

Social Relationships in a Group of Captive Wolves

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SYNOPSIS. The social organization of a group of wolves in a large outdoor enclosure was followed through several breeding seasons. During the breeding season conflicts become more frequent and the social hierarchy obvious. The more dominant animals restrict courtship activities by inferior wolves of their own sex. However, apparently as a correlate of their position, two alpha males have shown less mating activity than other males. Mate preferences exhibited by animals of both sexes also limit the number of matings. The preferences appear related to the social hierarchy existing when an animal matures. Cultural transmission of social status is suggested by some changes in ranking of wolves raised in the woods at Brookfield. Temporary removal of the original alpha male and death of the original alpha female appear to have promoted changes in social order and an increase in actual mating combinations. The probable consanguineous nature of wolf groups and facets of the social behavior suggest that some form of group selection could be operative in the wild.

The basic relationships and activities of a group of wolves held captive at the Chicago Zoological Park, Brookfield, have been reported in previous film showings and summaries (Rabb, *et al.*, 1962; Ginsburg, 1965). The present paper is an abbreviated account of the social relations within this group during the mating season and the changes that have taken place over the years.

The wolf woods at Brookfield is $\frac{3}{4}$ acre enclosed by a chain link fence. In this area, there are several large native trees, a moated open viewing area, an artificial waterfall and pool, and a cement block shelter. The wolves dig their own burrows. There are no other caged animals nearby. The wolves are not tame. They recognize the keepers, but shy away when one enters the enclosure. They are fed chunks of horse meat, canned dog food, and ground meat in mid-afternoon, and visitors ply them with marshmallows. Perhaps because of the feeding regime and daytime activity in the park, the wolves are largely diurnal, in contrast to some situations in the wild. In general, our observations agree with what little

is known of group relations in the wild, principally that recorded by Adolph Murie (1944) and Mech (1966). Thus, the Brookfield wolves have cooperated in raising the young of a single mother, they gang up on an outcast, they have a leader to whom all defer, etc.

The Brookfield females come in heat during the cold weather at the beginning of February. Intense courtship activity starts a week before and continues for three weeks. Most of this activity takes place in mid-afternoon, although there have been late morning matings. During the breeding season, we usually watch and make film records for 5 or 6 hr each day from across the moated viewing area. Observations made through binoculars from a nearby building indicate that our usual proximity has no apparent effect on the wolves' behavior. Except on Sundays, the few winter visitors and the non-scientific voyeurs rarely distract the animals. We and keepers have checked at night and found little activity and no courtship behavior then. As used in this paper, courtship actions include sniffing, licking, pawing, dancing, mounting, presenting, and certain kinds of nipping. The elements of communication used in these and other social activities have been well described by Schenkel (1947).

The group originally consisted of 2 males

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and 3 females, surviving offspring of six born in April, 1957 to a common father and two mothers, all of whom were then 2 years old. The parents, of Canadian stock, had come to Brookfield as pups. One mother was a very white animal, and it is likely that four of the young, who were similarly light, came from her. The other parents and the other young were well marked with dark features.

The exact early social relations in the group in the wolf woods, to which they were transferred in 1958, are not known. However, two of the females had young of their own when they were 2 years old. These two litters were brought by their mothers to a common shelter, the concrete block den. Amiable relations lasted one night. The next night all of the pups were killed, most of them being neatly pulled in half.

In subsequent seasons, only a single female mated successfully and gave birth. This bitch dominated the other two females by assaulting them physically or psychically whenever they solicited a male or were receptive to a male. The other females were confined by intimidation to small areas of the woods (Fig. 1). Consequently, only one of the others mated, and then only once, when the chief bitch was herself in copulatory tie. The alpha bitch,



FIG. 1. Low-ranking female wolf in a restricted area deferring to alpha bitch, 1963 season. Alpha animal, ♀1, is being followed by males. The squatting position of ♀2 often was succeeded by further fawning, including a belly-up posture on the ground, if ♀1 turned directly toward her.

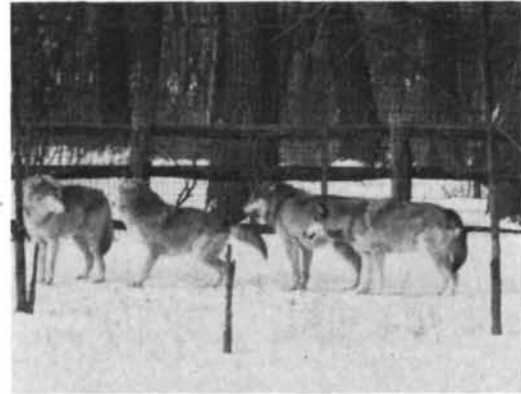


FIG. 2. Alpha female unsuccessfully soliciting alpha male, 1963 season. Left to right: ♂1, ♀1, ♂3?, ♂2.

♀1, preferred the alpha male, ♂1, and actively courted and solicited him (Fig. 2). So did ♀3. ♂1 reciprocated ♀3's attentions, but rebuffed ♀1. ♀1 thereupon accepted ♂2. ♂1 punished ♂2 while he was tied, as did ♀1. However, the punishment was not severe or lasting. ♂1 discouraged many mounting attempts by ♂2 simply by approaching the pair. Despite the increase of conflict in the mating season and restriction of lesser females' movements, the sociability of the group was maintained.

Change was built into this situation in that some of the pups produced were allowed to remain with the group. These included a male and a female from 1961, two males from 1962, and a female from 1963, all of them ♀1's offspring. However, there was no change in the relationships among the old adults in the mating seasons through 1963 (Fig. 3).

In 1964, we removed ♂1 shortly before the females showed vaginal blood, the sign of impending estrus. ♀1 accommodated quickly. She tied with ♂2 three times, and briefly with both of the 2-year-old males. However, ♀4, now 3 years old, and ♀2, one of the subordinate older females, were courted by the males. As in the past, intimidation by ♀1 prevented actual mating by them. Often the lesser females simply sat down when mounted, effectively terminating the mating attempt. As before, there were some cross-sexual dominance actions, principally ♀1 dominating the lesser males.

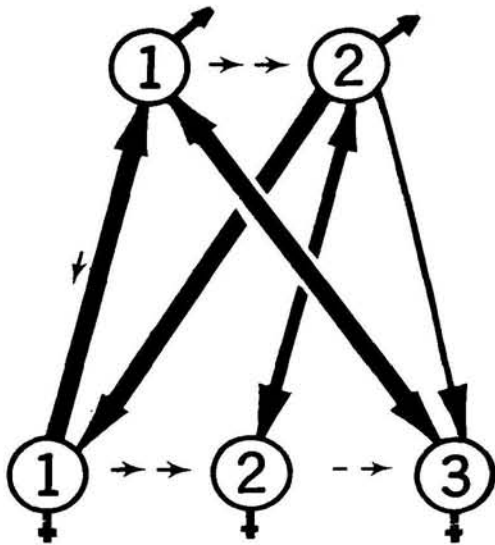


FIG. 3. Relations of original group of wolves at Brookfield in mating season, 1963. Small arrows indicate direction of dominance actions; large arrows, courtship actions. Relative frequency of courtship actions is suggested by width of lines.

♂1 broke a lower canine tooth while in solitary confinement. Perhaps partly because of this, as well as his absence during a critical period, he was no longer dominant the following season. Although he still patrolled the area, deference went to ♂2. We had next planned to remove ♀1 to determine how complete a release in mating activities would result for the other animals. However, this was done for us in a natural fashion at the end of 1964 in the period of pre-mating rivalries and status adjustment (*cf.* Schenkel, 1947, p. 84-86). ♀1 died from infection of leg wounds apparently inflicted by the most repressed animal, ♀3, as she was being badgered by ♀1. Despite suppression by ♀4, who was now the alpha female, ♀3 mated eight times with ♂1 in the 1965 season. ♂2 mated with ♀3 twice. ♂1 generally rebuffed the attentions of ♀4, and she in turn rebuffed her two young suitors, ♂4 and ♂5 (Fig. 4). ♀3 gave birth to a litter, which was cared for by ♀2 and ♀4.

In the 1966 season ♀5, a 3-year-old, was very important because of her new alpha status in partly restricting the other females' activities, but particularly in thwart-



FIG. 4. Alpha female rejecting suitors, 1965 season. Left to right: ♂5, ♂2, ♀4, ♂4. ♂5 has one paw on the female's back. If males persisted after initial snarl, ♀4 often whirled upon them in a snapping attack.

ing continuing dominance by ♀4. All of the animals mated except ♂3 and ♀5 (Fig. 5). In addition to ties in the reciprocal courtship relations, two males succeeded in tying with two females who did not court them and usually rejected them. All three females that mated gave birth.

Among points worth noting from our observations is the effect of dominant animals in restricting the courtship activities of lesser animals. This applies not just to the alpha animals, but to other relationships, such as ♀4 in the 1966 season to ♀2 and ♀3 (Fig. 6). Or ♂5 to ♂1: for the 1965 and 1966 seasons, ♂5, the beta male, was chiefly responsible for repressing ♂1.

A second point is the lasting nature of mate preferences, which is outstanding in the case of ♂1 and ♀3 (Table 1). Mate preferences seem to be related to the order of dominance in the group when the young first become mature. Thus, ♀4 prefers ♂1, and ♀5 prefers ♂2. ♂4 and ♂5 preferred ♀1, but switched to ♀4 when ♀1 was no longer available (about $\frac{1}{3}$ of their recorded courtship actions were directed to ♀4 in 1964, $\frac{2}{3}$ in 1965, and $\frac{4}{6}$ in 1966). The relation of ♂3 to ♀2 is apparently also linked indirectly to the dominance hierarchy. In 1963 he split his attentions between ♀1 and ♀2. He later concentrated on ♀2 after his initial rebuffs and domination by ♀1. These younger

TABLE 1. *Mate preference in Brookfield wolves, mainly based on frequency of courtship activity.*

Season	♂ 1	♂ 2	♂ 3	♂ 4	♂ 5
1961	c ♀ 3	a ♀ 1	—	—	—
1962	c ♀ 3	a ♀ 1	—	—	—
1963	c ♀ 3	a ♀ 1	a ♀ 1	a ♀ 1	—
1964	—	a ♀ 1	c ♀ 2	a ♀ 1	a ♀ 1
1965	d ♀ 3	c ♀ 2	c ♀ 2	a ♀ 4	a ♀ 4
1966	c ♀ 3	c ♀ 3	d ♀ 2	b ♀ 4	b ♀ 4

	♀ 1	♀ 2	♀ 3	♀ 4	♀ 5
1961	a ♂ 1	?	a ♂ 1	—	—
1962	a ♂ 1	?	a ♂ 1	—	—
1963	a ♂ 1	b ♂ 2	a ♂ 1	a ♂ 1	—
1964	a ♂ 2	a ♂ 2	0	0	—
1965	—	a ♂ 2	e ♂ 1	e ♂ 1	a ♂ 2
1966	—	a ♂ 2	d ♂ 1	d ♂ 1	a ♂ 2

—, animal was present but not mature; 0, animal present but no preference evident; ?, data lacking.

Letters before individual symbols indicate dominance rank within sex.

males, of course, were not very experienced competitors for ♀'s favor. However, lesser males can, and do, partly thwart a superior male's attentions to a mutually preferred female by blocking and fawning maneuvers.

Also noteworthy is that some kind of filial or allegiance-bond is seen in males. Thus, ♂³ has always sided with ♂¹, protecting him when he was being attacked while in tie. Likewise, ♂⁴ and ♂⁵ seem to shield ♂² from other animals at such critical times. These allegiances may be related to the dominance hierarchy when the young males mature. The recent decline of ♂³ in the rank order may thus be in part a result of the fall of ♂¹. In respect to this, Table

TABLE 2. *Changes in dominance rankings of Brookfield wolves. Separate rankings within sexes.*

Wolf	Birth year	1961	1962	1963	1964	1965	1966
♂ 1	57	A	A	A	—	E	D
♂ 2	57	B	B	B	A	A	A
♂ 3	61	—	C	C	B	B	E
♂ 4	62	—	—	D	D	D	C
♂ 5	62	—	—	D	C	C	B
♀ 1	57	A	A	A	A	—	—
♀ 2	57	B	B	C	C	C	D
♀ 3	57	C	D	D	D	D	C
♀ 4	61	—	C	B	B	A	B
♀ 5	63	—	—	—	?	B	A

?, animal present (*contra* report in Ginsburg, 1965) but not enough interactions with other animals to assign rank (definitely below ♀ 1).

2 is slightly misleading in giving linear rankings—♂³ was not truly dominant to ♂¹ in 1965 in terms of conflict, but he definite-

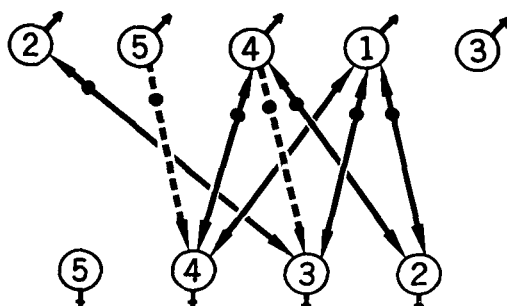
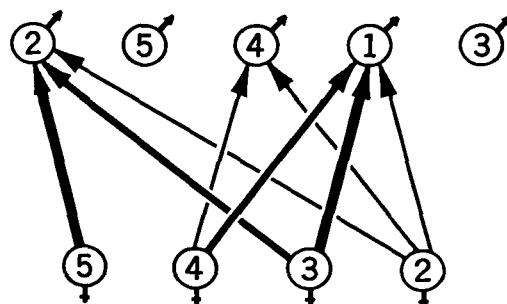
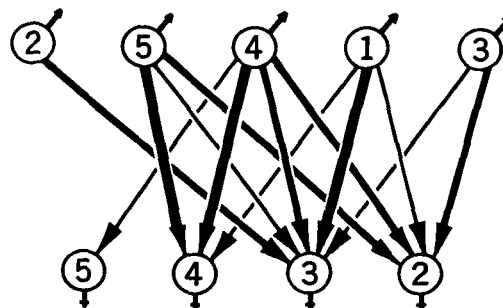


FIG. 5. Summaries of courtship relations in wolves at Brookfield, 1966 mating season. Top, male actions; middle, female actions; bottom, reciprocal courtships and ties. In top and middle, width of lines indicates relative frequency of courtship. In bottom, bulbs on arrows represent copulatory ties; dashed arrows are non-reciprocal courtships that resulted in ties. Symbols for individuals arranged in order of dominance, alpha animals at left.

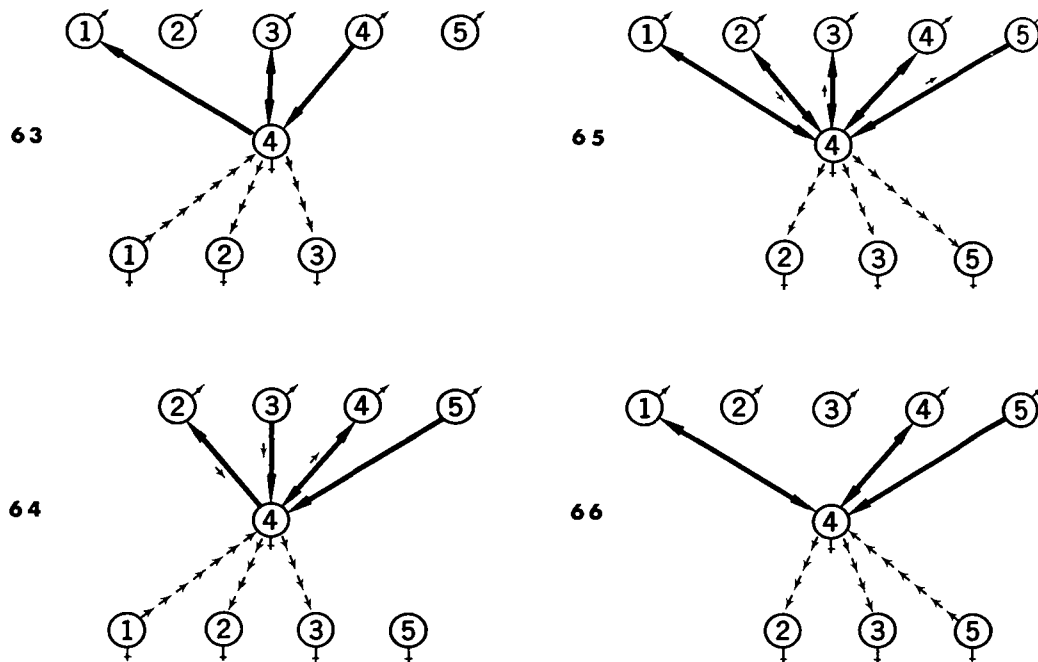


FIG. 6. Principal relations of ♀4 to other wolves at Brookfield in four mating seasons. This female became mature in 1963. Small arrows, dominance actions; large arrows, courtship actions.

ly was superior to ♂4 and ♂5 at that time. The rapid rises in rank of ♀4 and then ♀5 also suggest cultural transmission of status. As pups they apparently adopted their alpha mother's attitude to the other adult females, and upon growth were able to enforce this attitude.

We previously remarked on the lesser mating activity of the alpha male, when we had evidence from only one animal (Ginsburg, 1965). However, in the 1966 season, the second alpha male in the group's his-

tory tied only once, and was the most inactive of all the males in courting activity, continuing a trend from his previous two alpha seasons. Admittedly, his preferred female was no longer in the group in 1965 and 1966. In both of these seasons, he tied with the first female to come fully into heat, and thereafter showed relatively little interest in the proceedings. Conversely, in the last two seasons, the former alpha male has increased his courtship activity (Table 3.)

TABLE 3. Courtship actions and number of ties in Brookfield wolves. Courtship figures are percentages of total bouts recorded for each season. Active indicates animal initiated behavior, passive, that animal was object of courtship.

Season	Behavior	♂ 1	2	3	4	5	N	♀ 1	2	3	4	5	N	
1966	Active	23	7	10	34	26	279		12	47	16	25	146	
	Passive	54	38	0	7	1	146		17	39	43	1	279	
	Ties	2	1		3	2	8		2*	3*	3*		8	
1965	Active	9	18	19	36	18	363		15	50	32	3	117	
	Passive	81	14	2	3	0	117		23	16	60	1	363	
	Ties	8	2				10			10*			10	
1964	Active		31	9	35	25	187		40	35	5	20	0	20
	Passive		45	35	10	10	20		59	19	2	20	0	187
	Ties		3		1	2	6		6*					6
1963	Active	14	47	19	16	4	135		43	16	35	6		49
	Passive	70	14	16	0	0	49		69	15	13	3		135
	Ties	1	5		1		7		6*		1			7

* Female subsequently gave birth.

Not enough young have grown up in the woods at Brookfield to give many clues to social relations between maturing litter mates. For the first 3 years, the brother and sister of 1961, ♂3 and ♀4, had a mutually tolerant and rather playful relation. He was dominant to her, but also he fended off some courting attentions to her by younger males. In the midst of the 1965 mating season, ♀4 somehow, and for unknown cause, subjugated her brother. This gave rise to amusing failures in communication as the younger males mistook his submissive gestures for deference to themselves. Between these younger males, ♂4 and ♂5, there has been strong, and even savage, rivalry. However, in the 1966 season, there was more tolerance, and even some evidence of mutual support.

Fig. 6 shows graphically the relationships of one of these young, ♀4, through four mating seasons to give an idea of the changes that occur and the complexity of the social structure. However, graphs cannot convey the flavor of each wolf's personality, which displays some characteristics not linked to the hierarchical order. For example, ♂4 was sexually precocious compared to his brother, ♂5, and has always been more acceptable to the females.

Simple effects of density or crowding are not obvious in the reproduction of this captive group, where food is amply provided. Seven litters have ranged in size from 3 to 6, average 4.3; a total of 12 young was born in 1966 when three females gave birth. However, females born after the group was established have not bred or even shown full estrus in their second year, despite high social ranking.

The Brookfield wolves are not in a natural situation, but there are indications from the literature that similar relationships and behavior are seen in the wild. For example, judging from Murie's account, the dominant male of his most closely studied pack was not the father of the young. Similarly, Ognev (1931) reported that N. A. Dmitriev-Mamonov found that a female mated for four consecutive years with a small, lame male in apparent preference to other males in the area. Other studies in

captivity also lend support. Mr. George Wilson of St. Louis, Missouri, who has kept two males and two females outdoors in a rather natural setting, has told us that the dominant male was not the father in his group. In the group of five studied by Frädrieh and Göltenboth (1965), the mother was the beta female.

The significance of these matters in the biology of wolves is not fully clear. However, the existence of strong mate preferences alone patently restricts the reproductive potential of a pack. Dominance within the sexes also has contraceptive value, but the actions of the alpha male do not necessarily amount to psychological castration of the lesser males, as has been suggested by Etkin (1964, p. 275) on the basis of studies of the dog. However, our chief bitch, for all practical purposes, did achieve this state of control over lesser females. When the original strong dominance hierarchy broke down, there were relatively numerous cross-sexual combinations, although the result was obviously not a wholly promiscuous or random mating situation (Fig. 5).

It appears that captive groups composed of litter mates untutored by their parents can show complex group organization, which we infer arises through genetically determined behavior (*cf.* Scott and Fuller, 1965, p. 415). The group at Brookfield, despite persecution of an occasional outcast, shows strong evidence of natural cohesiveness in assembling for greeting ceremonies, in howling together in response to artificial wolves in the form of local sirens, through group assaults, etc. Again, there is close correspondence to behavior reported in the wild, which even includes situations where outcasts do not leave the group (see Mech, 1966, p. 63-64).

The ritualized group activities, the altruism shown in the care and raising of the young by non-parents, and the low level of reproductive activity apparent in some male leaders suggest that wolves have evolved their social structure with some selective pressure for traits of value to the group, and not just the individual.

It may be impractical or impossible to determine whether such selection operates

mainly on individual wolves as adaptive units within a social environmental unit (Wiens, 1966), or as bearers of common genes in a kinship group (Williams, 1966). It has been presumed that the basic social unit in wild wolves is composed of litter mates (*e.g.*, Scott and Fuller, 1965, p. 416). But is it? Does a litter that starts hunting together become an enduring reproducing group? Even if so, what are the genetic and social relationships to the basic group of the apparent strangers that are accepted and rejected on occasion? There is obviously a need to know much more about the formation of wolf groups in the wild.

The natural and induced changes of social structure in the wolves at Brookfield demonstrate that a fascinating range of relationships is possible in a captive group. We hope this and related work on similar groups (*e.g.*, Schönberger, 1965) will provide reference points for studies in the wild, where biotelemetry and marking techniques promise eventually to give a definitive picture of wolf life.

If we need additional stimulus to tackle problems implied and touched on in this report, the ideas of recent years concerning man's early evolution from a pack-hunting primate seem an ample challenge to us. The social organizations of wolves, lions, and Cape hunting dogs may be more relevant than those of most primates to the human situation.

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