, Alaska (H. Reynolds, Alaska Department of Fish and Game, Fairbanks, Alaska, USA, personal communication, 1998).

crepancies. First, the food was provided and, although there was competition, food was abundant. The size of the food (chicken carcasses in contrast with large prey carcasses in the wild) probably played a role in the severity and solution of the bear–wolf conflict. Second, wolves normally outnumber bears in interactions in the wild. In the Bear Forest bear density was exceptionally high, resulting in a higher potential danger for the wolves. Third,

Table 8. Comparison of bear–wolf interactions in the wild (Table 7) and in Bear Forest for a 1997 behavioral study of 13 brown bears and 7 wolves in a 2-ha enclosure at Ouwehand Zoo, Rhenen, the Netherlands.

Interaction	Item	Bear Forest	Wild
Context	bear den	4	3
	wolf den	6	9
	food	15	20
	cubs	0	3
	unknown	54	10
Actor	bear	22	17
	wolf	57	28
Loser	bear	18	16
	wolf	61	10
	none	0	3
	unknown	0	16

neither bears nor wolves could leave the area. Fourth, no reproducing bears or wolves were kept so no interactions concerning cubs could be recorded. Fifth, bears and wolves in the enclosure were familiar with each other, a situation that hardly will occur under wild conditions. This familiarity implies that social contacts between individuals include more learned (predictable and controllable) aspects, and hence implies less exploration and emotional reactions. Bears and wolves seemed to tolerate each other in the Bear Forest, as sometimes also occurs in natural situations (Lent 1964).

MANAGEMENT IMPLICATIONS

During the research no severely injurious bear–bear and bear–wolf interactions were recorded. However, wolves sometimes bit and injured other wolves in attacks that could be fatal. Recently, Mech (1999) pointed to differences in social organization of captive wolf packs and natural wolf packs. The typical natural wolf pack is a family, a breeding pair with 1–3 generations of offspring. This may imply that a stable organized wolf pack should be setup from the start from a pair that develops stable relations by breeding.

As long as there are no reproducing animals in the enclosure, no severe problems are expected from having bears and wolves together. However, we had 2 concerns. The distances between bear and wolf dens were unnaturally small, and because young bears, wolves, and cubs seem to induce bear–wolf interactions in the wild, wolf and bear cubs in enclosures may cause severe management problems. Also, the feeding schedule should be varied to keep the animals more active, so that they do not expect food every day at the same time.

To keep a wolf pack as natural as possible, the males should not be castrated — sterilized if necessary — to maintain a natural hormonal level within the pack. Thus, the pack will be more stable and activities will be more equally distributed among the wolves. Whether the same is true for bears is not clear. If a group of intact bears and intact wolves are kept together, many interactions should be expected. It is probably difficult — maybe even impossible — to keep intact animals in such an enclosure.

CONCLUSIONS

Brown bears in the Bear Forest developed a social hierarchy based upon sex and age. The blind bears occupied a lower rank than expected based on their age and sex. As in a free–ranging pack, the rank order of the wolves was sexually related. The linear hierarchy in the females was: (1) alpha female Brenda, (2) beta female Noeska and (3) lowest ranking female Sylvia. The interactions among these females were very aggressive.

Bear–wolf interactions occurred more often in the Bear Forest than at first thought. Interactions of an unknown origin were more common than in the wild, and may have been play interactions between bears and wolves familiar with each other. However, more research concerning specific behavior sequences is needed to elucidate this question.

Comparing our results of interactions in the enclosure to interactions in the wild, we found that (1) the dominance hierarchy in bears is similar to that found in the wild during salmon fishing, that (2) the wolf hierarchy is most probably similar to that found in the wild, and that (3) bear–wolf interactions are less severe in the enclosure than in the wild. In the enclosure wolves killed no bears and bears killed no wolves. There seemed to be a high tolerance level, as was sometimes described for natural interactions between bears and wolves.

ACKNOWLEDGMENTS

Special thanks are due to Ouwehand Zoo, Rhenen, and the Netherlands. Funding for the project and travel to the Eleventh International Conference on Bear Research and Management in Graz in 1997 came from the International Bear Foundation, The Netherlands. Also thanks are due to 2 referees and H. Reynolds who provided information about bear–wolf interactions in the wild and stimulated us to explore the comparison of interactions in the 2-ha enclosure with interactions between bears and wolves in the wild.

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Received: 4 September 1997.
Accepted: 7 June 2002.
Associate Editor: Kate Kendall.