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Social organization in juvenile bison bulls (*Bison bison*): Non-linear dominance and dyadic associations

Rothstein, Aron, Ph.D.

City University of New York, 1988

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SOCIAL ORGANIZATION IN JUVENILE BISON BULLS (*BISON BISON*): NON-LINEAR DOMINANCE AND DYADIC ASSOCIATIONS

by

Aron Rothstein

A dissertation submitted to the Graduate Faculty in Biology
in partial fulfillment of the requirements for the degree of
Doctor of Philosophy, The City University of New York

1988

This manuscript has been read and accepted for the Graduate Faculty in Biology in satisfaction of the dissertation requirement for the degree of Doctor of Philosophy.

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Chairman of Examining Committee
Prof. Joseph G. Griswold

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Date

Executive Officer
Prof. Peter Chabora

Prof. Carol Simon, City College

Prof. Howard Topoff, Hunter College

Dr. Richard Van Gelder, The American Museum of Natural History

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ABSTRACT

Interspecific comparisons of social development suggest that the types of social interactions engaged in by juveniles may be related to the adult social organization. The objective of this study, conducted at Wind Cave National Park in South Dakota, is to describe the social behavior and organization of juvenile bison bulls (*Bison bison*). Based on the social behavior of adult bulls, it is predicted that juvenile bison bulls will form an aggressively interacting social sub-group within the cow/juvenile herd.

Calf and yearling bulls were found to interact preferentially with social partners of their own age. Yearlings also interact more than expected with 2-year-old females. It appears that young males choose partners of their own size. The juvenile males interacted more aggressively with male than with female partners.

Dominance relations among the yearling males were investigated using several methods. The yearlings have stable dyadic relationships without an overall linear order. Significant transitivity in the relationships suggests that a combination of physical attributes and social experience is responsible for the outcome of agonistic interactions. There is a correlation between dominance and horn size.

A method is developed and used to analyze pair association data for the 16 male yearlings. Dyadic associations were found among the yearlings, representing pairs that were in the same group and/or interacted more than expected under the hypothesis of random association. These relationships involved 15 of the 16 individuals. Yearlings were more likely to associate with partners of differing dominance rank than with rank neighbors. Because these pairs have well established dominance relationships, they may be able to engage in vigorous agonistic interactions with reduced chance of escalation and injury.

Young bulls form a sub-group within the herd. They interact with each other in ways that maximize their experience in intermale agonistic encounters and minimize the risks involved in serious fights. This picture of yearling bull social organization is consistent with the hypothesis that the pattern of male bison social development should reflect the social structure among adult bulls and not the structure of the cow/juvenile herd into which they are born.

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Chapter 1

INTRODUCTION

Social living is employed by many ungulate species in order to exploit food sources and avoid predation (Estes, 1974; Jarman, 1974; Eisenberg, 1981; Krebs & Davies, 1981). Because of the constant presence of conspecifics, the behavior of group-living animals must be adapted to the social environment as well as the physical one. Social behavior is thus an important factor in an individual's ability to survive and reproduce. For example, red deer stags defend groups of hinds during their breeding season. A stag's ability to compete with other males determines his reproductive success for the year (Appleby, 1981; Clutton-Brock *et al.*, 1982). American bison bulls, although they do not collect harems, differ widely in the number of cows they breed during the rut. This variation is closely related to the bulls' ability to dominate others, and thus gain access to estrous cows (Lott, 1979).

Interactions are the basic units of social behavior. The concept of *interaction* is difficult to define rigorously. Interaction implies that an animal directs behavior at another animal (that is, "does" something to the social partner); the second animal may or may not respond overtly. In an interaction, the pattern of each animal's behavior is in some way contingent on the behavior and responses of the other. Hinde & Stevenson-Hinde (1976) note that interactions are "events that could not be fully understood by observation of one partner alone."

Two animals that repeatedly interact with each other over time, and whose behavior in interactions is in some way affected by their previous encounters, have a relationship. Relationships are defined by a pattern of type and frequency of interaction. For example, the mother-young relationship in bison involves frequent nursing and contact-maintaining behavior that is unique to this class of relationship (McHugh, 1958; Engelhard, 1970; pers. obs.). The agonistic interactions of adult bison bulls result in dominance relationships among the individuals. These relationships are characterized by predictable patterns of dominant and subordinate behavior by the partners in an interaction (McHugh, 1958; Lott, 1974; 1979;

1981; pers. obs.). The total of all the relationships between group members then defines the social structure of the group.

This group social structure imposes demands on the behavioral development of young animals. In addition to developing behavior and skills to deal with the physical environment, a young animal must develop the ability to interact with and enter into species-typical relationships with group members. In mammals, this ability typically develops through experience gained in interactions between the young animal and other group members. Ample evidence that differences in early social experience lead to differences in later social behavior highlights the importance of a young animal's social interactions (Harlow, 1959; Harlow & Harlow, 1962; Gilbert, 1968; Scott *et al.*, 1974; Bekoff, 1977a).

Social behavior development and group social organization are intimately connected. The social interactions in which a young animal can engage are limited by the social structure of the group; the limits include age and sex classes of potential partners and types of interactions that will be tolerated by other group members. At the same time, the group's social organization is a product of the social development of individual group members. This interdependence of social structure and social behavior development suggests that there should be certain patterns of development associated with specific types of social structures. That is, one might be able to predict the type of interactions involved in social development from knowledge of a species' normal social structure, and *vice versa.*

Bekoff (1977b) compared early social development and adult social organization among species of canids. He found a positive correlation between the sociability of a species, as measured by group size and frequency of interaction, and the amount of non-aggressive social play by the young. He hypothesized that, for canids, social play functions to develop bonds that continue into the adult social structure.

Inter- and intraspecific work on ungulates has addressed similar questions. Berger (1979) found that bighorn lambs from more social populations play more and with less aggression than do lambs from less social populations. Comparison of goats and sheep shows that lambs participate in more social play than do kids (Scott, 1945; Collias, 1956; Rudge, 1970; Geist, 1971). This difference is correlated with differences in adult behavior: sheep are more gregarious and interactive than goats.

Byers (1983), building on these ideas, predicted that since collared peccaries live in extremely social groups (by mammalian standards), juvenile peccaries should have frequent non-aggressive interactions with each other. He found, however, that juvenile peccaries interacted with other juveniles only infrequently. Moreover, when they occurred, interactions between juveniles were largely agonistic. Most interactions involving young peccaries were with adult group members. Thus, in at least some ungulates there appears not to be such a simple relationship between the pattern of social development and the adult social organization. As data on the development of social behavior of more species become available, this relationship will become clearer.

The present study is an investigation of social interactions and relationships among young American bison bulls (*Bison bison*). Bison are valuable subjects for such a study. They represent an extreme in gregariousness for bovids. Herds may once have numbered in the hundreds of thousands (early literature, concerning bison before the populations were hunted into near extinction, is reviewed by Roe (1951)). At present, herds number in the hundreds, putting bison still at the extreme end of bovid social organization. The bovid family encompasses a range of social organizations, from solitary species to herding species (Estes, 1974; Jarman, 1974). Information on social development in bovids is thus valuable in that it provides a base for comparisons among a group of related species whose ecology and social organization has been well studied.

Bison social organization involves adult segregation by sex for most of the year. Cows and young males live in large groups while adult bulls are solitary or in small all-male groups; bulls join the cow/juvenile herd for extended periods only during the mid-summer rut (McHugh, 1958; Petersburg, 1973; Lott, 1974). Young bulls therefore must move into a social group with a structure radically different from that found in their natal group. Based on the work mentioned above, this fact leads to the hypothesis that young bulls will form a distinct social sub-group within the cow/juvenile herd. As adults their most frequent social interactions will be with other bulls; they will have few day to day interactions with cows. As juveniles, their most important interactions are predicted to be with other young bulls, in preparation for future competition with them. Additionally, these interactions are expected to be largely agonistic, as is the case between adult bulls.

My objective is to test these predictions by examining the interactions among young bison bulls. In chapter 3 I examine preferences by young bulls as to the age and sex of social partners they choose. Chapter 4 is an investigation of the dominance relationships among yearling bulls. Chapters 5 and 6 concern associations among yearling bulls; that is, the formation of pairwise relationships between preferred social partners. Throughout I have tried to relate the observed behavior of young bulls to the known behavior of adult males.

Chapter 2

GENERAL METHODS

STUDY AREA

This study was conducted in Wind Cave National Park (WCNP) in southwestern South Dakota, USA. The park is located at the southern edge of the Black Hills, 9.7 km north of Hot Springs, South Dakota.

The park was created by an act of Congress in 1903 in order to protect the limestone cave that gave the park its name. The above-ground area of the park encompassed 4274 ha. In 1931, the park boundaries were extended to include a total of 4742 ha; this enlargement included Beaver Creek canyon and thus added a natural source of water to the park. In 1946 the park was enlarged to its present size of 11,355 ha. The park shares its northern boundary with Custer State Park, which is administered by the state of South Dakota. Figure 1 shows the current park boundaries.

The altitude of the park ranges from 1529 m in the northwest to 1112 m in Red Valley in the eastern section. The northwest section of the park is composed of a series of valleys separated by timbered ridges, while the eastern and southern sections include expanses of rolling grasslands. In the center of the park are several steep canyons and draws.

Annual precipitation at WCNP averages 48 cm; 70% of this occurs between 1 May and 30 September. There are two natural, year-round sources of water in the park: Beaver Creek, entering from the west, and Highland Creek, entering from the North. Both streams disappear underground within the park boundaries. Each year there are a number of wallows and depressions that remain filled with water throughout the summer. These waterholes are favorites with the bison, but their number, size, and location change from year to year, depending upon local rainfall patterns. The park also maintains several spring-fed dish tanks that supply year-round water. In addition, there are two artificial ponds that remain from when the more recently added sections of the park were private ranches.

WIND CAVE NATIONAL PARK

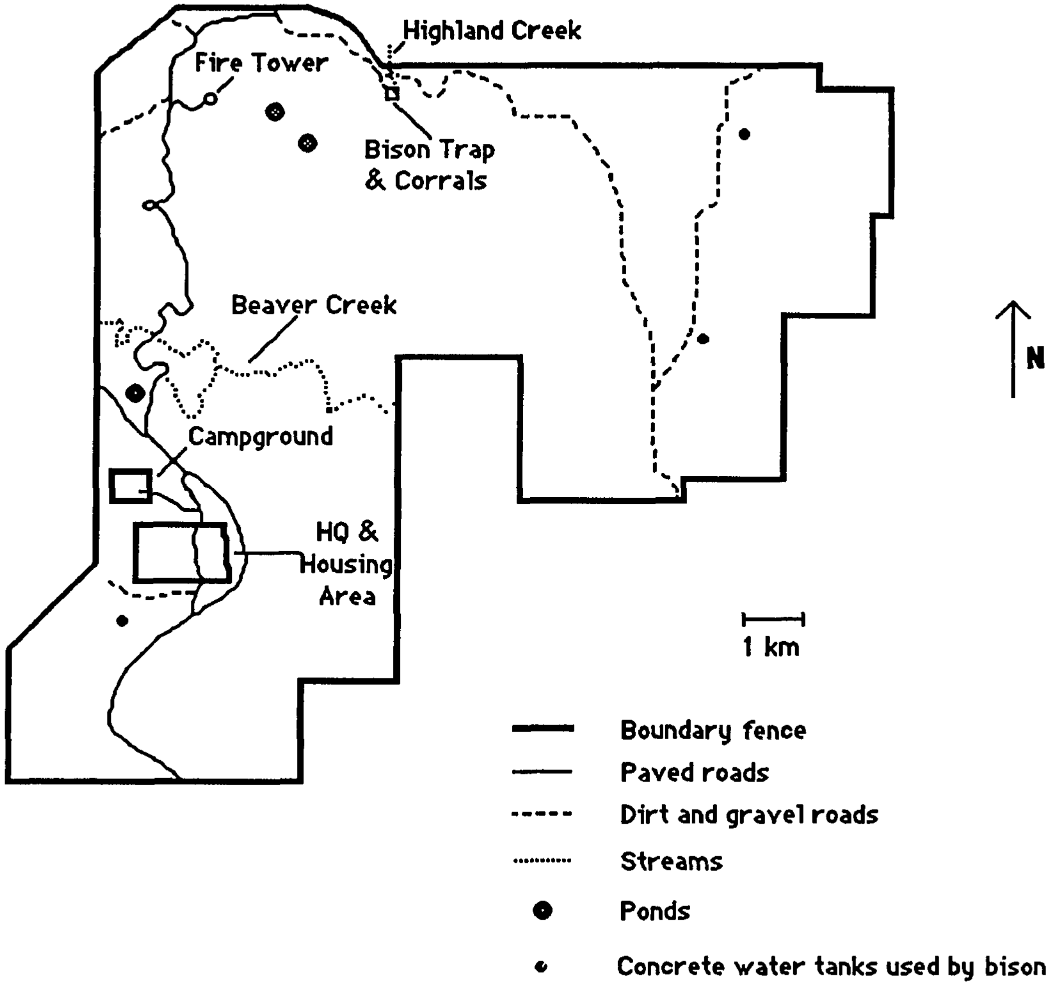


Figure 1: Map of Wind Cave National Park.

The park is enclosed by 55 km of boundary fencing. The fence is 244 cm high woven wire except for 4.8 km of 122 cm fence on the west boundary. The lower fence allows movement of elk between the park and the Black Hills National Forest to the west. The lower fencing is adequate to keep bison within the park, especially since they do not spend much time near the western boundary. Paved roads enter the park over cattle guards which serve to restrict bison movement in most cases. In addition, two areas are separated from the rest of the park by 244 cm high fencing: 1) the park headquarters and employee housing area, comprising about 174 ha, and 2) the visitor's campground, which encompasses 13 ha (see Figure 1). Aside from these areas, the bison have freedom to move anywhere within the park.

There are 29 km of paved roads within the park; an additional 14.5 km of secondary gravel roads are open to the public and are passable in dry weather. Annual visitation at the park averaged approximately 1 million for 1982 to 1984. Most visitors come to view the cave and then leave the park using only the paved roads; there is little use of the surface of the park by the public. There are 45 km of fire trails that cover most of the interior of the park. These trails are closed to public vehicles but were open to researchers. The trails are generally passable in a pick-up truck with good ground clearance.

Vegetation

The park represents an ecotone between the coniferous forest, which covers much of the Black Hills, and the South Dakota grasslands. Pine forest, predominantly ponderosa pine (*Pinus ponderosa*), covers 20% of the park. Deciduous trees are found scattered throughout the park along draws and other wet areas.

The remaining 80% of the park is covered by grassland with scattered timber. The grassland is a mixture of mid- and short-grass prairie. Predominant grasses are big bluestem (*Andropogon gerardii*), little bluestem (*Andropogon scoparius*), wheatgrasses (*Agropyron* spp.), needlegrasses (*Stipa* spp.), blue grama (*Bouteloua gracilis*), hairy grama (*Bouteloua hirsuta*), side-oats grama (*Bouteloua curtipendula*), and buffalo grass (*Buchloe dactyloides*). Sedges are predominantly *Carex* spp. Common forbs are scurfpea (*Psoralea* spp.), goldenrod (*Solidago* spp.), sweetclover (*Melilotus* spp.), and fetid marigold (*Dyssodia papposa*). Common shrubs include fringed sage (*Artemisia frigida*), wild rose (*Rosa* spp.), snowberry (*Symphoricarpos occidentalis*), and lead plant (*Amorpha canescens*).

Other mammals

Beside bison there are several mammalian grazers in the park. The most numerous are black-tailed prairie dogs (*Cynomys ludovicianus*). In 1982 there were 11 active dog towns in the park; two of these were poisoned out leaving 9 towns that occupied 6% of the park area. During spring and summer bison prefer to graze on dog towns. There is some evidence that the grass on dog towns has a higher nitrogen (and thus protein) concentration than off-town grass (Krueger, 1983).

Pronghorn antelope (*Antilocapra americana*) are numerous and often graze next to or within bison herds. In 1983 there were approximately 160 pronghorn within the park but during the winter of 1983-84 about 100 left the park over a cattle guard that was filled in because of higher than average snowfall. There are 375-400 elk (*Cervus elaphus*) in the park. Elk are occasionally seen grazing with bison in the early mornings and late evenings.

In 1983 there were an estimated 120 mule deer (*Odocoileus hemionus*) in the park. White-tailed deer (*Odocoileus virginianus*) are also occasionally seen. The deer rarely interact with bison and are most commonly found in and around the headquarters enclosure.

Mammalian predators in the park include coyote (*Canis latrans*), badger (*Taxidea taxus*), bobcat (*Felis rufus*), and, perhaps, cougar (*Panthera concolor*). Coyote are the most common and are frequently found in and around bison herds. It appears that coyote could kill a young bison calf, but I found no evidence of this during the course of the study. By the time calves are a week old they are too fast and big to be taken by a single coyote. Cows with young calves do, however, chase coyotes away from the herd. The coyotes seen in the herds were usually engaged in hunting prairie dogs and other small rodents; the bison may benefit the coyotes indirectly by providing cover and by stirring up mice and voles in the grass.

Cougars certainly could represent a threat to bison. In the summer of 1986 there were two reliable sightings of a lion in the park (probably the same animal in both sightings). In previous winters there were signs of lions found (i.e., tracks) but no obvious lion kills have been found within the park. Badgers and bobcats are seen infrequently. Neither are potential predators of bison.

BISON HERD AND MANAGEMENT

History of herd

The following information is a summary of the herd history given by Shult (1972). Although bison were originally present in the Black Hills and surrounding area, they had been exterminated by the end of the 19th century. Bison were reintroduced to WCNP on November 28, 1913. Fourteen animals, 7 male and 7 female, were obtained from the New York Zoological Society and released in the park. In 1915, 2 male and 4 female bison from Yellowstone National Park were added to the Wind Cave herd.

In February of 1936 the herd numbered 171 and the first round-up was held to reduce the herd size. Animals culled were delivered to the Pine Ridge Indian Reservation for meat. Since that time, the park has conducted periodic round-ups; the excess animals are shipped to slaughter and the meat given to the Bureau of Indian Affairs for distribution.

In 1965 a brucellosis eradication program was started. Bison seem well adapted to brucellosis; there is little evidence of its causing abortions among bison cows. There is, however, concern that it could spread from bison herds to cattle. The park's program involves vaccinating heifer calves and testing all bison at round-ups; all reactors are culled from the herd and shipped to slaughter. In 1984 a concerted effort was begun to have the herd certified brucellosis-free. This goal has been achieved as of 1987, but testing will continue at all future round-ups.

In 1969 four males from Theodore Roosevelt National Park in North Dakota were added to the WCNP herd. This was the last planned transfer of animals into the park. There are, however, occasional exchanges between the WCNP and Custer State Park herds, across their mutual boundary. This is mostly due to bulls walking or jumping across the cattle guards. The state park bison are branded so they are easily identified. Each year of the study at least one new state park bull was observed in the Wind Cave herd; it is assumed that a similar number of Wind Cave bulls moves into Custer State Park each year.

The addition of stock from different herds over the years has led to the formation of a genetically diverse herd. This was confirmed by blood tests conducted at the 1983 round-up. The Wind Cave herd had more variation than any other U.S. herd tested (C. Stormont, pers. comm.). It is impossible to know how much diversity was lost when the herds were decimated in the 19th century.

Current herd management

Current management policy at WCNP is to keep total herd size at about 350 animals. The cow-juvenile herd, which consists of all females plus males 2 years old and under, numbers about 250 and there are 80 to 100 older males. The herd is reduced through culling at biennial round-ups (because of the brucellosis program, round-ups were held annually between 1983 and 1986, but culling for herd reduction took place only at alternate round-ups). At the round-ups animals can be weighed and measured; numbered metal eartags are placed in all calves and yearlings. These tags can be used for accurate aging of animals from park records.

During the 1960's park personnel placed salt blocks at various locations in the park. These led to the establishment of some mineral licks that are still used by the bison. Other frequently used licks appear to be natural in origin. At present, the herd is not supplied with food or salt. Water is kept available through periodic cleaning of the dish tanks throughout the park.

Other park management practices that affect the bison are programs of fire prevention and prescribed burning, and limiting new colonization by prairie dogs. Each spring there is a prescribed burn of a section of the park, the goal being to burn the entire park on a 12 to 15 year cycle. This burning prevents the encroachment of pine trees onto the grassland. It also affects bison movement; the bison prefer the new growth after a fire and, during the summer, spend large amounts of time in the burned area. Prairie dog colony control may also affect the herd by limiting these preferred grazing areas (see above).

OBSERVATION AND DATA RECORDING

Field work

I began field work for this study in April, 1982. Prior to that I attended the round-up in January, 1982, to familiarize myself with bison of different ages and eartag a number of animals (see below). Field work continued from April to November, 1982 and then from March, 1983 to August 1984. I returned to WCNP in October, 1984 for the round-up and also for short periods in the summers of 1985 and 1986 to make follow-up observations on the study animals. Finally, I attended the round-up in October, 1986 to get weights and physical measurements of subjects.

During the summer months, I either arrived at the park at dawn and stayed with the bison until their mid-afternoon rest (usually 1300 or 1400 Mountain Standard Time) or arrived in mid-afternoon and stayed with the animals until dark. In the summer of 1983 I conducted 10 all-night observations using a night vision scope. The results of these observations were unsatisfactory because individual animals could not be recognized through the scope.

Individual identification

My study subjects were 12 bulls born in 1982 and 11 bulls born in 1983. In addition, I collected some data on several individually identifiable bulls born in 1981, and made opportunistic observations on older bulls that I did not recognize individually.

Apart from older bulls, most animals could be identified individually by sight. This was usually accomplished through natural variation in appearance. Animals varied in horn length and shape, body size and shape, and hair patterns. I made sketches of animals and kept a record of day to day changes in their appearance (e.g., loss of a horn or loss of some winter hair).

In addition to natural variation, I was able to attach colored eartags to animals during the round-ups. The number and size of the tags had to be kept small so that visitors to the park would not be disturbed. I found these tags most helpful in 1982, when first learning to identify individuals, and after 1984, when I was away from the field for long periods.

Identifying young animals born between round-ups was difficult. Young bison are very similar in appearance and individuals change quickly as they grow. I tried several ways of marking them in the field and settled on hair bleach as the best. The bleach was applied to the ends of blunt arrows which were then shot from a 45 lb. bow. This method produced circular light spots of hair that allowed positive identification. The marks lasted about 6 months, until the coat was shed in either spring or fall. I reapplied the marks as necessary until I became able to identify the individuals through natural variation, usually by the time they were 1 year old.

As a check on my ability to identify animals, I made use of both the colored eartags and the park's numbered tags. Bison identified by natural characteristics could be checked when they turned so that the colored tag, in the right ear, became visible. At round-ups, the numbered eartags could be checked. In every one of these instances, my identification was correct. In all, I was able to identify 250 individuals. This included almost the entire cow/juvenile herd.

Locating and observing bison

In general, I located groups of bison in the park by driving the roads and fire trails in a 4-wheel drive pick-up truck. The fire tower on Rankin Ridge (the highest point in the park, see Figure 1) provided a view of much of the park, and I would often go there myself or contact the fire ranger by radio to find out if bison were visible. Additionally, reports on bison locations were often available at the park visitor center; I made use of these whenever possible. After 1982, however, I became familiar enough with local bison movements that I could usually find a group quickly from knowledge of their position over the previous several days. This was possible because for short periods of time the bison would adopt a pattern of movement within a sub-section of the park.

Subjects were observed from a pick-up truck or on foot, depending on their location. Observation distances varied from less than 10 m, when the herd could be approached in the truck, to 200 m. Because the fire trails cover most of the park, I was often able to drive into the middle of a group to conduct observations. Bison at Wind Cave are habituated to vehicles; at the close approach of the truck, the nearest animals show an increase in vigilance (i.e., frequent looks directed at the truck) for a period of 2 to 3 min. They then resume their normal behavior, and appear to take no further notice of the observers or the truck.

In certain parts of the park I found it necessary to approach bison on foot. Observers on foot have a greater effect, especially in areas near the middle of the park where contact with humans is not common. An observer can approach to 50 m without greatly disturbing the animals, provided that he moves slowly and sits down as soon as the bison begin watching. I found this method of openly approaching a group preferable, in most cases, to attempting a concealed approach. Although a group could be observed from concealment for a while, discovery was all but inevitable. This usually resulted in the bison becoming agitated and walking (if not running) away.

Data collection

On first approaching a group I would record group size and the identity of all individuals (unrecognized individuals were aged and sexed). Subjects were observed through 10 x 50 binoculars and a 25x spotting scope. Observations were spoken into a tape recorder and transcribed later. This allowed subjects to be kept in constant view throughout an observation period.

Most behavioral data were collected during focal animal observation periods (Altmann, 1974). In small groups of bison (i.e., 30 or less) I was able to watch up to 3 subjects simultaneously without missing behavior. In larger groups, only one animal at a time could be followed. Focal animals were selected from a list that held the names of the 23 subject animals in random permutations generated by repeatedly drawing the names from a hat. Upon arrival at a group, I selected the active animal highest on the list as the focal animal. Subjects remained focal until they went out of sight for more than 5 minutes or until they became inactive (i.e. lay down) for more than 5 minutes. If no other active subjects were present in the group, observations resumed when the original animal became active again; otherwise, a new subject was chosen from the list.

During an observation period, all interactions involving the focal animal were recorded. The data collected were: (1) the time and duration of the interaction, (2) the behaviors involved, (3) the identity of the social partner(s), and (4) the result of the interactions. The last category included changes in distance between the partners, the winner and loser of an agonistic interaction, and the behavior of the individuals after the interaction.

During focal periods I took scan samples around the subject every 5 minutes. I recorded the identity, behavior, and distance of all neighbors out to 20 m. If no individuals were within 20 m, the identity of the nearest neighbor was determined. I was able to accomplish the identifications without a break in the focal observation. Twenty meters was chosen as the cutoff distance for two reasons. First, in a large group there were enough individuals within 20 m that I could not identify animals at greater distances in a reasonable amount of time. Second, when a male yearling was involved in an interaction his partner almost always came from the animals recently within the 20 m boundary.

In addition to the focal observations, I used all-occurrences sampling (Altmann, 1974) to collect data on interactions involving any of the study animals. A record was also made of the number of adult bulls roaring and tending females (see below), changes in the weather, and any unusual occurrences, such as tourist activity, that might affect the herd.

SOCIAL BEHAVIORS RECORDED

A good description of bison behaviors can be found in McHugh (1958). In focusing on social behavior of the young males, I employed more detailed categories of behavior than McHugh. Brief descriptions of the social behavior patterns that I recorded during focal animal and all-occurrences sampling follow.

Non-aggressive interactions

This category includes interactions not usually seen in agonistic encounters between bison. Some of the behaviors do occur in agonistic interactions, but appear to be ancillary to the conflict.

close graze	after an approach, the partners graze within 1 meter of each other.
non-aggressive contact	one animal contacts another in a non-agonistic context. This includes rubbing, licking, and nosing of one animal by another.
nosing rear	the animal approaches and rubs its nose on the rear of the partner. The partner is almost always a female, so it is the vulva which is nosed; the noser can be male or female. A urinating female is a strong stimulus for this; an animal will approach and wet its nose in the urine stream. This behavior is almost always followed by flehmen.
flehmen	also known as lip-curl. After nosing the rear of a cow, the animal stands with its back curved concavely, its neck extended, its chin up, and its upper lip curled back. The tail is often raised, especially when the behavior is performed by a male. It is assumed that flehmen allows the substances picked up on the nose to be drawn over the vomeronasal organ, and that this organ is used to analyze the reproductive state of the female.

following	one animal walks and a second animal trails, orienting toward the first. The distance between the two animals will constantly change, with the follower catching up and then lagging behind but not passing the leader.

Sexual behavior

These behaviors are not as common in young bulls as in adults, but they do occur. Mounting is frequent in young animals but it appears to be aggressive rather than sexual, especially when both partners are male.

tending	During the rut, a bull will follow a near-estrous cow and attempt to keep other bulls away until she is ready to breed. The bull will attempt to control her movements by butting her and obstructing her. Tending may continue for an hour to a day after the pair have bred. This behavior is also performed by juvenile bulls with juvenile cows during the rut. The cows tended by juveniles are not ready to breed; the juveniles will eventually be chased away by bulls when the cows approach estrus.
mounting	one animal approaches another from behind and rears on its hindlegs as it places its chest on the partner's rump. The forelegs scrape along the back of the partner. This behavior precedes copulation. Many adult cows have oval scars on their backs from the hooves of bulls. Although in this context mounting is clearly a sexual behavior, it also occurs between males and, less frequently, between females. In these cases it seems to be involved with dominance. For example, the winner of a head-twisting bout between male 2-year-olds will often mount the loser. Young bulls will try to mount adult cows but the cows are quick to spin away or horn the males. Even when mounting occurs between males, there seems to be a sexual component because the mounter will often have a partially erect penis.

Aggressive displays

In this category are postures and behaviors that occur within social interactions and appear to function in communication between social partners.

headswing	the animal swings its head sideways toward the social partner while standing parallel to the partner. This presents the horns to the partner and is used by a dominant animal to displace a subordinate. In young bulls this often is followed by a head-twisting bout.
headwag	the animal rotates its head, shifting back and forth from clockwise to counterclockwise directions, around the axis of its neck while oriented toward the partner. In young bulls this appears to be an invitation to head-twist (see below); in older animals it occurs during displacement of an animal that has not moved away at the approach of the displayer.
headbob	the animal quickly raises and lowers the head while facing the partner. This is often done while walking quickly toward the partner, and may precede a lunge (see below).
broadside	two animals stand parallel to each other, less than 10 m apart. They may be facing the same or opposite directions. This is most often seen between bulls 2 years and older. It appears to be an agonistic display in which the bulls "size each other up." In most cases one of the bulls will turn and walk away, ceding ground to the other. Adult bulls roar (see below) while displaying. If neither bull walks away, a fight may ensue.
paw ground	a standing animal scrapes his front hoof along the substrate, kicking up dirt. This usually precedes rolling and is also seen when an interaction escalates from a broadside display. In this case, the back is arched and the tail is elevated.

rolling	The animal lies on the ground, usually in a bare patch of dirt, and rolls onto its side while kicking its legs out and up; the roll is often repeated several times. Bison do not roll completely over, probably because the hump makes it impossible. As the legs kick out, the forelegs scrape up dirt and throw it onto the animal's stomach and side. During the rut, adult bulls will usually urinate on their front hooves and into the dirt as they are lying down to begin a roll, eventually picking up a very pungent odor. I have included rolling under aggressive displays because: 1) the dirt kicked up by a bull can be seen for over a mile across flat land, 2) bulls tend to roll when the herd they are in is approached by another bull, and 3) bulls often roll as a prelude to other aggressive displays and/or fights.
chin up	the animal approaches the partner with its neck extended and chin elevated. If the partner does not give way, this leads to a chin-on-back or mounting (see below).
tail up	the animal elevates its tail above the horizontal (the tail is usually carried below the horizontal). This is seen when bulls are approaching cows during the rut or when bulls aggressively approach other bulls, and appears to be indicative of a high state of arousal. During a fight the tail may be up or, frequently, it is switched back and forth quickly. The lack of the tail up posture when calves headtwist (see below) is one of the indications that it is a playful interaction (see chapter 3).
roar	this is a deep bellow given by adult bulls around the time of the rut. If several bulls are in a rutting group, the roaring will be constant throughout the day. Bulls roar when they are tending cows, when other bulls approach, during rolling, and during broadside displays. While roaring, the bull sticks out its tongue, which is light colored and provides a sharp visual contrast against the bull's dark head. I once heard a cow roar but the sound was shorter and much higher-pitched than a bull's roar; I could not ascertain the stimulus for it, and it was never repeated.

Aggressive interactions

The following behaviors occur in agonistic encounters between individuals.

approach	one animal moves to within 3 m of another. The animal is oriented toward, and walks directly at, the partner (as opposed to two animals coming close together while grazing). This precedes most aggressive interactions. Sometimes an approach occurs without further interaction. In this case it was scored as non-aggressive.
stand over	when an animal approaches another that is lying down, he often stands with his head and neck over the lying animal. This is often followed by aggressive behavior such as displacement or head-twisting (see below). If standing over was not followed by an aggressive interaction, it was scored as non-aggressive.
chin-on-back	one animal approaches another from the rear or the side with chin up and then places its chin on the partners back. This is usually a mounting intention movement; when used in an agonistic interaction the partner often spins away and tries to evade being mounted. This behavior sometimes does not lead to mounting; the animal will chin-on-back and then stand next to the partner.
displacement	one animal approaches another and the approached animal moves away, yielding its spot (for grazing, licking dirt, lying, or just standing) to the approaching animal. This is seen very frequently whenever the herd is active. Simple displacements are as just described but, if the second animal does not move off, the interaction can increase in intensity. The would-be displacer will perform other aggressive behaviors such as headswinging, headwagging, lunging, or butting to displace the partner. In evenly matched pairs, a fight may ensue.
pushing	the animal places its head and horns against another animal and pushes. It is fairly gentle, not as strong as a butt.

butting	the animal strikes the partner quickly and firmly with its head and horns. The partner may be struck anywhere on the body. This may occur if a displaced animal is too slow in moving away or if it was unaware of the approach of a dominant animal.
horning	one horn is placed against the partner, usually against the flank, and lightly dug in. This occurs during displacements.
kicking	one animal strikes another with one or both hind feet. The kick is generally directed posteriorly.
lunging	the animal rushes toward the partner with head down and horns forward. Sharp contact ensues if the partner does not get out of the way.
head-twisting	the animal approaches the partner, the two lock horns and begin twisting their heads back and forth, pushing each other, and attempting to flip the partner's head sideways. The overall motions are the same as in a serious fight but the body postures are more playful (i.e., legs stiffer on the approach, tails down; see chapter 3). Among older juveniles (2-year-olds and older) a long bout often escalated into a fight with the animals apparently trying to injure each other.
fighting	two animals lock horns and attempt to spin the other around, in order to get a clear path to the side of the opponent. Occasionally the partners separate and then charge each other, crashing their heads together. This is seen in full intensity only between adult bulls around the time of the rut. Injuries and deaths resulting from these fights are not uncommon at Wind Cave.
chasing	the animal holds head and horns low and runs after a retreating partner. This is usually over a short distance right after a fight or head-twisting bout, with the winner chasing the loser away. Among calves it occurs over long distances in play, with up to four or five calves chasing each other through the herd.

driving	a dominant animal walks, forcing a subordinate animal to move ahead of it. This may be confused with following, but the behavior of the driven animal is a clue: the animal will look from side to side for a way to get around the driver, and usually takes the first opportunity to do so. Driving a subordinate often appears to be inadvertent on the part of the dominant animal.

Chapter 3

AGE AND SEX PREFERENCES IN SOCIAL PARTNER CHOICE

INTRODUCTION

Young bison bulls spend their first two years in cow/juvenile herds under social conditions distinctly different from those of adult bulls, which live in small all-male groups. Nevertheless, within this environment young bulls develop species-typical patterns of adult behavior. In this chapter I address the following questions. What is the pattern of young bulls' social interactions; specifically, with whom do they interact and in what types of interactions do they engage? How does this pattern compare with that of adults?

Herd structure and juvenile bison

Cow/juvenile groups consist of females of all ages and males 2 years old or less. Three-year-old males are occasional members, but, for the most part, are found in separate bull groups. Discounting lone cows or single cow/calf pairs, the size of cow/juvenile groups ranged from 6 to 236. Between December, 1983 and July, 1984 the mean group size was 52.8 (n=359). This mean is biased toward the high end because not all animals were seen every day and large groups were more likely to be seen; it does, however, indicate that large groups are found frequently at Wind Cave.

Males have a different type of social organization. Bulls three-years-old and up are found alone or in small groups. Petersburg (1973), working at Wind Cave, found bull groups ranging in size from 1 to 15 with one sighting of a group of 25. The largest bull group that I saw during the present study was 22. The mean group size reported by Petersburg (calculated every 2 weeks) ranged from 3.3 to 1.0, with the low value being found during the rut when most of the adult bulls become associated with the cow/juvenile herd.

Thus, although early development of both males and females occurs within a similar social environment, the adults live in different types of social systems for most of the year. After two years of age, the young bulls begin to spend more and more time in bull groups. By four years of age, they have entered the adult bull social organization, being found mostly in small groups and joining the cow/juvenile herd only during the rut.

Adult social interactions

As evidenced by the larger size of cow/juvenile groups, adult cows show more cohesiveness than bulls. This suggests that the relative frequency of agonistic (space increasing) interactions among bulls is greater than among cows. Rutberg (1983) compared his interaction data for cows with Lott's (1979) for bulls and found that this was indeed the case. In fact, a higher frequency of aggressive behavior between males seems to be a general finding for ungulates (see, e.g., Eccles and Shackleton, 1986).

Observable interactions among adult bison bulls are almost always aggressive. During the rut, bulls frequently fight with and injure one another. At this time of the year bulls are drawn together by the presence of estrous cows; it is the only time that large numbers of bulls are found together. When not interacting with each other or chasing cows, bulls maintain greater interindividual distances than do cows (personal observation). This seems to be a result of their aggressive behavior, which also may lead to small sized groups.

Interactions between adult bulls and cows are generally sexual. There are some low level agonistic interactions; these are usually uncontested displacements of cows as bulls move through the herd.

Juvenile social interactions

The existence of play is an important issue in dealing with juvenile behavior. While there is no general agreement on its function, play is usually identified as behavior that closely resembles other species-typical behavior patterns but is performed outside the usual functional context of these patterns (Symons, 1978a). To the observer there is no immediate function apparent in play. An example is playfighting. Young animals use many of the behavior patterns seen in adult fights, but there is an absence of agonistic displays and the use of weapons (e.g. teeth or horns) is inhibited. Playfights do not take place over disputed resources or result in changes in dominance status; in fact, dominant individuals often assume a subordinate role in playfighting (Symons, 1978b; Fagan, 1981).

Young bison calves engage in solo locomotor-rotational play during their first week of life. This play consists of running, bucking, and twisting. In addition, calves appear very curious about any object they come in contact with, whether inanimate or living, and investigate it by nosing and pushing (Egerton, 1962; personal observation). Toward the end of the first week, calves begin to play with other calves. They race through the herd, sometimes chasing each other. Although Egerton (1962) describes this play as chasing, at Wind Cave it had the appearance of solo play: up to 5 calves would race in and out among other herd members, but they did not seem to be actively chasing specific individuals. I rarely saw prolonged running or chasing play in calves older than 4 weeks.

Calves begin to playfight during their second week. This behavior is immediately identifiable as play because of the postures and movements used by fighting calves, and because of the existence of invitations to play from one calf to another. The calves push and twist their heads together, as do adult bulls, but there are often short bouts of running and jumping between headtwisting bouts. Calves often wag their tails during playfights, and they invite other calves to fight by approaching with a stiff-legged gait and wagging or bobbing their heads. A standing calf will push and nose a lying one, often inciting the second calf to get up and begin a playfight.

This fighting continues as the young bulls mature but, as early as 3 to 4 months, it becomes unclear whether it is still play. The animals continue to show some of the behavior seen in playfights, such as invitations to fight and inhibited use of horns. There are, however, aspects of the fights that do not fit in the category of play. Winners and losers are clearly identified, the fights often take place over a contested resource such as a mineral lick or a prairie dog mound, and dominance relationships are rarely reversed (see chapter 4). Egerton (1962) observed this and suggested that one function of playfighting is for calves to establish dominance relationships. This hypothesis has little support; Symons (1978a&b) reviewed hypotheses about animal play and determined that the establishment of dominance is probably not a function of play, in part because behavior used to contest access to a resource has an immediately apparent function and should be classed as agonistic rather than play behavior.

Yearlings and older calves may send mixed signals to each other during interactions. Adult bulls' hair patterns, especially their beards, pantaloons and head hair, appear to serve as aggressive signals during agonistic encounters (Lott, 1979). Calves begin to change from their natal orange to a darker coat color between 3 and 4 months of age. Yearlings have beards, head hair and pantaloons to varying degrees. In interactions, young males cannot help presenting their partners with these aggressive signals; as a result, it may be difficult for two young bulls to have a non-aggressive playfight.

Although interactions among juvenile bulls are not clearly play, the behavior involved is still different from that seen among adults. Therefore, I have examined sub-adult bull social behavior in the light of hypotheses, developed from play research, that address the possible functions of social interaction between juveniles (see Symons, 1978b and Fagan, 1981 for discussions of the possible functions of play).

Byers (1980) examined play partner preferences in Siberian ibex kids. He found that male kids directed play toward equally aged partners. This was interpreted as supporting a motor training hypothesis; kids appeared to seek partners of their own size and experience, allowing them to have sustained interactions. Partner preferences allow the kids to obtain optimum levels of motor training in social behavior patterns.

There are two hypotheses concerning the function of early social experience that I will address here. The first is that for juvenile bulls, social interactions provide experience with adult behaviors; the interactions are thus a form of practice. This hypothesis is equivalent to Byers' (1980) motor training hypothesis. The second is that the primary importance of social interactions is more immediate: they establish the young bulls' social positions within the herd. This hypothesis is similar to Byers' (1980) second hypothesis, that individuals learn the strengths and weaknesses of future competitors and initiate dominance relationships through play.

The practice hypothesis predicts that young bulls will choose social partners from a limited subset of the available animals. The subset should consist of those individuals of similar size and experience; this would allow vigorous interactions to be sustained so that the practice value of the behavior is maximized. The second hypothesis predicts that social partners will be selected from a larger subset (or the whole herd), especially including smaller animals over whom the initiator of the interaction can easily assert dominance. This outcome is not sufficient to support the second hypothesis unambiguously. Individuals might interact with a large subset of the population, but the quality of interactions could differ among classes of partners. Young bulls might practice with partners of similar size and attempt to dominate smaller partners.

My objectives in this chapter are to describe patterns of social interaction in juvenile bulls, to compare them with the adult behavior, and to test the predictions generated by the two hypotheses outlined above.

DATA

Observation and data collection methods are described in chapter 2. The data reported here were collected between March 31 and November 1, 1983 inclusive. The data include all interactions initiated by 12 yearling bulls and 11 male calves during approximately 1100 hours of focal observation.

ANALYSIS AND RESULTS

Frequency of interaction with different sex/age classes

I examined the frequency of interactions initiated by the young males with different sex/age classes. Each social partner of the focal animal was classified into one of 7 sex/age classes:

Male	Female
calves (<1 year)	calves
yearlings	yearlings
2-year-olds	2-year-olds
	older females (3+ years).

Older males were excluded from the analysis because they are not normally members of the herd and, in general, young males do not initiate interactions with them. Additionally, I excluded interactions between the young bulls and their mothers; these are rare for yearlings but, because of the unique nature of the cow-calf bond, make up a large proportion of a calf's interactions.

Data were pooled for each subject class (i.e. yearlings and calves) and tested for the proportion of interactions initiated by subject animals with members of each sex/age class using a χ^2 statistic. Expected values are based on the frequency of interaction that would occur if partners were chosen randomly with regard to age and sex; these frequencies were derived from the sex/age distribution of the total cow-calf herd.

Although the sex/age distribution of smaller groups varied somewhat from day to day, there is no significant difference between the average distribution of herds containing male yearlings and that of the herd taken as a whole ($\chi^2 = 8.82$, df = 6, $p > 0.1$).

Both yearling bulls and bull calves show a preference for social partners of their own age (figures 2 & 3; $\chi^2 = 753.10$, df = 6, $p<.001$ for yearlings; $\chi^2 = 98.37$, df = 6, $p < .001$ for calves). Within their own age class there is no preference, based on frequency of interactions initiated, for one sex or the other. These results, however, are based on pooled data. A contingency table analysis of individual (yearling or calf) vs. sex/age class of partner shows significant variation among individuals ($\chi^2 = 247.86$, df = 66, $p<.001$ for yearlings; $\chi^2 = 95.19$, df = 60, $.001<p<.005$ for calves). Closer examination reveals that the major difference among individuals is in the proportion of interactions they initiate with adult females. All show the pattern of greater than expected interactions with animals of their own age (see Appendix).

Type of interaction and sex of partner

Using a contingency table, I examined the relationship between the type of interaction initiated and the sex of the partner. This dependency was tested with a χ^2 statistic. Again, data are pooled for the 11 calves and for the 12 yearlings. Interactions with older males and between each individual and his mother are not included. Interactions are classified into the following groups (see chapter 2 for descriptions of the individual behavior patterns):

1) Aggressive - the following behaviors were recorded separately and then lumped together for this analysis: fighting, butting, chasing, horning, and aggressive display.

2) Mounting

3) Following

4) Displacement

5) Non-aggressive - all other interaction types.

INTERACTIONS INITIATED BY MALE CALVES

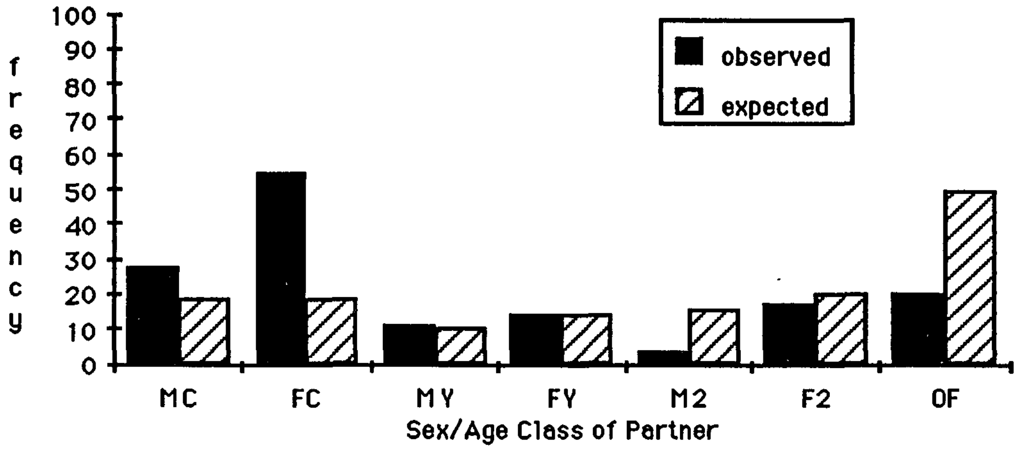


Figure 2: Interactions initiated by male calves with social partners of different sex/age classes. Expected values represent random interaction with herd members. MC, MY, & M2 are male calves, yearlings and 2-year-olds. Female age classes are the same plus OF for females older than 2 years. Note that calves interact more than expected with other calves.

INTERACTIONS INITIATED BY MALE YEARLINGS

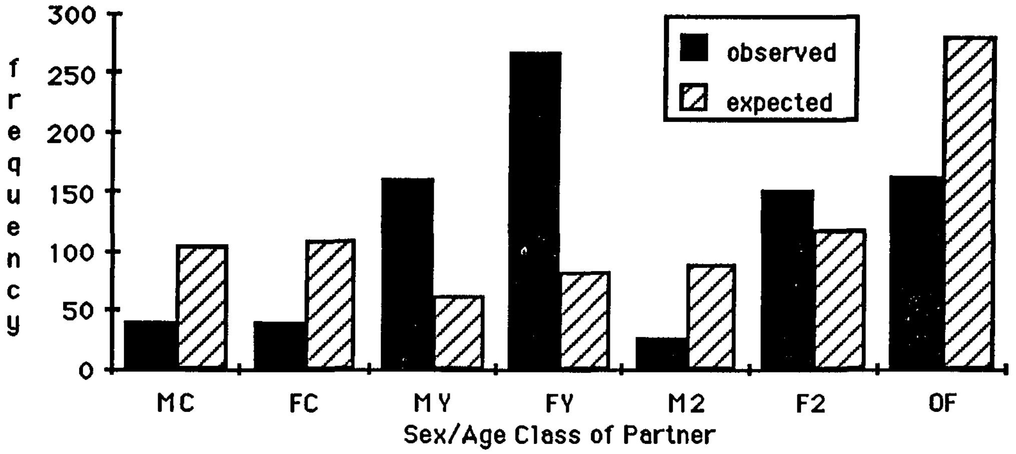
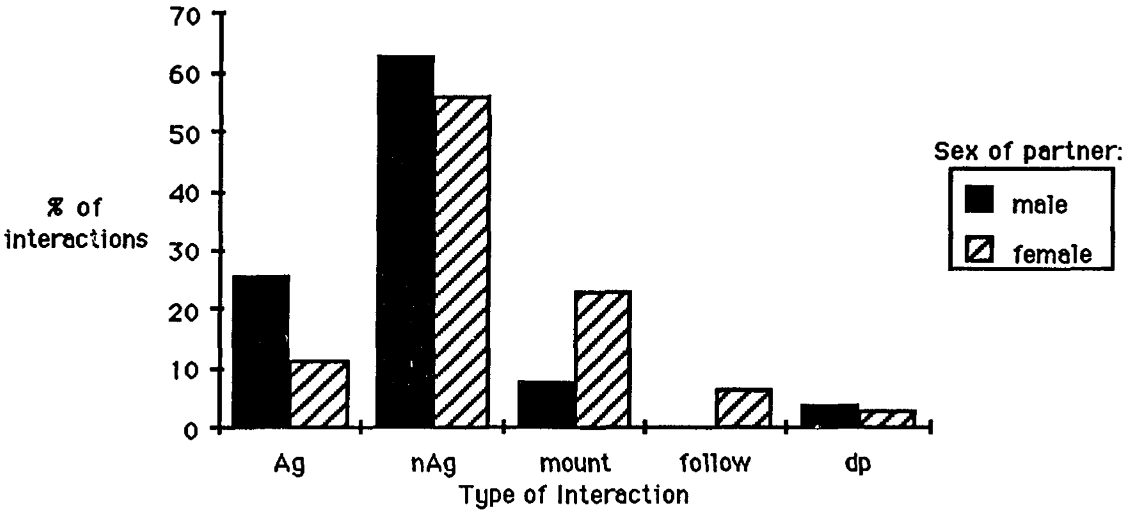


Figure 3: Interactions initiated by male yearlings with social partners of different sex/age classes. Expected values represent random interaction with herd members. MC, MY, & M2 are male calves, yearlings and 2-year-olds. Female age classes are the same plus OF for females older than 2 years. Note that yearlings interact more than expected with other yearlings.

Following was treated separately because it occurs in both aggressive and non-aggressive interactions. This behavior is often seen while the herd is on the move, in a non-aggressive context. Following also occurs after a fight, when it appears that the winner uses it to drive the loser away; in this case following seems to be an aggressive behavior. Mounting was treated separately because of its sexual component. Adult bulls mount cows in a sexual context only. Juvenile bulls often mount each other, especially after agonistic encounters, and attempt to mount females of all ages. When one young male mounts another male, it appears to be an aggressive behavior. The mounter, however, often has an erection; the motivation (sexual, aggressive, or both) is often unclear, so a separate category was used for this behavior.

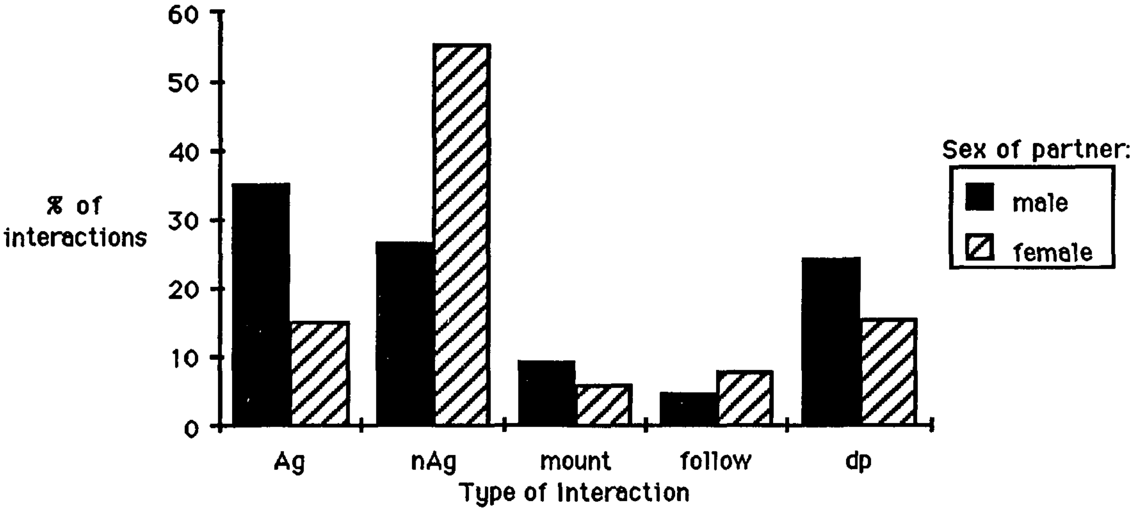
Although there was no preference for either sex when the frequency of interactions was considered, there is a relationship between type of interaction and sex of partner ($\chi^2 = 12.32$, df = 4, $p<.025$ for calves; $\chi^2 = 74.36$, df = 4, $p<.001$ for yearlings; see figures 4 & 5). In both age groups, the young males initiate relatively more aggressive interactions with males than with females. For the calves (figure 4), the percent of non-aggressive interactions is similar for both male and female partners, but with male partners there is a higher percentage of aggressive interactions while with females there is more mounting. The yearling bulls (figure 5) show a decrease in the proportion of non-aggressive interactions they have with male partners, and a corresponding increase in the proportion of aggressive and displacement interactions.

There is again, however, significant individual variability. Of the 12 male yearlings, 4 showed no significant difference in type of interaction between male and female partners. These 4 were more aggressive overall than the other 8; when they initiated non-aggressive interactions, the 4 bulls almost always chose female partners, but in aggressive interactions the partners were female as often as they were male. There were not enough interactions initiated by bull calves to treat each individual separately.



TYPE OF INTERACTIONS INITIATED BY MALE CALVES

Figure 4: Percent of each type of interaction initiated by male calves with male or female partners. Total is 100% for each sex. Ag is aggressive, nAg is non-aggressive, dp is displacement (see text). Note that interactions with other males are more likely to be aggressive than interactions with females.



TYPE OF INTERACTIONS INITIATED BY MALE YEARLINGS

Figure 5: Percent of each type of interaction initiated by male yearlings with male or female partners. Total is 100% for each sex. Ag is aggressive, nAg is non-aggressive, dp is displacement (see text). Note that when male yearlings interact with other males, it is most often aggressively but with females it is most often non-aggressively.

DISCUSSION

Age and sex of social partners

Young males show a preference for interacting with a small subset of the herd; specifically, they choose partners of their own age. This supports the hypothesis that juvenile social interactions function as 'practice' for adult behavior. The prediction that young males would choose to interact with others of similar size is borne out. In addition to partners of their own age, male yearlings initiate interactions more often than expected with 2-year-old females (Figure 3). In body size, male yearlings are larger than female yearlings and slightly smaller than female 2-year-olds. There is a similar body size relationship in Siberian ibex between male kids and female yearlings, and male kids often play with female yearlings (Byers, 1980). For a young bison bull, body size is important in agonistic encounters because he has little chance of sustaining an interaction with an individual that outweighs him by several hundred pounds. In the case of a bull under the age of 5, this would include almost any older male. So, young bulls appear to choose social partners of approximately their own size.

The second hypothesis, that juvenile interactions serve primarily to establish an individual's social position in the herd, receives less support. This hypothesis led to the prediction that young bulls would choose to interact with individuals that they could easily dominate; i.e., those smaller than themselves. Figure 3 shows that this is not the case; in fact, male yearlings have fewer interactions than expected with calves.

Characteristics of interaction between male yearlings and calves provide further evidence against this hypothesis. The interactions are always much shorter than those between yearlings, and the older bull appears to be handicapping himself in order to sustain the behavior. The conflict is usually ended by the older bull, who appears to lose interest and then walks away.

In competition for estrous females, size is an important factor for juvenile bulls. They are sexually mature by 3 years of age but, in free-ranging herds, are not able to breed until they reach full size between 5 and 6 years. The narrow choice of social partners made by young bulls, limiting themselves to partners of similar physical attributes, insures that they will be able to participate in vigorous agonistic encounters resembling those that occur between adult bulls. Furthermore, they are not handicapped by large differences in size or competence. Experience gained in these interactions could be crucial when the bull reaches physical maturity and is competing for estrous cows.

Type of interaction and sex of partner

Beginning in the first year of life, young males make a distinction in the sex of their social partners, showing different types of behavior in interactions with males and females. This pattern becomes even more pronounced in the second year. The behavior is similar to that seen in mature bulls: interactions with other bulls are likely to be aggressive while those with cows are usually sexual.

The data collected here do not indicate how young males distinguish between male and female social partners. The early and widespread occurrence of flehmen (lip-curl), a behavior in which secretions from the partner's perineum are brought in contact with the vomeronasal organ, indicates that chemical cues may be involved. This behavior is seen in rudimentary form even in 2-week-old calves, and by the end of the first year it is well developed.

Thus, while they are maturing within the cow/juvenile herd, young males choose social partners that allow them to behave in ways similar to adult bulls. They sustain interactions with animals of similar size, and behave appropriately with regard to the sex of the partner. In the following chapter I examine one of the consequences of aggressive interactions among yearling bulls: the establishment of dominance relations among the yearlings.

Chapter 4

DOMINANCE RELATIONSHIPS OF YEARLING MALES

INTRODUCTION

As shown in the previous chapter, young males frequently interact with each other, and these interactions are most often aggressive. This raises the question of what kind of social structure arises out of the agonistic interactions. A structure would be revealed by predictable patterns of social behavior within pairs of individuals. I have two objectives in the present chapter: 1) to describe the social dominance structure among male yearlings, and 2) to determine for the same group if there are physical correlates of dominance.

Social structure and dominance

Agonistic behavior is common to most social species (see Barash, 1977 for a review). The intensity of aggressive behavior between individuals is generally related to the nature of the resources that are being contested. If a resource is limited and defensible, so that an individual can prevent others from gaining access to it, then agonistic interactions may be extremely violent (Barash, 1977). Schnebel and Griswold (1983) found this to be the case in a group of captive wild pigs. Interactions between males were more intense over an estrous female, a limited defensible resource, than over feeding or resting places, which were widely spread out.

In most avian and mammalian social groups, stable agonistic relationships exist; one individual of a pair is usually the aggressor and/or winner in agonistic encounters (see Wilson, 1975; Brown, 1975 for reviews). This phenomenon is referred to as dominance. It is possible for dominance to be time and context dependent; for example, animal A is dominant in encounters over food while animal B is dominant in conflict over access to potential mates. This dependence on context occurs when the value of a disputed resource differs for two individuals (Popp & DeVore, 1979). An animal that values a resource highly should be willing to sustain an agonistic encounter longer than one that values it less. In the example given above, animal A may value food more highly than mates at the time in question.

Hinde (1983) points out that the concept of dominance has greater explanatory value if it can be shown that dominance relationships hold in different contexts, such as yielding priority of access to food and mates, or that dominance is correlated with independent measures such as differences in physical characteristics of the animals. In addition to describing the outcomes of agonistic interactions in a given context, dominance then becomes a factor in explaining the observed social organization.

The dominance structure within a social group can take one of several different forms. A linear hierarchy is most commonly reported. In this type of dominance structure one animal dominates all others, another dominates all but the first, and so on to the last individual, who is subordinate to everyone. This organization is common in primates and in captive groups of birds; it has received the most attention and will be discussed further below. A second type of dominance structure involves non-linear, stable dyadic relationships. Each pair of individuals, called a dyad, has an established dominant-subordinate relationship, but there is no linear ordering of animals. This arrangement is found in free-ranging adult bison bulls (Lott, 1979). In the bison there is also a temporal component to dyadic relationships; dominance is stable in a dyad for short periods only, reversing when the relative conditions of the bulls change (Lott,1979; see below for more detail).

Several hypotheses have been suggested concerning the importance of dominance to social organization. One is that dominance serves to reduce aggression within a group because, once dominance relationships are determined, agonistic encounters are settled quickly and without fights. This allows group activities to take place without constant disruption. Dominance does appear to reduce the frequency and intensity of aggressive behavior that occurs, but this hypothesis suggests that subordinate animals must sacrifice their own needs for the good of the group. Except when applied to small groups of close relatives, in which kin selection can operate, this group selection argument is not in accord with current understanding of the evolution of behavior.

A more parsimonious explanation results from examining the benefits and costs of dominance to individual group members. The benefit to dominant individuals is easy to see: priority of access to limited resources, especially food and mates. Access to mates is particularly important for male ungulates: dominant males often do most of the breeding (Geist [1971], on bighorn sheep; Lott [1979], on bison). The benefits to subordinate animals are less immediately clear but include a decreased chance of injury in agonistic encounters and continued group membership. Group membership can provide protection from predators, increased foraging efficiency, and a chance to mate on the sly. This chance to mate may be greater than a subordinate animal would have on its own. In addition to these benefits, there is the possibility of increasing one's dominance status due to aging, injury, or death of the dominant individuals (see Brown, 1975).

Dominance in bison bulls

For adult bison bulls a major advantage of being dominant is that it provides access to estrous cows. Lott (1979) studied bulls during the rut at the National Bison Range in Montana. He found that over the three weeks of the rut, the dominant bulls, as determined by success in fights and other agonistic encounters, bred more cows than did the subordinate bulls. The implication is that there will be strong selection for any heritable traits which enhance a bull's ability to dominate others.

There are, however, costs associated with maintaining dominance, especially during the rut. These costs arise from the need for constant defense of estrous cows against challenges by other bulls. During the rut, much running and fighting is required, leaving little time for feeding and resting; the physical condition of dominant bulls deteriorates (Lott, 1979).

During the rest of the year, the benefits enjoyed by dominant bulls are not as obvious because there appear to be no limited and defensible resources. It is possible that dominant animals can obtain better forage by displacing subordinates from favored feeding sites. In this way dominants could regain superior physical condition, allowing them to withstand challenges by other bulls during the ensuing rut. Just such a situation was found in red deer by Appleby (1980). Red deer stags have a linear hierarchy both in and out of the rut. Outside of the rut, dominant stags have first access to food which, in the study area, had a patchy distribution. Appleby (1980) suggested that dominant stags would gain more weight in the spring, especially after a bad winter. Body weight was correlated with dominance and breeding success.

A major difference between the situation found in red deer and that in bison is group size. Non-rutting red deer stags stayed in a group of about 60. The large number of animals would decrease the availability of food and increase the effective patchiness of the resources. In small groups of bison bulls, patchiness is not a problem; two bulls feeding alone in an area of 15 or 20 hectares are unlikely to compete for small feeding sites.

It is not known to what extent dominance relationships exist among free-ranging adult bison bulls outside of the rut. Petersburg (1973) could not determine an overall dominance hierarchy for the bull population at Wind Cave. He did write that "indications of such a hierarchy were evident" and that "secondary hierarchies were often readily identifiable within herd sub-units such as bull groups," but he did not elaborate.

In female bighorn sheep, Eccles and Shackleton (1986) could find no benefit to dominant animals in terms of weight gain, foraging efficiency, or reproductive output. The situation for these sheep appears similar to that for non-rutting bison bulls. In both cases the only apparent contested resources are feeding sites and resting places, which are usually not in short supply. Priority of access to them would not seem to confer a measurable advantage in physical condition. There may be a benefit to dominant animals under conditions of stress or heavy predation, but it is not evident under present-day conditions. Even if dominance were strongly established, interactions might occur so rarely or be so subtle that identification of dominance relationships from observations in the field would be difficult.

Another possibility is that dominance itself is a resource (Schnebel and Griswold 1983). Non-rutting bulls would try to maintain dominance during the year to obtain an initial advantage at the beginning of the rut. Among rutting bull bison, Lott (1979) found a non-linear hierarchy that shifted over time. It appeared that dominant animals were worn down through constant challenges. The instability of the relationships may indicate that dominance serves primarily to establish access to females. Breeding must take place over such a short period that the potential benefits to a subordinate bull in challenging a dominant one become worth the risk of injury (Lott, 1979). Because mating opportunities become rarer as the rut progresses, leading to more fighting among the bulls, males that are dominant at the beginning of the rut would have a great advantage. They could breed as many cows as possible early on, and then leave the herd to avoid possible injury.

Physical and behavioral factors and dominance

An intuitively attractive explanation for a linear dominance hierarchy is that it might result from intrinsic physical or behavioral differences among individuals. These differences could be measured independently of the dominance relationships that exist within the group. Important intrinsic factors might include body height or weight, and aggressive behavior toward non-group members. Several mathematical models indicate that such differences are unlikely to result in linear hierarchies (Landau, 1951a&b; Chase, 1974). These models show that the assumptions necessary for intrinsic differences to produce linear hierarchies are very strict. For example, in order to account for a linear hierarchy there must be a correlation coefficient of at least 0.9 between a ranking based on some independent measure, such as success in pairwise interactions, and the distribution of the actual numbers of individuals dominated in the group. A coefficient of correlation of 0.9 is much larger than those that have been measured in actual situations (Chase, 1974).

Linear hierarchies would be more likely to form if experiential factors are involved; that is, if the outcomes of current interactions are dependent on the results of preceding ones. In domestic hens, Chase (1985) found that during the formation of dominant-subordinate relationships in groups of four individuals, the direction of interactions that occurred was usually such that a linear hierarchy would form. In other words, current interactions were dependent on previous ones; the experiences of individuals with other group members could explain hierarchy formation.

Measuring dominance

In determining the type of dominance structure that exists within a group, one can use several methods. Early work on dominance showed that dominance relationships were transitive, resulting in strongly linear hierarchies (see Brown, 1975). In this context, transitivity means that if A dominates B, and B dominates C, then A will also dominate C. These studies were conducted on domestic chickens that were held in captivity and divided into artificial groups.

Subsequently, data collected in the field on many species have been used to arrange group members into linear dominance hierarchies, usually with some success. The method (as outlined by Brown, 1975 and

Lott, 1979) begins with the assumption that a linear hierarchy exists; the animals are then arranged into a ranking that minimizes the number of reversals. A reversal is an interaction that goes against the dominance order; for example, if animal B is below A in the hierarchy, as determined by the majority of interactions, then any interaction in which B dominates A is a reversal.

The problem with this method, which I shall refer to as the *dominance matrix method*, is that although a linear hierarchy can be developed in most cases, this hierarchy conceals irregularities in the relationships. Most groups have at least one circular triad (A dominates B, B dominates C, C dominates A). These triads are not evident when the hierarchy is presented. In addition, most data collected in the field contain missing values for cases where no interactions were observed between a given pair of animals. In some of these unobserved cases the relationship might be a reversal in the hierarchy, but the assumption of transitivity does not take this into account.

In order to deal with a situation in which they did not observe interactions involving all possible dyads in a group of dairy heifers, Beilharz and Mylrea (1963) developed a ranking index called *dominance value (DV)*. The DV is based on the proportion of observed social partners that an animal dominates. An assumption inherent in the concept of the dominance value is that this proportion represents some meaningful social characteristic of the animal. The advantage of the DV is that it allows a comparison of animals without assuming transitivity of dominance, and therefore makes no assumptions about the direction of dominance in unobserved interactions. There is a corresponding disadvantage in that the DV does not take into account the identities of the individuals dominated. It would be possible for a low-ranking individual to have a high DV by avoiding interactions with all animals dominant to him.

A third approach is to rank individuals by the number of animals each one dominates (Kendall, 1955). If interactions are observed among all possible dyads, the rank-order obtained is the same as would be found using DV. In this initial ordering by number of subordinates, it is possible for an individual to be ranked lower than one he has beaten. Kendall (1955) shows a method by which the competitive ability of opponents can be incorporated into the ranking (see Analysis and Results section below). This has the advantage that the social characteristics (i.e., the "quality") of opponents are taken into account, but the method shares disadvantages with the dominance matrix in that it makes assumptions about unobserved interactions and it produces a linear ordering of individuals that obscures any circular triads that exist.

The three methods outlined above each make different assumptions and measure different aspects of dominance. Where a true linear hierarchy exists, rankings obtained from the methods will be highly correlated, especially those derived from DV and number of subordinates ranking. When the relations among group members are not transitive, and especially if some otherwise low-ranking individuals are dominant to specific high-ranking ones, the three methods result in uncorrelated rankings. Thus, the correlation between the three methods provides a measure of transitivity inherent in the dominance relations within the group.

Chance effects

An interesting property of dominance has been pointed out by Appleby (1983). The probability of getting a hierarchy by chance when dominance relationships are really random is much higher than is intuitively expected. For example, in a group of three animals there are 6 possible patterns of dominance relations. Four of these are linear arrangements, the remaining two are circular triads. Thus, if dyadic relationships are stable but are completely independent of other dyadic relationships, there is still a 75% chance that the relationships will be linear (i.e., dominance will appear to be transitive).

As group size increases, the probability of linearity decreases, but is still appreciable. This is especially true if one is willing to accept as linear a hierarchy showing one or two reversals, or if there are missing data.

It is, therefore, important to be able to test for transitivity in the observed relationships before using them to develop a ranking. Appleby (1983) supplies such a test (adapted from Kendall, 1962). The test determines whether the number of circular triads in the data is less than would be expected by chance. The number of circular triads can also be used to calculate two indicies, h (Landau, 1951a) and K (Kendall, 1962), that measure the degree of linearity in a dominance matrix. Details are given in the Analysis and Results section.

In order to present a complete picture of the dominance relations among young bison bulls, I have used the three ranking procedures mentioned above. A high degree of similarity among the three rankings would strengthen any conclusions drawn about the dominance structure among the yearlings. Secondly, I have examined the transitivity and linearity of the yearlings' dominance relations. Significant linearity would indicate the existence of an overlying structure, above the level of dyadic interactions. Finally, I have examined the relationship of individual physical characteristics to success in agonistic encounters.

METHODS

Field observation methods are described in chapter 2. In addition, physical measurements were taken of all male yearlings and calves at a round-up that took place in November, 1983. Animals were run through narrow chutes and over a scale. The following measurements were made: height at hump, weight, horn length, and horn diameter. The absolute weights are not completely reliable because the calibration of the scale was suspect. The relative order of the weights should still be reliable, and it is this rank-order rather than the weights themselves that is used in the following analyses. It should be noted that the weights obtained were within the range reported in the literature for bull calves and yearlings.

The following analyses were carried out only for the yearlings because the calves did not interact with one another frequently enough to support a meaningful analysis. The behaviors used to determine dominance are all aggressive interactions and displacements among yearling bulls in which a clear winner and loser could be determined. The winner of an interaction was the individual that eventually displaced his partner. The dominant member of a pair was the individual that won the majority of the interactions. All 16 members of the male yearling cohort are included in the analysis.

ANALYSIS AND RESULTS

Dominance matrix

A 16 × 16 dominance matrix of winners and losers in the interactions was created from the data. The best linear hierarchy was then determined by assuming transitivity of dominance and varying the ranking of individuals in order to minimize the number of entries below the diagonal of the matrix. Entries below the diagonal represent reversals and provide a rough measure of the degree of linearity in the computed hierarchy.

The dominance matrix with the best linear hierarchy is shown in Table 1. The order is also shown as ranking #1 in Table 2. Out of 120 possible pairs among the 16 yearlings, I was able to collect data on 81. Of these, only 10 pairs (12.3%) showed any reversal in status over the period of the study. In seven of these (8.6%) one animal was dominant at the beginning of the study and the other was dominant at the end. In the remaining 3 pairs (3.7%) the relationship continued to be ambiguous throughout the study period. Dominance relations among the yearlings are extremely stable over time, especially when compared with those reported for adult bulls.

Although Table 1 shows the best linear order, 11.85% of the observations are below the diagonal. This represents a degree of non-linearity in the hierarchy. By comparison, Lott (1979) found that the best linear order for the adult bulls he observed had 22% of the observations below the diagonal. While yearling dominance structure appears to be more linear than that for adult bulls, there remains a number of relationships that cannot be fit into a linear hierarchy.

Dominance value

A dominance value (DV; Beilharz & Mylrea, 1963) was calculated for each individual. $DV=\arcsin(\sqrt{x})$ where x is the ratio of animals dominated by the individual to the total number of social partners the individual had. The arcsine transformation gives the DVs a normal distribution, but does not change the rank ordering of values of x. If there are reversals within a pair, then the number of wins divided by the number of interactions for that pair is used in calculating the number of subordinates. For example, if yearling Z beat yearling Y 5 times and Y beat Z 4 times, then Z receives 5/9 of a subordinate and Y receives 4/9 of a subordinate for the relationship.

Dominance values for the 16 yearlings are listed as ranking #2 in Table 2. Because DV is a measure of the proportion of social partners that are dominated, it does not depend on the assumption of transitivity of relationships, as does ranking #1 in Table 2. The DVs are not in the same order as ranking #1, but they are close. As a group, the 7 top animals are the same in both rank orders.

Rank by number of subordinates

I calculated a third ranking by using the number of subordinates. The dominance matrix was converted into a matrix of 1s and 0s (Table 3). Entries in the cells of the matrix are either 1, meaning the row individual is dominant to the column individual; 0, meaning the column is dominant to the row; or 0.5, meaning the individuals are tied. Cells for pairs of animals that were not observed in agonistic interactions receive a value of 0.5. The row totals then indicate the number of individuals that each animal has dominated, so individuals can be ranked by number of subordinates (Kendall, 1955).

This method yields ties between individuals, and can also rank an individual lower than one he has beaten. For example, in Table 3 **RSC** is ranked below **RC** (10.5 subordinates for **RSC** against 12 for **RC**) but in dyadic interactions, **RSC** is dominant to **RC**. One way to incorporate this additional information into the ranking is to compute a new score for each animal by adding together the scores of each animal he has beaten plus one-half the score of each one he has tied. These new scores take into account the "quality" of the opponents that an individual has dominated; i.e., an individual that wins over a few dominant individuals receives a higher score than one that dominates many low-ranking individuals. Algebraically this recomputation is identical to squaring the original matrix (Kendall, 1955). In order to square the matrix, one change must be made: the cells on the diagonal receive a value of 0.5 (each animal tied with himself). With repeated powering of the original matrix, the ranking of individuals converges to an unchanging one. As the matrix is powered, the scores for each animal increase geometrically. However, the absolute value of the scores is of no interest; it is the rank order that is important.

The number of subordinates for each animal is shown in Table 3. It can be seen that there are many ties in the number of subordinates. When the matrix is powered to account for the "quality" of opponents, these tied values disappear. After the matrix was raised to the 5th power, the rank order of individuals remained constant. The resulting order is shown in Table 2 as ranking #3. Again, the rank order is slightly different from the other two, but the same 7 individuals are at the top.

DOMINANCE MATRIX

Loser

Winner

Animal	RC	STC	RSC	HTC	RN	A	PC	QC	NC	TC	IC	KC	LC	EC	BRC	GC	wins
RC	-	3	1		6	4	1	2	7	5	2	2		3	5	2	43
STC	1	-	2		5		2	1		2			1	2		4	20
RSC	4		-		8			1	3	5					8	3	32
HTC				-	2	2			1	5	1				2	4	17
RN					-		1	4	3	3	2		3	1	3	2	22
A	2					-		4	8	3		1	1	1			20
PC	2	2					-	4		2			1		3	4	18
QC								-	8	1					6		15
NC			2	1					-	18	1				3		25
TC									2	-	2	1	1	3	2	1	12
IC								1			-			2			3
KC		1										-	2		1	2	6
LC													-	2	11	3	16
EC				2										-	1	4	7
BRC														2	-	2	4
GC									4	1	5					-	10
																	270

Proportion of entries below diagonal: 11.85%

Table 1: Dominance matrix for 16 male yearlings in 1983. The rank order shown gives the best linear arrangement, with the fewest reversals. Entries below the diagonal represent reversals.

DOMINANCE RANKINGS

		Ranking	
Animal	1 dominance matrix rank	2 DV	3 rank by # subordinates
RC	1	66.60	1
STC	2	61.68	5
RSC	3	63.43	2
HTC	4	64.34	3
RN	5	56.31	7
A	6	62.84	6
PC	7	61.40	4
QC	8	33.21	13
NC	9	38.06	9
TC	10	37.66	14
IC	11	30.00	10
KC	12	49.11	8
LC	13	35.26	11
EC	14	28.88	12
BRC	15	21.88	16
GC	16	26.01	15

Table 2: Dominance rankings based on 3 different methods. DV is dominance value (see text). Note close agreement of all rankings: the top 7 animals are the same. DV (rank #2) is ranked from high to low values, the other two rankings are from 1 (most dominant) to 16.

NUMBER OF SUBORDINATES MATRIX

		Subordinate																
	Animal	**RC**	**STC**	**RSC**	**HTC**	**RN**	**A**	**PC**	**QC**	**TC**	**NC**	**IC**	**KC**	**LC**	**EC**	**BRC**	**GC**	**Total No. of Subordinates**
	RC	-	1	0	0.5	1	1	0	1	1	1	1	1	0.5	1	1	1	12
	STC	0	-	1	0.5	1	0.5	0.5	1	1	0.5	0.5	0	1	1	0.5	1	10
	RSC	1	0	-	0.5	1	0.5	0.5	1	1	1	0.5	0.5	0.5	0.5	1	1	10.5
	HTC	0.5	0.5	0.5	-	1	1	0.5	0.5	1	0.5	1	0.5	0.5	0	1	1	10
D	**RN**	0	0	0	0	-	0.5	1	1	1	1	1	0.5	1	1	1	1	10
o	**A**	0	0.5	0.5	0	0.5	-	0.5	1	1	1	0.5	1	1	1	0.5	0.5	9.5
m	**PC**	1	0.5	0.5	0.5	0	0.5	-	1	1	0.5	0.5	0.5	1	0.5	1	1	10
i	**QC**	0	0	0	0.5	0	0	0	-	1	1	0	0.5	0.5	0.5	1	0.5	5.5
n	**TC**	0	0	0	0	0	0	0	0	-	0	1	1	1	1	1	0.5	5.5
a	**NC**	0	0.5	0	0.5	0	0	0.5	0	1	-	1	0.5	0.5	0.5	1	0	6
n	**IC**	0	0.5	0.5	0	0	0.5	0.5	1	0	0	-	0.5	0.5	1	0.5	0	5.5
t	**KC**	0	1	0.5	0.5	0.5	0	0.5	0.5	0	0.5	0.5	-	1	0.5	1	1	8
	LC	0.5	0	0.5	0.5	0	0	0	0.5	0	0.5	0.5	0	-	1	1	1	6
	EC	0	0	0.5	1	0	0	0.5	0.5	0	0.5	0	0.5	0	-	0	1	4.5
	BRC	0	0.5	0	0	0	0.5	0	0	0	0	0.5	0	0	1	-	1	3.5
	GC	0	0	0	0	0	0.5	0	0.5	0.5	1	1	0	0	0	0	-	3.5

Table 3: Number of subordinates for each yearling. This is developed from Table 1 (see text). The matrix is used to calculate ranking #3 in Table 2.

Correlation of rankings

Next I examined the consistency of the rankings obtained by the three methods outlined above. Spearman rank-order correlation coefficients were used to make this evaluation.

The Spearman rank-order correlation coefficients (r_s) for the three rankings shown in Table 2 are as follows:

for ranking 1 with 2 $r_s = 0.906$
for ranking 2 with 3 $r_s = 0.941$
for ranking 1 with 3 $r_s = 0.906$

Each of the correlations is highly significant ($p < 0.01$). The strong correlations between the three methods indicate that there are no major anomalies in the relations among the yearlings, and suggest that there is a degree of transitivity in the relationships. Because of the consistency between rankings, I will use only the dominance matrix rank (#1 in table 2) in the following sections.

Transitivity of relationships

The rankings examined in the preceding sections are measures of each yearling's relative ability to dominate others. By themselves, these rankings do not provide evidence for a linear hierarchy. As was shown in the dominance matrix, there is evidence that the yearlings' relations are not linear. To investigate the structure of the dominance relations, I used a test that measures transitivity in the interactions among the individuals (Appleby, 1983). The procedure addresses the question: In all possible triads A,B,C in the group, if A dominates B and B dominates C, does A dominate C more often than expected by chance? The data for this test are the number of subordinates for each animal (as shown in Table 3). First the number of circular triads (d) is calculated as follows:

$$d = \frac{N(N-1)(2N-1)}{12} - 1/2 \sum (S_i)^2$$

where N is group size (16 in the present case) and S_i is the number of subordinates for each animal. Next, degrees of freedom and a χ^2 value are computed:

$$df = \frac{N(N-1)(N-2)}{(N-4)^2}$$

$$\chi^2 = \frac{8}{N-4}\left[\frac{N(N-1)(N-2)}{24} - d + 1/2\right] + df$$

This value is tested against a standard χ^2 distribution.

The number of circular triads (d) is 112, yielding a χ^2 value of 42.33 with 23 degrees of freedom for the test of transitivity ($p < 0.025$). This result shows that the number of circular triads in the data is significantly less than what would be expected if the direction of dominance in a relationship was random with respect to other relationships involving the same individuals. Appleby (1983) points out that this test is actually conservative when there are a number of unknown relationships, as in the present case. The significant transitivity indicates that among the male yearlings there are some characteristics that lead to dominance. An animal dominant in one dyad has an increased probability of being dominant in other relationships.

Linearity

Significant transitivity in dominance relationships is one indication of linearity in a hierarchy. To investigate this directly, I calculated two measures of linearity for the data: **h** (Landau, 1951a) and **K** (Kendall, 1962 described in Appleby, 1983). They are computed as follows:

$$h = \frac{12}{N^3-3} \sum_{a=1}^{N} \left[V_a - \frac{N-1}{2}\right]^2$$

where V_a is the number of animals that individual **a** dominates. **K** is identical to **h** for odd values of N; for even values, as in the present case, **K** is:

$$K = 1 - \frac{24d}{N^3-4N}$$

where d is the number of circular triads (see above). Both measures are based on the variance of the distribution of V_a. If each individual dominates a different number of others, the variance of V_a is at a maximum and the hierarchy is linear. For example, in a group of 5, if one animal dominates all others, another dominates all but the first and so on, the distribution of V_a is {4,3,2,1,0}. This distribution has the maximum possible variance and implies linearity in the hierarchy. The measures **h** and **K** range from 0, indicating a complete lack of linearity, to 1, indicating a strict linear hierarchy. Chase (1974) suggests using 0.9 as the target value for a linear ranking.

The two measures of linearity agreed well with each other: **h**=0.35 and **K**=0.33. This agreement is not surprising because the measures are not independent. The low values indicate a lack of linearity in the dominance relationships among the yearlings. This finding is interesting when combined with the significant transitivity in the relationships. It suggests that there are certain attributes, such as physical differences, that account for a portion of the success each animal has in dominating others. Some individuals are more likely to be dominant, but not to the extent that a linear hierarchy develops.

Physical attributes and dominance

To examine the relationship between dominance rank and physical attributes of the yearlings, I calculated Spearman rank-order correlations between dominance and body weight, body height, and the two measures of horn size.

Table 4 shows that there is no significant correlation between weight or height and dominance rank but that there are significant correlations between rank and horn length (r_s=0.814, $p < .01$) and between rank and horn diameter (r_s=0.722, $p < .01$). The correlation between rank and horn length accounts for 66% of the variance whereas that for horn diameter accounts for 52%. This suggests that there is an effect of certain physical factors, namely horn size, on a yearling's ability to dominate others.

The previous analysis forced the animals into a linear ranking so that a correlation coefficient could be calculated. Since the dominance relations in the group were shown not to be linear, I felt that a less biased approach would be to examine each dyad separately, without ranking individuals. If physical differences are irrelevant to the establishment of dominance, then in 50% of the dyads the dominant animal should be physically larger and in 50% he should be smaller. I tested the observed versus the expected proportions using a G–statistic (which is tested against a χ^2 distribution).

DOMINANCE AND PHYSICAL ATTRIBUTES

Animal	rank	weight (kg)	height (cm)	horn length (cm)	horn diameter (cm)
RC	1	268	130	29.2	7.4
STC	2	264	132	--	--
RSC	3	--	--	33.0	7.4
HTC	4	--	--	31.8	7.6
RN	5	257	130	29.2	9.9
A	6	202	137	30.5	7.4
PC	7	209	140	30.5	7.9
QC	8	232	130	27.9	6.6
NC	9	243	132	26.7	7.4
TC	10	268	132	29.2	7.4
IC	11	211	124	27.9	6.9
KC	12	286	135	17.8	6.9
LC	13	--	--	27.9	6.6
EC	14	175	127	25.4	6.6
BRC	15	180	118	24.1	6.6
GC	16	--	--	26.7	6.9
Mean:		233.0	130.5	27.9	7.3
		r=0.376 n.s.	r=0.383 n.s.	r=0.814 p<.01	r=0.722 p<.01

Table 4: Dominance rank compared with physical measurements. The rank is the same as ranking #1 in Table 2. Spearman rank-order correlation coefficients (r) between dominance rank and each physical attribute are shown. Only horn length and horn diameter are correlated with dominance rank.

There were 45 dyads with complete data for dominance and body weight. In 28 the heavier animal was dominant and in 17 the lighter animal was dominant. This is not significantly different from what would be expected by chance ($G=2.688$, $df=1$, $0.1<p<0.5$). Forty-one dyads had complete data for height. In 26 the taller animal was dominant and in 15 the shorter animal was. This is not different from the null hypothesis ($G=2.936$, $df=1$, $0.05<p<0.1$).

In examining horn size, I used only dyads that had more than a 2.54 cm difference in horn length. This was the smallest reliable difference, given the conditions under which measurements were taken. There were 44 dyads with complete data. In 38 the animal with longer horns was dominant. This is a highly significant departure from expected ($G=25.655$, $df=1$, $p<<0.001$). The probability of being dominant over an animal with shorter horns is about 0.86.

The results of the correlation analysis and the dyadic analysis reveal the same relationship between horn size and dominance. The dyadic analysis, in addition, shows the high probability of a longer-horned yearling being dominant.

DISCUSSION

The previous chapter and the present one show that there are antecedents to adult bull social behavior in the interactions of juvenile bulls. The young bulls treat male and female social partners differently, interact aggressively with each other, and establish dominance relationships. These behaviors are all similar in many regards to those of mature bulls. The dominance structure that arises among the yearling bulls is, however, different from that seen in adults. Young bulls develop stable dominance relations that are characterized by low levels of agonistic behavior. As bulls mature there is a shift to less stable dominance relations. High levels of aggression, especially during the rut, are associated with more frequent shifts of status within pairs. Social instability could be temporary, with adults having more stable relationships outside of the rut. The data to test this hypothesis are not available.

The dominance structure of the yearlings is stable and non-linear, yet there is a significant degree of transitivity within it -- some yearlings can be ranked above others with regard to their overall social status. This pattern of relationships can be explained best by a mixture of physical factors and social experience.

The importance of physical factors to success in agonistic interactions leads to a bias for transitivity in the relationships; animals with certain characteristics are more likely to be dominant. For yearling bulls there is a significant relationship between horn size and social status. However, the fact that in 14% of pairs with differences in horn size the smaller-horned animal was dominant, and the existence of stable dominance relationships in pairs with no difference in horn size strongly suggests that some non-physical factors are involved. A history of interaction with specific individuals combined with the ability to remember the outcomes of previous interactions would favor the establishment of stable dyadic relationships.

Because physical factors alone can not completely account for the observed relationships, it seems best to consider yearling social organization to be composed of individual dyadic relationships without an overlying structure. A similar conclusion was reached by Lott (1979) in his study of adult bulls. A yearling pair's relationship, once established, does not change over the year. Dominance within a dyad is established early on; it may be that the first interaction sets the stage for a relationship. In this case chance can play a role in determining the direction of dyadic relationships: initial success may depend on the previous experience of the individuals, and not simply on their physical differences. For example, a yearling having just displaced another may carry that success over by approaching and displacing a third individual. Chase (1985) found that this type of interaction was common in the development of relationships among hens.

Several observations in the field suggested a possible mechanism for the effect of horn size on dominance. Yearlings' horns are straight and grow away from their heads. On several occasions I have observed a yearling being hit on the eye by his opponent's horn during a head-twisting bout. This contact results in his backing off and losing the encounter. In this way, long horns might determine dominance within that pair. As the males grow, the horns curve back toward the top of the head and no longer poke opponents in the eyes.

For adult bulls, Lott (1979) found no correlation between weight and dominance. However, he measured weights after the rut. Because the physical condition of dominant bulls appears to decline during the rut, a rank-order based on weights taken afterward may not be the same as one determined at the beginning (Lott, 1979). Petersburg (1973) saw no relationship between horn size and success in agonistic encounters between bulls, but his judgement of horn size was made visually. Differing head sizes and hair patterns of bison bulls make accurate judgement of horn size differences difficult under field conditions. The relationship between physical factors and dominance in adult bulls is still an open question. It is, however, true that many older males at Wind Cave win fights and are able to displace others even though their horns are only broken stumps (personal obs.). This suggests that previous experience within dyads is important in determining dominance.

What are the advantages of dominance for bison yearlings? There are few apparent resources to be gained. Although many encounters take place in mineral licks or on prairie dog mounds, at which bison also lick dirt, the displaced animal is always able to use the lick either by moving to a different spot or by waiting until the dominant animal moves on. In an environment with heavy predation, a subordinate's having to wait until the group moves on in order to get a chance at the lick might be a disadvantage. This possibility could not be examined under the conditions at Wind Cave.

Yearlings do appear to go out of their way to engage other yearlings agonistically. In a study of captive wild pigs, Schnebel & Griswold (1983) found that dominant individuals went out of their way to engage subordinates. This lead them to suggest that dominance itself was a resource worth defending. In bison, relationships that may have developed before the rut become less stable during the rut, when a limited resource becomes available. Defense of dominance during most of the year is therefore no guarantee of success, but it might provide an initial advantage at the start of the rut.

It may be that the stability of dyadic relationships is not especially meaningful to the yearlings themselves. If the purpose of yearling interactions is to provide experience in adult behavior patterns, as discussed in chapter 3, then the stable relationships that emerge may provide no benefit in and of themselves to the yearlings. The stability may be a result of the fact that there are no limited resources worth fighting for, so there is no reason to challenge the status quo. When defensible resources, in the form of estrous cows, become available to the maturing bulls, previous experience may provide certain individuals with an initial advantage. As soon as a bull reaches full physical maturity, he must compete with all adult bulls, not just those of his own age class. Experience with dominance could then allow him to breed at a younger age than lower-ranking peers.

The stability of dyadic relationships among young bulls raises the issue of individual recognition. For specific relationships to develop, yearlings must be able to recognize each other. This issue will be addressed in the succeeding chapter.

Chapter 5

DYADIC RELATIONSHIPS AMONG YEARLINGS: ASSOCIATIONS IN SPACE

INTRODUCTION

In the previous chapter I found what appear to be individual dyadic relationships among male yearlings, as indicated by the stability of dominance within pairs of animals. There are two mechanisms that might account for the appearance of these relationships. First, individuals might recognize each other and develop social relationships based on their histories of interaction. Behavior in the current interaction would be influenced by previous experience with that same partner. In this case there exists a social relationship between two specific individuals. Second, an animal's actions could depend on a combination of behavioral and physical cues received from the partner. In this scenario, an individual's behavior is a response solely to the partner's actions and appearance; the identity of the partner is immaterial.

The latter mechanism can still be dependent on previous interactions. For example, an animal's experience might indicate that bulls with long horns who approach quickly with an aggressive display are likely to dominate him in an agonistic encounter. Consequently, he responds submissively when confronted by a social partner meeting these criteria. The identity of the partner is of less concern than his behavioral and physical characteristics. In a small group this would lead to predictable outcomes in pairwise interactions between the group members; an observer could easily conclude that the animals did, in fact, have relationships based on individual recognition.

Two animals may be thought of as having a relationship when they are involved in a series of interactions over time, and the results of previous interactions affect subsequent ones (Hinde, 1983). In field observations of male bison it is difficult to determine whether an interaction has been affected by previous encounters between the individuals. However, if the partners have been involved in such a relationship over time, a pattern of interaction should develop. The relationship can then be identified by the following criteria: 1) a pattern (type and frequency) of interaction that is unique, or, at least, different from the pattern of interaction that either individual exhibits with most other group members, and 2) a pattern of association in space and time that differs from that with most other group members. An example of the first criterion would be a frequency of non-aggressive interactions between two individuals that was greater than either had with other group members. An example of the second would be a greater than average frequency of membership in the same group for two individuals.

In chapter 4 I examined agonistic interactions among a group of 16 male yearlings. The present chapter is devoted to patterns of association in space among the same individuals. The main thrust of the investigation is to determine whether there are certain pairs of male yearlings that associate (i.e., are seen together) more often than would be expected by chance. This presents some difficulties because bison at Wind Cave are found in groups of shifting size and composition; therefore, the problem is to determine how often two individuals would appear in the same group if they were actually associating randomly, and then to compare the observed frequencies of same group membership with the expected values.

Lott & Minta (1983) addressed this question with the bison on Santa Catalina Island in California. They marked 16 cows and 8 calves for identification and periodically sampled the island, recording which of the subjects were seen in each group encountered. This allowed them to calculate a coefficient of association for each of the 276 possible pairs of subject animals. The coefficient represented the proportion of total sightings in which the pair members were seen together. They also calculated an expected probability for the population as a whole, which represented the probability of any two animals being in the same group given the size distribution of groups in the population. It is important to take this distribution into account because if the population is in a few large groups, the probability that two animals will be together by chance is larger than if the population is in many small groups. They called this probability the *CDP (calculated dyadic probability).*

When the mean coefficient of association for the 24 animals was compared with the CDP for the population, it was found that the values were almost identical. Lott & Minta (1983) concluded that association between the subjects could be explained by chance encounters alone. They hypothesized that group membership for bison is dependent on the physiological needs of the animals and not on individual social bonds. For example, a thirsty animal in a resting group will join a group headed for water, rather than wait for its group to finish a rest period. This might be adaptive on the plains where resources, especially water, are patchy and unpredictable. Thus the formation of bonds with other individuals would be selected against (Lott & Minta, 1983).

Although there may be random association among bison, the approach outlined above has some flaws. The fact that the mean coefficient of association does not differ from that predicted by a random model does not demonstrate a lack of specific associations between individuals. If each of 24 animals has one partner with which it regularly associates, and associates with the other 22 randomly, there will be 12 pairs with a high coefficient of association and 264 pairs with random values. When only the mean is examined, values for these 12 pairs are overwhelmed by the 264 random ones. Lott & Minta's (1983) own data illustrate this. Each calf had a high coefficient of association with its mother, as one would expect given the obvious social bond between them. Yet, the mean coefficient of association did not differ from random; these pairs were swamped in the comparison.

To avoid overlooking a small number of associated pairs, one must compare the overall distribution of the association values with a distribution based on a random model. In the present analysis of group membership, I use an approach which examines these distributions to determine whether male yearlings associate non-randomly.

There are two general hypotheses to account for an individual's membership in a group. The first is that group membership is determined by the presence of specific social bonds between pairs of animals; an individual joins or remains with a given group because of who is in it. The presence of a calf in a group with its mother is an obvious example. This hypothesis leads to the prediction that non-random association, as measured by a valid procedure, will be found when group composition is examined. I will refer to this hypothesis as the *social bond hypothesis*.

The second hypothesis is that group membership is based on the individual needs of the animals, which are unrelated to the identities of other group members. One class of needs is physiological, as suggested by Lott & Minta (1983, also see above). Another class is individual social needs. An animal may prefer groups of a certain size, or groups consisting mainly of individuals from a certain age/sex class of the population. (See chapters 3 & 4 for a demonstration of an age/sex preference for social partners.) I will refer to this as the *mutual needs hypothesis*.

Upon first examination, this hypothesis seems to predict random association between individuals, but this need not be the case. Certain pairs of individuals might have similar physiological or social needs. For example, two animals might have a preference for small groups while two others prefer large groups. Alternatively, two small animals may need to drink more frequently or eat less often than two large animals; each pair then shares similar physiological needs. If the home range of the animals is not unlimited (as is the case for bison at Wind Cave), then some pairs will be found to associate non-randomly because of their common needs. Thus, the only prediction that the second hypothesis makes is that associating pairs will share some characteristics that can be measured independently of group membership.

One additional possibility is that group composition is shifting and may be random, but that individual relationships still exist. Individuals may join groups for reasons unrelated to the identity of other group members, but social relationships would still be evident in preferential association between two individuals when they find themselves in the same group. As demonstrated in chapter 4, male yearlings interact preferentially with other yearlings; there may be non-random spatial association as well.

Because an individual's social partners are generally chosen from the animals surrounding him (pers. obs.), close proximity between animals could be one manifestation of a social relationship. This raises a question: Are there non-random associations among male yearlings, as measured by time spent near each other, when they find themselves in the same herd? If so, this would provide evidence that individual social bonds do exist and, therefore, that some type of individual recognition occurs.

My objectives in this chapter are to determine whether there is non-random association between male yearlings as measured by: 1) membership in the same group, and/or 2) spatial proximity between certain individuals when they are members of the same group. If such associations are evident, I will try to identify physical or social characteristics that could account for the associations in order to distinguish between the social bond hypothesis and the mutual needs hypothesis.

METHODS

Subjects and data collection

Subjects for this investigation are 16 male yearlings from 1983. This was the entire male yearling cohort for that year. Twelve of these animals were subjects of focal animal observations, but group membership data were collected on all 16. The data presented here were collected between 5 May and 6 August, 1983.

Whenever a group was encountered, the identity of as many members as possible was determined. In most cases this included all group members, but in all cases every male yearling present could be identified. If an animal was within 100 m of any member of a group (distances were estimated visually), it was recorded as being in the same group. It should be noted that this does not limit the area a group may occupy, but in practice few groups were larger than 300 m across. In general, animals within sight of each other coordinated their movements and eventually ended up in the same group.

The record of group membership among the male yearlings yielded the following information about each of the 120 possible pairs:

1) the frequency that the pair was sighted together
2) the frequency that at least one member of the pair was seen without the other
3) the sum of 1 and 2 which is the total number of sightings of at least one pair member.

In analyzing the data I assume that the probability of sighting an individual is independent of the presence or absence of other male yearlings in the group.

Using these data, I calculated an **association index** (I will refer to this as the **AI**) which was simply the number of times a pair was sighted together divided by the total number of sightings of at least one member of the pair. This value ranges from 0, indicating that the pair is never together, to 1 which indicates that they are always found together.

For the analysis of association between individuals in the same group, I used data from focal observations of 12 yearlings. During the focal observation periods I took scan samples every 5 minutes which included the identity and distance of all neighbors within 20 m. If no other animal was within 20 m, I recorded the identity of, and distance to the nearest neighbor. Twenty meters was chosen as the cutoff distance for two reasons. First, in a large group there were enough individuals within 20 m that I could not identify animals at greater distances in a reasonable amount of time. Second, when a male yearling was involved in an interaction his partner almost always came from the animals recently within the 20 m boundary.

ANALYSIS AND RESULTS

Graphical analyses

I used two graphical procedures to visualize the relationships among the 16 yearlings. A hierarchical cluster analysis, using the AIs as measures of similarity between individuals, was conducted to identify pairs of individuals that were often together (De Ghett, 1978). The results reported below are from the single linkage technique; additional analyses using average linkage and complete linkage gave similar clusters. The SAS Cluster procedure was used with options selected so that the input data were not normalized (SAS Institute, 1985).

The data were then subjected to multidimensional scaling (MDS) to produce a three–dimensional representation of the associations among the yearlings. The SAS procedure ALSCAL was used with the options RATIO and NOSQUARE selected (SAS Institute, 1986). For this analysis dissimilarities are required so I converted the AIs to 1-AI (this gives the proportion of times that members of a pair were sighted in different groups).

The results of the single linkage cluster analysis are shown in Figure 6. In this dendrogram, animals are linked at their AI value (top scale). The single linkage algorithm includes an object in a group at the level of the shortest distance between it and any member of the group. For example, in Figure 6, A is grouped with TC, STC, RN, NC, HTC, RSC, and GC at an AI of about 0.46. This indicates that A has an AI of .46 with at least one of the other group members. This dendrogram illustrates which pairs and groups of animals are found together more often than others, but does not indicate whether the pairs have significant relationships; RN and STC are together 66% of the time but this may not be more than one would expect by chance.

Figure 7 shows the results of an MDS analysis. MDS takes observed distances between objects and attempts to represent the objects in a low–dimensional space in which the geometric distances between objects are proportional to the observed distances (Kruskal & Wish, 1978). An example would be deriving a map of 10 cities given only the distances between each pair of cities. In the present case, objects are 16 male yearlings and distances between them are the proportion of times that each of the 120 possible pairs were seen apart (i.e., 1-**AI** for each pair).

Figure 7 shows a 3–dimensional solution. This solution is within acceptable limits: it has a stress value of .198. Stress measures the distortion of the original data and .20 is about the maximum acceptable value (Kruskal & Wish, 1978). The solution has an $\mathbf{R}^2$ of .719. This latter value means that almost 72% of the variance of the scaled data (i.e. the points shown in Figure 7) is accounted for by the original distances between individuals. A 2–dimensional solution, though perhaps easier to visualize on paper, is not presented because the stress value is greater than .20.

The dimensions in Figure 7 are in themselves arbitrary, being derived from the data. The axes could be rotated to an infinite number of positions without disturbing the spacing between the points. One way of interpreting an MDS diagram is to attempt to identify meaningful axes through the space. For example, if animals tended to associate with others of similar body weight, one would be able to find an axis in the space that had light animals on one end and heavy ones on the other. I could identify no such axes when I looked at body weight, height, or dominance rank.

Cluster analysis and MDS are descriptive tools. In the present case they show that certain pairs of yearlings are more likely to be found in the same group than are other pairs, but do not indicate whether these pairs have a significant association. If no groupings had been apparent, there would be no reason to continue the analysis. Since there are some groupings evident, I proceeded with tests for significant association.

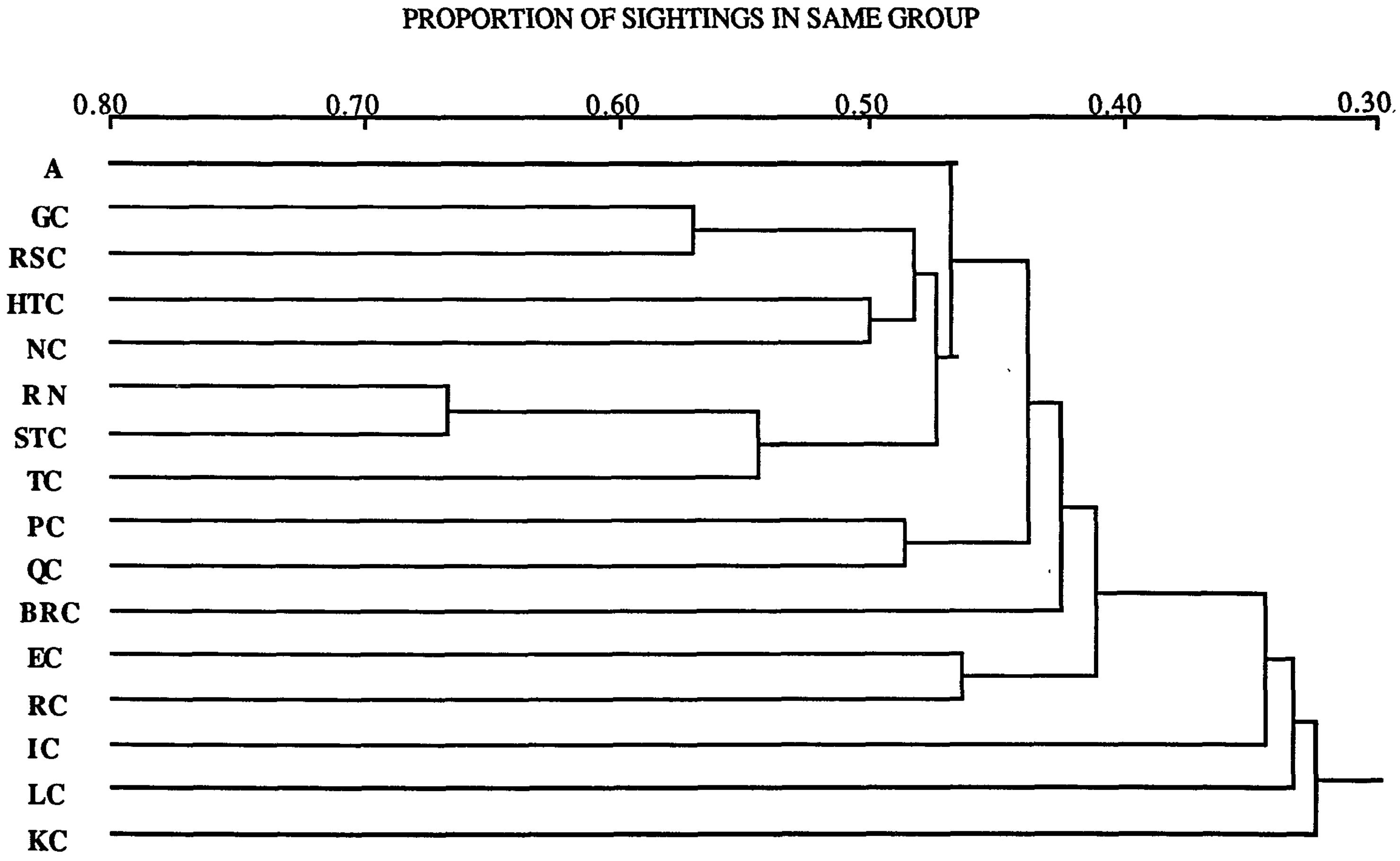


Figure 6: Results of single linkage cluster analysis of yearling group membership. Individuals are joined at the proportion of sightings in which they were in the same group (AI, see text).

THREE-DIMENSIONAL MDS SOLUTION FOR GROUP MEMBERSHIP

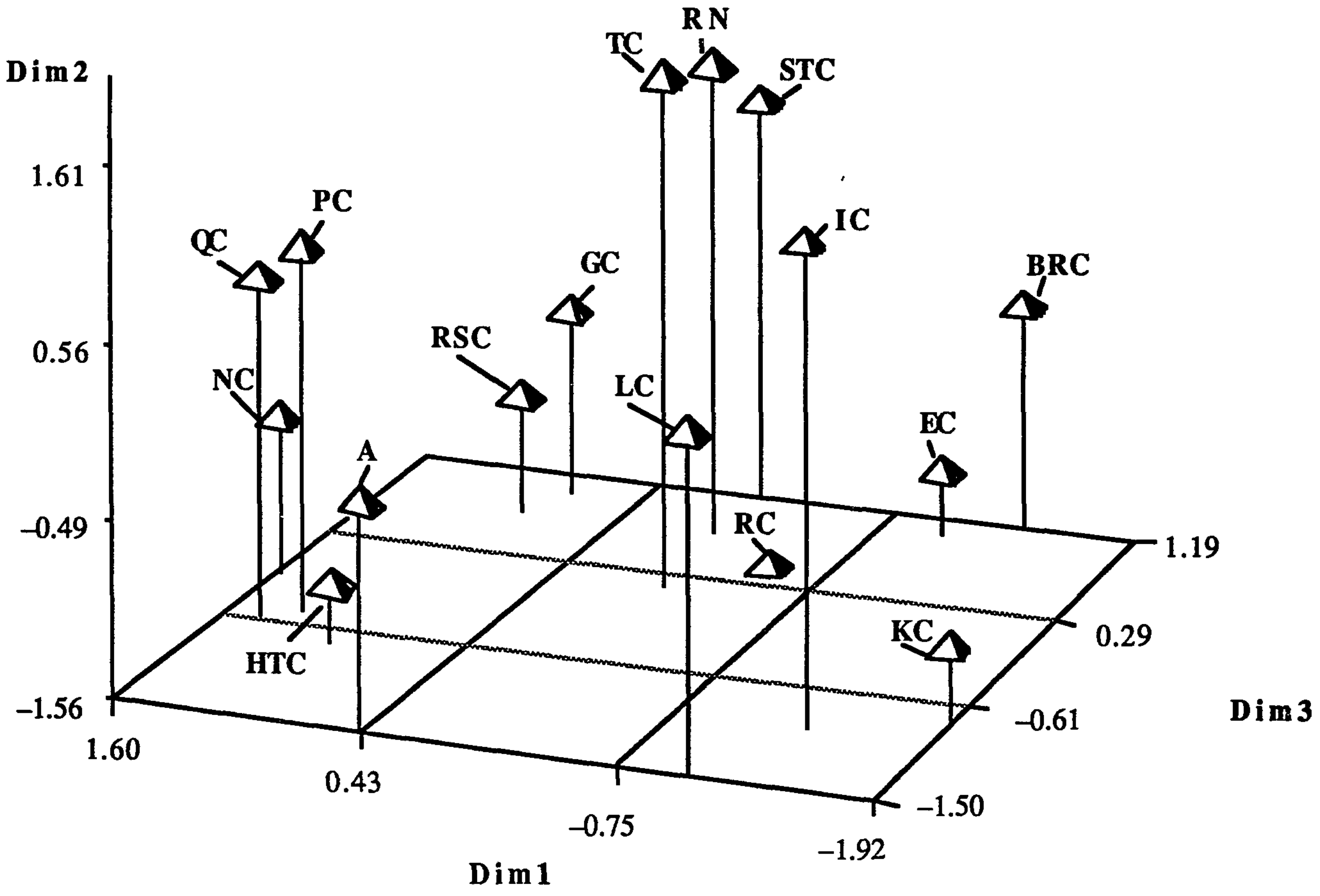


Figure 7: Multidimensional scaling of Association Index (AI) values for male yearlings (see text for explanation).

Group membership

I tested each individual to determine whether there were certain partners with whom he was found more often than expected by chance. To do this I set up 2-way contingency tables for each of the 16 yearlings (see Table 5 for an example). The rows represent the 15 other yearlings and the columns contain the number of days the subject was sighted in the same group as each other yearling, and the number of days that they were known to be in different groups (i.e., one or both were seen without the other). The χ^2 value tests for independence of row and column proportions. A non-significant value indicates that the proportion of same group to different group does not differ among the 15 possible partners. This is the null hypothesis, based on random association. A significant value indicates that the proportion of same group to different group differs for at least one of the possible partners. Note that this may be due to a pair's being together significantly more or less often than expected.

Because 16 non-independent χ^2 tests were conducted, tabled probability values for rejecting the null hypothesis cannot be used. This is because the 16 tests were examined and those with the highest χ^2 values were specifically chosen. By chance alone, some of these values would be expected to have an associated probability of less than .05, even if the null hypothesis were true. To derive the proper values for significance testing, I ran a Monte Carlo type simulation using a model of random association among 16 objects (representing the 16 male yearlings).

The simulation was conducted in the following manner. I determined the observed number of yearlings in each group seen on each day during the study period. Using this, I assigned individuals to groups at random until I had groups of the same size as those observed in the field. I then determined the number of days that each pair was together and that each was apart. These data are analogous to the observed data except that they represent a random process of group composition, given the observed distribution of male yearlings. I then did 16 contingency table analyses on the generated data, and recorded the highest χ^2 value obtained. This entire process was repeated for 1000 trials.

GROUP MEMBERSHIP FOR YEARLING EC

Partner	Same Group	Different Group	Total	AI
A	7	31	38	0.184
BRC	16	23	39	0.410
GC	13	24	37	0.351
HTC	10	25	35	0.286
IC	6	30	36	0.167
KC	8	27	35	0.229
LC	10	23	33	0.303
NC	9	28	37	0.243
PC	10	29	39	0.256
QC	5	36	41	0.122
RC	19	22	41	0.463
RN	11	29	40	0.275
RSC	10	29	39	0.256
STC	11	27	38	0.289
TC	8	33	41	0.195

χ^2=22.884, df=14, p>0.05

Table 5: The number of times EC was in the same group with each of the other male yearlings. AI is association index (see text).

The result was a distribution of χ^2 values that represent the expected highest values that would be obtained in 16 dependent tests if group membership were in fact independent of the identity of the individuals. The derived distribution is shown in Figure 8. The 10th largest value represents the cutoff for significance at the .01 level (i.e., 1% of the values fall above this) and the 50th largest represents the .05 level. These values are 29.763 and 25.439 respectively. In this case, the calculated values are very close to the tabled values for a χ^2 distribution with 14 degrees of freedom (29.141 and 23.685 respectively, Rohlf & Sokal, 1981). The values from the simulation were used to determine which of the 16 subjects showed significant differences in association among the possible partners.

Nine of the 16 male yearlings showed significant χ^2 values when tested for co-occurrence in groups with the other 15 yearlings. Representative data are shown in Tables 5 and 6. The χ^2 value for yearling EC (Table 5) is not significant while for **PC** (Table 6) it is. A significant value emerges when an individual is in the same group as some others more than expected and/or in the same group with some less than expected. Table 6 also lists the expected values for **PC** based on random association. It is seen that **PC** is in the same group as **BRC** less than expected (observed: 7, expected: 13.5) and with **QC** more often than expected (observed: 16, expected: 10.1).

To determine which animals were associated, I examined the individual cell contributions to the χ^2 value for each of the 9 significant tests. The cell contributions are in the final two columns of Table 6 and are calculated as

$$\frac{(\text{observed-expected})^2}{\text{expected}}$$

for each cell. I defined an association as a pair with a cell χ^2 of greater than 2.0 and a positive deviation from expected. Thus in Table 6 yearling **PC** is associated with **QC** (cell χ^2 of 3.42). He also shows high χ^2 values for **KC** and **BRC** but, as can be seen from the expected values, this is because he is found with them less often than expected. This analysis reveals specific associations between pairs of male yearlings in the sense that these pairs are found together in non-random patterns.

GROUP MEMBERSHIP FOR YEARLING PC

	observed values:			expected values:			individual cell χ^2 components:	
Partner	Same Group	Different Groups	\	Same Group	Different Groups	\	Same Group	Different Groups
A	12	20	\	9.8	22.2	\	0.49	0.22
BRC	7	37	\	13.5	30.5	\	3.12	1.38
EC	10	29	\	12.0	27.0	\	0.32	0.14
GC	13	25	\	11.6	26.4	\	0.16	0.07
HTC	13	19	\	9.8	22.2	\	1.04	0.46
IC	6	27	\	10.1	22.9	\	1.68	0.74
KC	3	35	\	11.6	26.4	\	6.42	2.84
LC	8	27	\	10.7	24.3	\	0.69	0.31
NC	14	18	\	9.8	22.2	\	1.79	0.79
QC	16	17	\	10.1	22.9	\	3.42	1.51
RC	12	35	\	14.4	32.6	\	0.40	0.18
RN	15	22	\	11.3	25.7	\	1.18	0.52
RSC	12	24	\	11.0	25.0	\	0.08	0.04
STC	12	24	\	11.0	25.0	\	0.08	0.04
TC	15	21	\	11.0	25.0	\	1.42	0.63

$\chi^2=32.159$, df=14, $p<0.01$

Table 6: Number of times PC was in same group with each of the other male yearlings. Individual cell components of total χ^2 are included. Expected values are derived from hypothesis of no partner preference (see text).

RESULTS OF TWO-WAY χ^2 SIMULATION

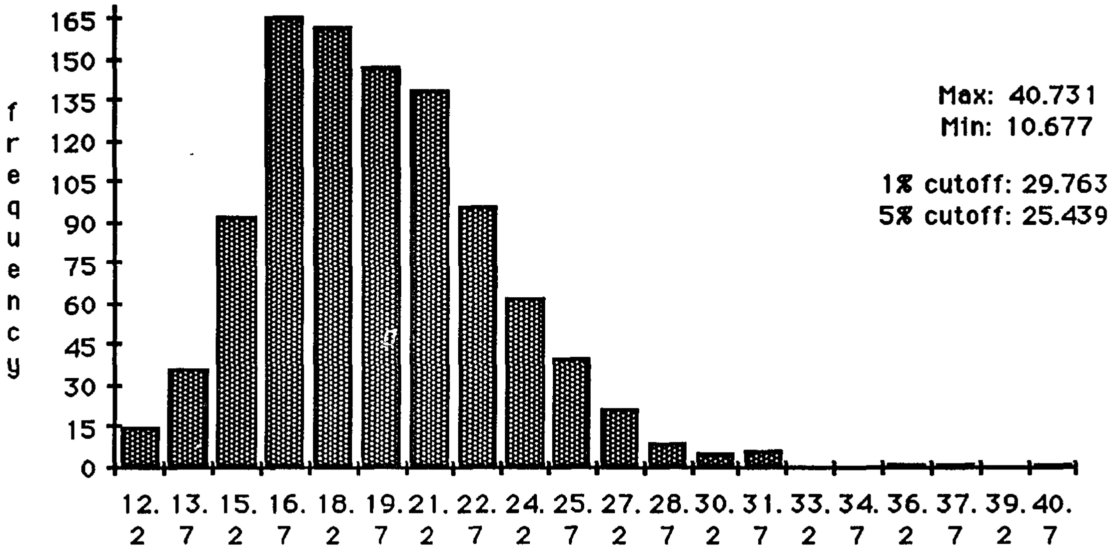


Figure 8: Results of a Monte Carlo simulation of association data assuming random group selection by male yearlings (see text for details). Values on the abscissa represent class midpoints.

Figure 9 is similar to Figure 7, except that associations found in the contingency table analysis are indicated by encirclement or dashed lines. From this it can be seen that among the 120 possible pairs, there are two triads and six dyads with significant association. There is good agreement between the MDS solution and the grouping derived from the contingency table analysis. Circled groups are generally also close on the diagram. In conclusion, the methods used reveal non-random associations within a group even when most pairs associate randomly. Although only 10% of the dyads are together more than expected by chance, these associations involve 11 of the 16 male yearlings.

Association within a group

Finally, I examined the degree to which male yearlings associate with each other when they are in the same herd. For each of the 12 yearlings that were focal subjects, I determined the days in which he was in a group with each of the 15 other yearlings. For each of these days, I found the number of scan samples in which the two were within 20 m and the total number of samples taken on either animal. I was then able to set up 2-way contingency tables similar to those used above except that the columns represent times within 20 m and times at distances greater than 20 m (see Table 7 for an example).

Ten of 12 animals tested showed significant differences among partners found within 20 m when in the same group. These differences, however, are probably not meaningful to the animals. The frequency with which male yearlings are found within 20 m of each other is extremely low compared to the total number of opportunities available. In Table 7, which shows the data for yearling A, we see that GC is within 20 m about twice as often as NC, but we are speaking of 11 times out of 167 possible times as opposed to 6 out of 160. These small differences are unlikely to be the result of preferences among the animals. The significant χ^2 values are most likely due to the large total number of scans (N=1310 in the example in Table 7) and do not provide unambiguous evidence of behaviorally significant differences.

THREE-DIMENSIONAL MDS SOLUTION FOR GROUP MEMBERSHIP

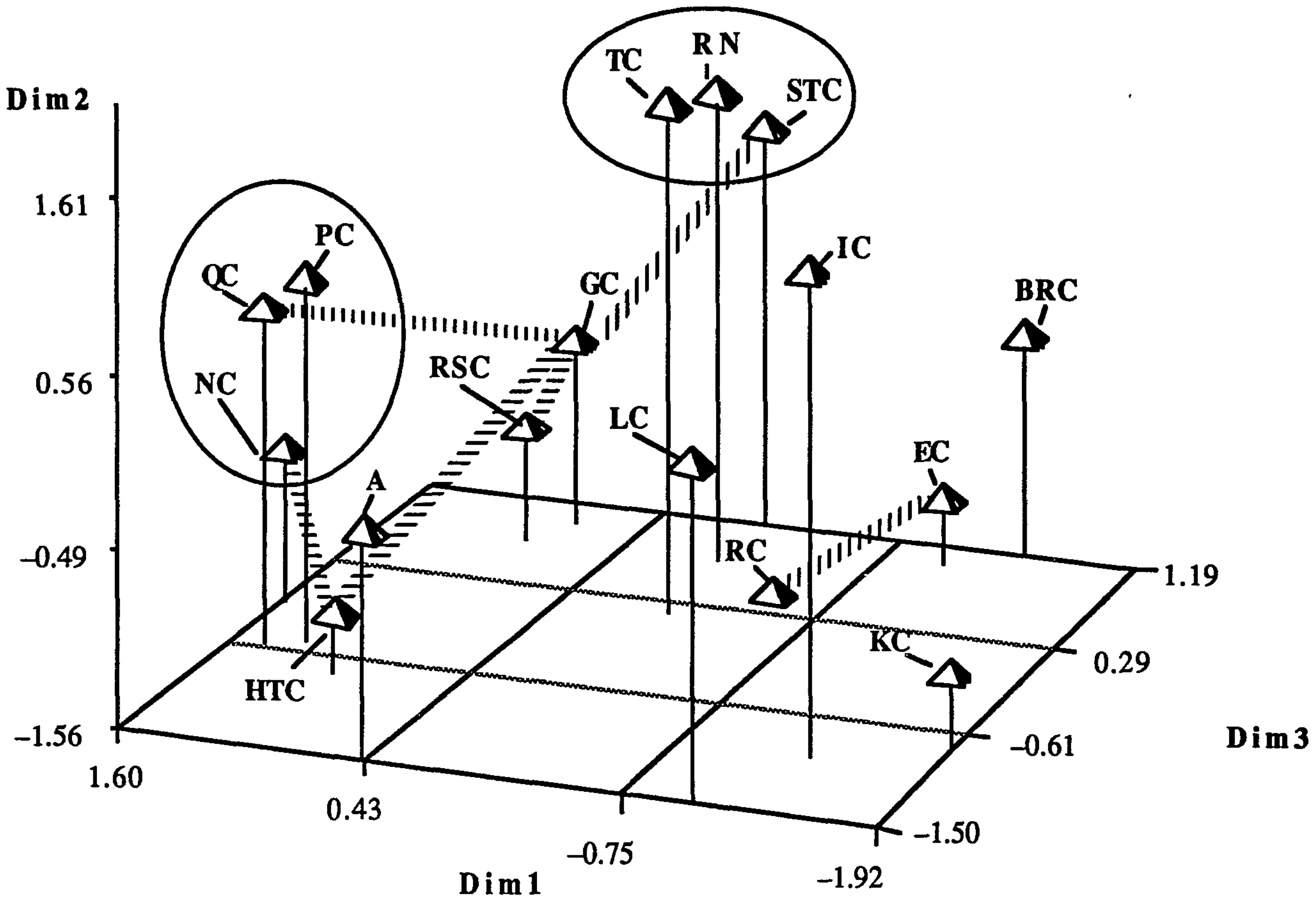


Figure 9: Multidimensional scaling of Association Index (AI) values for male yearlings. Animals with significant associations are indicated. Two triads are encircled and 6 dyads are connected by dashed lines.

PROXIMITY FOR YEARLING A

Partner	Scans <= 20 meters	Scans > 20 meters	Total scans
BRC	1	33	34
EC	2	53	55
GC	11	156	167
HTC	0	91	91
IC	1	31	32
KC	3	19	22
LC	3	37	40
NC	6	154	160
PC	4	87	91
QC	4	137	141
RC	7	84	91
RN	0	84	84
RSC	5	99	104
STC	0	67	67
TC	5	126	131
TOTAL	52	1258	1310

χ^2=23.922, df=14, p<.05

Table 7: Number of scan samples that each of 15 male yearlings were within 20 meters of the focal animal (A). χ^2 value tests hypothesis that partner identity is independent of the proportion of scans within 20 meters (see text).

DISCUSSION

The results of the analyses reported here provide good evidence of non–random association among male yearlings but limited evidence in support of individual recognition. It is clear that certain pairs of yearlings are found in the same group more often than predicted by a random process of group composition. It was also determined, however, that these same pairs do not show a significant association in space when they are in the same group. One interpretation of the lack of close proximity is that yearlings do not form social bonds. Alternatively, the 20 m criterion may have been overly restrictive.

Proximity among individuals is an often used measure of social relationship, especially in primates (see, e.g., Colvin, 1983). For this reason it was used as one of the criteria in the present study. It is, however, important to keep in mind that the expression of a social bond is dependent on the context of the relationship. When one observes spacing in groups of adult bulls (see chapter 3) it is clear that group members do not maintain close proximity to each other, even though they do coordinate their movements and activities. While close proximity is one of the most important characteristics of the mother–young bond in bison, and of many types of bonds in primates, it is not a characteristic of bonds that may form among adult bulls. Thus, demonstrating that pairs of yearlings do not maintain close proximity does not in itself indicate the absence of social bonds. Yearling social behavior may be similar to that of adult bulls, showing the same low frequency of close spatial association.

Although the remaining evidence, namely the existence of stable dominance relations and non-random group membership patterns, lends credence to the idea that young bulls do develop specific social relationships with others of their age/sex class, there is another possibility. The non–random associations among certain yearlings could be due to individuals joining the same group because of similar physiological or social needs (as suggested by Lott & Minta, 1983). However, if this were the case, one would expect to find some axis in the MDS diagram showing that animals grouped together are similar in some way. I was not able to do this when considering body weight, size, or dominance status, measures that might provide a gross indication of physiological and social requirements. This evidence, although negative, supports the hypothesis that bison yearlings can recognize each other and form some social bonds.

In the Analysis and Results section it was mentioned that some pairs of yearlings were together significantly less than expected. This brings up the interesting possibility that certain pairs actively avoid each other. I do not believe this to be the case. When a bison herd splits up, individuals follow one another into the two new groups. It seems more likely that an individual would follow a specific partner into a new group than that he would move out of a group in order to avoid one animal among perhaps 100 others. In any case, active avoidance, if it does occur, lends further support to the individual recognition hypothesis.

The difference between my findings and those of Lott & Minta (1983) may be due to several factors. First, Lott & Minta examined adult cows and their calves while I studied juvenile males. There may be age and sex differences in group membership patterns. Second, the habitats for the two herds differ. Santa Catalina, where Lott & Minta worked, is covered with steep slopes; the grazing areas seem much more patchily distributed than at Wind Cave (personal observation). These conditions result in smaller group sizes and may force individuals to move more independently in order to find enough food. In this situation the current behavior of other group members may be more important to an individual than their identities.

A third difference is in the methods of analysis. The method used in the present study is designed to identify a few associations amid a large number of random ones. The analysis used by Lott & Minta is not sensitive to a small number of non-random pairs. Using this second method, one may overlook a few pairs that associate and conclude that all associations are random.

The remaining distinguishing characteristic of a social bond, as outlined in the Introduction to this chapter, is the frequency and type of interactions between the individuals. In the next chapter I examine the interactions among pairs of male yearlings in order to delineate more precisely the nature of the relationships among them.

Chapter 6

DYADIC RELATIONSHIPS AMONG YEARLINGS: INDIVIDUAL PARTNER PREFERENCES AND THE ROLE OF DOMINANCE

INTRODUCTION

The present chapter addresses two main objectives. The first is to determine whether male yearlings have individual preferences with regard to social partners. The second is to examine the possible role of social status as an organizing factor in yearling social relationships.

Social partner preferences

In the previous two chapters I found that there were dyadic dominance relations and non-random associations among the male yearlings. These dyadic associations suggest, but do not unambiguously demonstrate, that young bulls develop relationships with specific individuals.

Stable dominance relations can arise through behavioral and physical differences among animals, without the existence of individual recognition or social partner preferences. Yearlings may simply react appropriately to the behavior and appearance of a social partner, without recognizing him. As long as the yearlings respond predictably to these cues, stable dominance-subordinance relationships will develop (see chapter 4).

Likewise, non-random group membership need not involve individual identification or partner preference. Yearlings may be found together because they have similar physiological (Lott & Minta, 1983) or behavioral needs (see chapter 5).

In the present chapter I examine interactions between young bulls in more detail. Specifically, I ask whether some pairs of yearlings interact with each other significantly more than others. If so, I will investigate whether the interactions within these pairs are more or less agonistic than those among individuals with no partner preferences. This, combined with the information on dominance and group membership, would provide strong evidence for the existence of specific social bonds among the yearlings.

Social status

In groups with strong dominance hierarchies, social status can affect many aspects of behavior. Appleby (1981) studied social behavior in red deer stags and found that dominance was a factor in most of his measures of interindividual association and interaction. The rank of individuals explained their leaving and joining groups, the identity of their nearest neighbors while in a group, the identity of their social partners, and the intensity of agonistic interactions. Stags tended to associate with partners closest in rank; in addition, agonistic interactions between individuals close in rank were of lower intensity than those between animals with large differences in rank.

Although not as strictly linear as in red deer, dominance relations among bison yearlings are strong and stable. These relationships may affect other aspects of the social lives of young bulls. My second objective in this chapter is to investigate the effect of dominance on social relations among yearling bulls. Can differences in social status among individuals explain spatial association patterns and dyadic interaction rates?

METHODS

Observation and data collection methods are described in chapter 2. The data were collected between 30 March and 31 October, 1983 inclusive. All interactions observed between male yearlings during focal observations of 12 subjects are used in the analysis. These include interactions involving all 16 male yearlings at Wind Cave in 1983. Because only 12 animals were focal subjects, data are available on 114 of the 120 possible dyads.

To investigate the effects of social status, I used the dominance values (DV) calculated in chapter 4. Because the yearlings do not have a strong linear hierarchy, I feel that the DVs are a better measure of social status than either of the rank orders derived in chapter 4. Additionally, the DV is a continuous variable and is normally distributed (due to the arcsine transformation) so that parametric methods such as regression and correlation can be used.

ANALYSIS AND RESULTS

Interactions

In 631 hours of focal observation, 341 interactions among male yearlings were recorded. The overall interaction rate was 0.54 interactions/hour. Of the 341 interactions, 270 were classed as agonistic; these are the same interactions analyzed in chapter 4. The remaining 71 (21%), non-agonistic, interactions were of two types: 1) approaches, in which one yearling orients toward and then moves to within 1 m of another, and 2) following, in which one yearling walks behind another while obviously orienting to the leader's movements. After an approach, the yearlings usually graze or stand close together without any agonistic displays. Unless otherwise mentioned, agonistic and non-agonistic interactions were combined for the following analyses.

Social partner preferences

To identify possible partner preferences I first developed a measure called *partner hours* for each of the 114 dyads. Partner hours is the number of hours both individuals were in the same group while one of them was a focal subject, divided by the number of male yearlings in the group (not counting the focal animal). For example, if on a given day A was a focal animal for 2 hours in a group with 3 other male yearlings, each other yearling would have 0.67 partner hours with A for that day. This is an estimate of the time that two yearlings had in which to interact. I used *partner hours* rather than the total hours each pair was together because my null hypothesis is that a yearling bull shows no partner preference in interactions. He is therefore expected to interact with each partner at the same rate. If a focal animal has an overall interaction rate of 1/hour, then in a group with 3 other yearlings he is expected to interact 0.33 times per hour with each partner, not once per hour. The measure of *partner hours* takes the number of potential partners into account.

The interaction rate for each dyad is computed as the number of interactions between the partners divided by the number of partner hours for the pair. The rates can then be compared to determine if some of the dyads interact more than would be expected if interactions are independent of the identity of the partner. Before grouping all 114 dyads, I examined the 12 focal subjects to see if they interacted with the same frequency. The total number of interactions and total hours of focal observation for each subject are shown in Table 8. Also shown in the table are the expected number of interactions if each subject interacted at the grouped rate of 0.54 interactions/hour. There are significant differences in interaction rates among the 12 animals ($\chi^2 = 33.00$, df = 11, p<.001).

Because of this variation among the subjects, they must be treated separately so that differences in dyadic interaction rates are not confounded with differences in overall sociality among the animals. Table 9 is an example of the data for one of the 12 subjects. The number of observed interactions and the partner hours for each of the 15 other yearlings are shown. The expected interactions are calculated as:

$$\frac{\text{total interactions}}{\text{total focal hours}} \times \text{partner hours.}$$

This gives the number of interactions expected if interactions are independent of partner identity, and thus dependent only on the amount of time that two individuals are available to each other. Because the expected values are so low, a normal χ^2 test would not be reliable. I therefore ran a computer simulation in order to derive values to test the observed interaction rates.

For each subject the simulation was run for a minimum of 1000 trials. In each trial interactions were assigned to the 15 possible partners without regard to identity. The only constraint was that the probability of an interaction being assigned to a given partner was equal to the observed partner hours for that individual divided by the total focal hours for the subject. For example, from Table 9 the probability of an interaction for A with KC is $3.96 \div 53.06 = 0.075$.

When the observed number of interactions had been assigned randomly, the interaction rate (interactions per partner hour) was calculated for each partner. The highest of the 15 rates was recorded and then the next trial began. At the end of the simulation there were 1000 values representing the highest rates obtained when partners were chosen at random. I used only the highest value for each trial because there was no *a priori* expectation that certain pairs would interact more than others. The pairs with the highest observed interaction rates were chosen *a posteriori*, so the test distribution had to reflect this. The 95th percentile of this distribution was then used as the test value (at p=.05) for the observed interaction rates.

TOTAL INTERACTIONS AND FOCAL HOURS FOR MALE YEARLINGS

Focal Animal	A	BRC	EC	GC	KC	LC	NC	QC	RC	RN	STC	TC	**Totals**
Total focal hours	53.06	61.86	52.02	60.87	41.37	32.92	65.38	63.43	58.82	47.68	37.99	55.94	631.34
Observed Interactions	18	28	28	31	11	29	29	36	39	42	15	35	341
Expected interactions	28.7	33.4	28.1	32.9	22.3	17.8	35.3	34.3	31.8	25.8	20.5	30.2	341.1

Table 8: Number of observed and expected interactions, and focal observation hours for 12 male yearlings. Expected values based on hypothesis that the interaction rate is the same for all yearlings.

INTERACTIONS FOR FOCAL YEARLINGA WITH EACH OTHER MALE YEARLING

Partner	BRC	EC	GC	HTC	IC	KC	LC	NC	PC	QC	RC	RN	RSC	STC	TC	Totals
Interactions	0	0	0	0	0	1	1	8	0	1	3	0	0	2	2	18
Partner hrs.	1.14	2.21	3.60	2.21	3.17	3.96	1.57	4.38	5.30	3.88	7.45	1.78	4.71	4.31	3.39	53.06
Interactions/hr.	0.00	0.00	0.00	0.00	0.00	0.25	0.64	1.83	0.00	0.26	0.40	0.00	0.00	0.46	0.59	

Table 9: Interactions and partner hours for each yearling with focal animal A.

For focal animal **A** the 95th percentile was 1.754 and the 99th percentile was 2.247. From table 9 it can be seen that only **NC** has an interaction rate (1.83) that is significantly higher than would be expected from his number of partner hours with **A**.

This procedure was repeated for each of the subjects. Three pairs were found to be associated at the 0.05 level: **A** & **NC**, **TC** & **NC**, and **RC** & **RN**. Although each of these dyads represents a relationship based on frequency of interaction, none of them has a relationship based on frequency of membership in the same group (see chapter 5). The twelve pairs previously found to be associated through group membership were subjected to an additional analysis.

Interaction frequencies for group membership dyads

The method of testing interaction rates for the 12 pairs found to be associated in chapter 5 is essentially the same as just described. The only difference is in the test value for significance. Because there is an *a priori* hypothesis that these pairs will interact preferentially, the correct distribution of test values includes all the rates calculated for each trial in the simulations, rather than just the highest rate for each trial. A simulation of 1000 trials thus produces 15,000 values; the 95th percentile of this distribution provides the cutoff value for the 0.05 level of significance. To illustrate, for focal animal **GC** the 0.05 test value for all partners is 1.896 while the value for comparing partners thought, *a priori*, to be associated is 1.111.

Using this method, I found 3 additional pairs that were associated: **QC** & **NC**, **GC** & **HTC**, and **STC** & **RN**. Overall, 9 of the 16 male yearlings (56%) were involved in a dyad characterized by a greater than expected rate of interaction. In addition, 6 dyads involving 4 of the yearlings could not be examined because these 4 were not focal subjects; the true number of individuals involved in relationships may be higher.

Type of interaction in associated pairs

Next I tested the 6 pairs to determine whether their associations are characterized by a different proportion of aggressive interactions than among the rest of the yearlings. The 6 pairs had 51 aggressive versus 16 non-aggressive interactions, while the rest of the yearling cohort was involved in 219 aggressive versus 55 non-aggressive interactions. These proportions do not differ significantly (2-way contingency table, G=0.462, df=1 p>0.1). Thus although these 6 dyads show an individual social partner preference, their relationships are not different in tone from dyads showing no preference.

Social status

Interaction rates and dominance

In the first analysis above, I found that there was significant variability in the overall interaction rates among the 12 focal subjects. This necessitated treating the individuals separately, but it raises an interesting question in its own right: Is the rate of interaction related to an individual's dominance status? Table 10 shows the total interaction rate and the dominance rank (see chapter 4) for each of the 12 focal animals. There is no association between the two variables (r_s=0.126, df=10, p>0.05). Although the yearlings show individually characteristic rates of interaction, this is not correlated with their social status.

Closest associates and dominance

Is there a relationship between an individual's closest associate and dominance? Two ways to determine an individual's closest associate are available: 1) the animal having the highest association index (AI, see chapter 5) with the subject, and 2) the animal having the highest interaction rate, as measured above, with the subject. The first is a measure of spatial association and the second a measure of social interaction. Table 11 shows the DV of each yearling and the DV of each yearling's closest associate. There is no correlation between DVs of animals that interact most frequently (r=0.009, p>0.9). There is, however, a significant negative correlation between the dominance values of animals that associate spatially (r=-.609, p=0.012). This indicates that, as far as group membership is concerned, a yearling's closest associate is likely to be of much different status: low-ranking yearlings are found in groups with high-ranking yearlings.

Proximity and dominance

Is there a relationship between individuals that spend time near each other when in the same group and their relative social status? For this analysis I used the proximity scans of animals within 20 meters that were introduced in chapter 5. For each of 117 pairs of yearlings I calculated the number of scan samples in which the pair were within 20 m and the total number of scans taken while the two were in the same group. Next, I determined the difference in DV for each pair; these dominance value differences ranged from 0.28 to 44.72. The range of DV differences was divided into 10 equal classes and the proportion of scans within 20 m calculated for each class. The proportions were transformed with an arcsine transformation:

$$y=\arcsin\sqrt{x}$$

where y is the transformed variate and x is the observed proportion. The data are shown in Table 12.

A regression analysis of time spent within 20 m on DV difference was not significant (slope=-0.01, F=0.135, p>0.5). Thus, the relative social status of the members of a dyad does not affect the time they spend near each other within the herd.

Interaction frequency and dominance

A similar analysis was undertaken with the frequency of interactions; that is:

$$\frac{\#\text{ interactions}}{\text{partner hours}}$$

where partner hours is calculated as outlined above. The data are presented in Table 13. A regression analysis showed no significant relationship between interaction rate and dyadic status differences (slope=-0.01, F=4.898, p>0.05).

DOMINANCE RANK AND INTERACTION RATE

Focal Animal	A	BRC	EC	GC	KC	LC	NC	QC	RC	RN	STC	TC
Interactions/Hour	0.339	0.453	0.538	0.509	0.266	0.881	0.444	0.568	0.663	0.881	0.395	0.626
Dominance Rank	6	15	14	16	12	13	9	8	1	5	2	10

Table 10: Dominance rank compared with total interactions per hour for 12 focal male yearlings. Ranks are those derived from the dominance matrix in chapter 4.

DOMINANCE VALUES OF MALE YEARLINGS AND THEIR CLOSEST ASSOCIATES

Subject	A	BRC	EC	GC	HTC	IC	KC	LC	NC	PC	QC	RC	RN	RSC	STC	TC
DV	62.84	21.88	28.88	26.01	64.34	30.00	49.11	35.26	38.06	61.40	33.21	66.60	56.31	63.43	61.68	37.66
Closest Associate (AI)	26.01	61.68	66.60	63.43	38.06	37.66	21.88	37.66	64.34	33.21	61.40	28.88	61.68	26.01	56.31	56.31
Closest Associate (Interactions/hour)	38.06	33.21	64.34	64.34	28.88	61.68	35.26	56.31	33.21	61.68	38.06	56.31	63.43	56.31	56.31	38.06

Table 11: A comparison of dominance values (DV) for 16 male yearlings and their closest associates. Closest associate (AI) is the animal with the highest Association Index (see chapter 5) with the subject. Closest associate (Interactions/partner hour) is the individual with whom the subject has the highest interaction rate.

RELATIVE RANK AND PROXIMITY FOR MALE YEARLING PAIRS

Pair DV Difference	Scans within 20 meters	Total scans	Total pairs	proportion scans within 20 meters	arcsine proportion within 20 m
0.28-4.72	220	5272	23	0.0417	11.79
4.72-9.16	214	4359	17	0.0491	12.80
9.16-13.60	150	3191	11	0.0470	12.52
13.6-18.04	88	2043	8	0.0431	11.98
18.04-22.48	76	1475	5	0.0515	13.12
22.48-26.92	195	4245	15	0.0459	12.38
26.92-31.36	157	3893	14	0.0403	11.58
31.36-35.80	95	2667	12	0.0356	10.88
35.80-40.24	113	1909	7	0.0592	14.08
40.24-44.68	40	1066	5	0.0375	11.17
Totals:	**1348**	**28772**	**117**		

Table 12: Number of scan samples within 20 meters for male yearling dyads. Grouped by the difference in dominance value (DV) of the dyad members. Arcsine transformation is $\arcsin\left(\sqrt{x}\right)$ where x is the proportion of scans within 20 m.

RELATIVE RANK AND INTERACTION RATES FOR MALE YEARLING PAIRS

Pair DV Difference	Interactions	Partner Hours	Total pairs	Interactions per partner hour
0.28-4.72	59	109.98	21	0.536
4.72-9.16	59	79.12	17	0.746
9.16-13.60	49	70.23	11	0.698
13.6-18.04	22	52.52	8	0.419
18.04-22.48	20	27.54	5	0.726
22.48-26.92	48	86.10	15	0.557
26.92-31.36	28	77.83	14	0.360
31.36-35.80	23	48.19	11	0.477
35.80-40.24	21	51.90	7	0.405
40.24-44.68	12	27.92	5	0.430
Totals:	**341**	**631.33**	**114**	

Table 13: Interaction rates for male yearling dyads. Grouped by the difference in dominance value (DV) of the dyad members.

DISCUSSION

Combining the results of the present chapter with those of the previous one shows that 15 of the 16 male yearlings were involved in a dyadic association based on group membership and/or interaction frequency. Under the conditions of shared home range and limited dispersal found at Wind Cave, young bison bulls establish individual relationships among each other. These relationships are based on social partner preferences but they are not defined by different patterns of social behavior; dyads that associate more than expected do not show different types of behavior from pairs that associate randomly. It is likely that individual recognition occurs between yearlings, allowing them to maintain these partner preferences and stable dominance relationships.

Dominance status has an effect on yearling bull social behavior. The status of an animal is negatively correlated with the status of his closest associate: yearlings associate with partners that are opposite to them in dominance. This situation is different from that found for other ungulates, in which more interactions occur between social partners of equal rank (Appleby, 1981 on red deer; Schnebel & Griswold, 1983 on wild pigs).

This difference may be understood by examining the relative importance of dominance in bison and red deer. For bison bulls dominance is not as important an organizing factor as it is for red deer stags. The bison cannot easily collect and defend estrous cows; the value of dominance to a bull's reproductive success is therefore not as great as it is for red deer stags, who defend harems of hinds. Outside of the rut, red deer stags live in large groups (compared with bison) and dominance allows individuals to gain access to limited food supplies and disrupt the feeding of subordinates (Appleby, 1981). Bison bulls live alone or in small groups during most of the year; their ability to defend food supplies is very limited and there is a correspondingly low frequency of dominance interactions.

The importance of dominance may explain why red deer stags of close rank associate while bison bulls prefer partners of distant rank. The intensity of aggressive interactions is higher between red deer stags of differing rank than between stags of similar rank, perhaps because aggression between closely ranked individuals is more likely to lead to dangerous fighting. Subordinate stags are thus at a disadvantage in groups of dominant stags, so they tend to leave such groups and find others of similar rank (Appleby, 1981).

For yearling bison bulls, maintenance of dominance does not appear to provide immediate benefits in the form of access to limited resources. Because there is little to contest, there is no strong pressure to assert dominance over low ranking individuals. Relationships between animals far apart in status are very predictable and thus may be safer than those between animals of similar status, leading to a preference for social partners of different rank. This hypothesis has also been suggested to explain the finding in many primate species that aggression is common between animals of similar dominance rank (Clutton-Brock & Harvey, 1976).

Yearling bison bulls develop individual relationships that to some extent are affected by social status, with individuals of differing ranks associating. However, contrary to the situation in some other ungulates, dominance does not seem to be a strong organizing factor at any level other than the dyad. This can be understood in light of the contribution of dominance to reproductive success, which is less for bison than for species in which dominant males can collect and monopolize estrous females.

Chapter 7

CONCLUDING DISCUSSION

The analysis of social structure presents methodological problems, especially where measurement of dominance and association is concerned. Dominance relationships can appear to be linear even when no real hierarchy exists (chapter 4). By utilizing tests of linearity and transitivity I was able to describe dominance relationships with greater accuracy than is possible through the construction of a dominance matrix alone. The identification of dyadic associations within groups of shifting membership is even more problematic. A few pairs are expected to be together with high frequency simply by chance. The method of analysis presented in chapter 5 is capable of identifying a few associated dyads within a large number of randomly associating ones. These methods provided a detailed description of yearling bison bull social organization.

The results reported here demonstrate that in the Wind Cave population: 1) young bison bulls choose to interact with animals of similar size; 2) young bulls interact more aggressively with male than with female partners; 3) yearling bulls establish stable dominance relationships among themselves; 4) yearling bulls establish dyadic relationships with preferred social partners, evidenced by preferential association in space and in social interactions; and 5) the dyads are likely to be composed of two bulls that differ in social status, rather than of rank neighbors.

The prediction presented in chapter 1 is borne out. Yearling bison bulls form a social sub-group within the cow/juvenile herd. The bulls choose to interact with each other, and their interactions are mostly agonistic; this pattern of interaction was expected based on the known behavior of adult bison bulls. Through these interactions, yearlings develop dyadic relationships with each other. There does not appear to be a higher level of organization, such as a linear dominance hierarchy, involved in the yearlings' relationships. Horn size was found to be a factor in the outcome of agonistic interactions, but the overall non-linearity of dominance among yearlings, coupled with the existence of social partner preferences, indicates that relationships are based on social experience with specific individuals.

Although yearling bull social relations are similar to those of adult bulls, there are age-related differences in agonistic behavior that point out an important difference in the nature of dominance for the two age classes. Both adults and yearlings establish dominance relationships, but there are indications that the attainment of high rank is not as important to young bulls as it is to adults. Yearling dominance relationships are more stable than adult ones: there are few reversals after dominance is established between two young bulls. Male yearlings are evidently not motivated to challenge the status quo in the same manner as adult bulls do during the rut.

The tendency for yearling bulls to associate with others of distant dominance status provides a clue to the importance of their social interactions. In many species agonistic encounters are more frequent between rank neighbors than between animals of distant rank (Clutton-Brock & Harvey, 1976; Appleby, 1981; Schnebel & Griswold, 1983; Reinhardt *et al.*, 1986). By choosing to associate with distantly ranked individuals, with whom the outcome of an agonistic encounter is predictable (Clutton-Brock & Harvey, 1976), young bison bulls can engage in vigorous aggressive interactions with a lowered probability of dangerous escalation. This choice of social partner may explain some of the ambiguity of play fights that was described in chapter 3. Because the partners differ in dominance status, few role reversals occur during the fights; this maintenance of dominant/subordinate roles was taken as evidence that the fights were not completely playful (chapter 3). However, because there is no threat to social status, the interactions do not resemble adult fights. There are invitations to interact, the fights last longer, and the result of the fight is often not an increase in distance between the partners. These characteristics are traditionally associated with play (Fagan, 1981).

In other ungulates, such as red deer stags (Appleby, 1981) and cattle (Reinhardt *et al.*, 1986), maintenance of social status appears to be an important factor in inter-male interactions. In these species individuals associate with, and direct more interactions toward, partners of similar rank. Dominant animals may interact with the closest ranked subordinate because this animal represents the most immediate threat to their status. Subordinate animals avoid association with animals of much higher rank in order to minimize interruption of their behavior by dominant animals (Appleby, 1981). In this way, animals of similar rank tend to associate with each other. The difference between yearling bison bulls and species such as red deer is in the benefits of being dominant. For red deer, dominance confers an immediate advantage on an individual in competition for limited resources such as food and, during the rut, mates (Appleby, 1981). At Wind Cave, there do not appear to be limited resources of interest to young bison bulls; therefore, they receive little, if any, immediate benefits from dominance. Gains in status are not a top priority (chapter 6).

Two studies of bison cows illustrate the change in dominance relations that occur with changing availability of resources. Rutberg (1983) found that cows on the National Bison Range in Montana had a linear dominance hierarchy that was not correlated with weight, which is assumed to be indicative of fighting ability, but was correlated with age. He interpreted this to mean that cows learn their social status at an early age, when all older cows are dominant to them. As they mature (and gain weight) they do not challenge the established relationships; thus, dominance comes to be correlated with age. Lott & Galland (1987) found that on Santa Catalina island in California, dominance among adult bison cows was correlated with weight but not age. On Santa Catalina conditions are much harder for cows than at the National Bison Range, as evidenced by the lower average weight of the Catalina cows and the lower annual reproductive rate of the Catalina herd. The scarcity of resources on Catalina leads to more frequent challenges to the hierarchy, dominance thereby becomes correlated with weight (Lott & Galland, 1987).

I expect a similar type of change to occur in maturing bison bulls as they reach breeding age and begin to compete for estrous cows. This should cause a shift in dominance relationships, from the stable ones of yearlings to the more volatile relations of adult bulls. In the summer of 1987 I observed a series of interactions between one of my study animals, KC (then 5 years old), and an older adult bull whose age I estimated at between 10 and 15 years. The rut was just beginning and there were many bulls with the cow/juvenile herd. KC and the older bull were engaged in a broadside display that ended ambiguously: both turned away and began grazing. A second broadside display followed; this time the older bull turned away and began to move with the herd. KC followed quickly, driving the older bull ahead of him. Each time the older bull turned aside, KC displayed to him until he turned farther away. This is the first instance I have seen of one of my study animals challenging an older bull. It is important to note that it occurred at the beginning of the rut, when estrous cows are just becoming available.

The evidence indicates that young bison bulls' social interactions function to provide experience with the agonistic behavior required for successful competition as adults. By choosing partners of similar size and strength, and avoiding challenges to dominance rank neighbors, they are able to sustain vigorous agonistic interactions with less risk of injury than is present in fights between adult bulls. This pattern of juvenile interaction is in contrast to that observed in young collared peccaries by Byers (1983). Peccaries live in groups of mixed age and sex, characterized by a high degree of sociality. Juvenile peccaries were found to interact mostly with adults, rather than with each other. Adult bison, on the other hand, live in sexually segregated groups for most of their lives. The young animals of both species are thus involved in interactions that resemble what they will experience as adults: peccaries interact with individuals of all ages and sexes while bison bulls interact with other males of similar size.

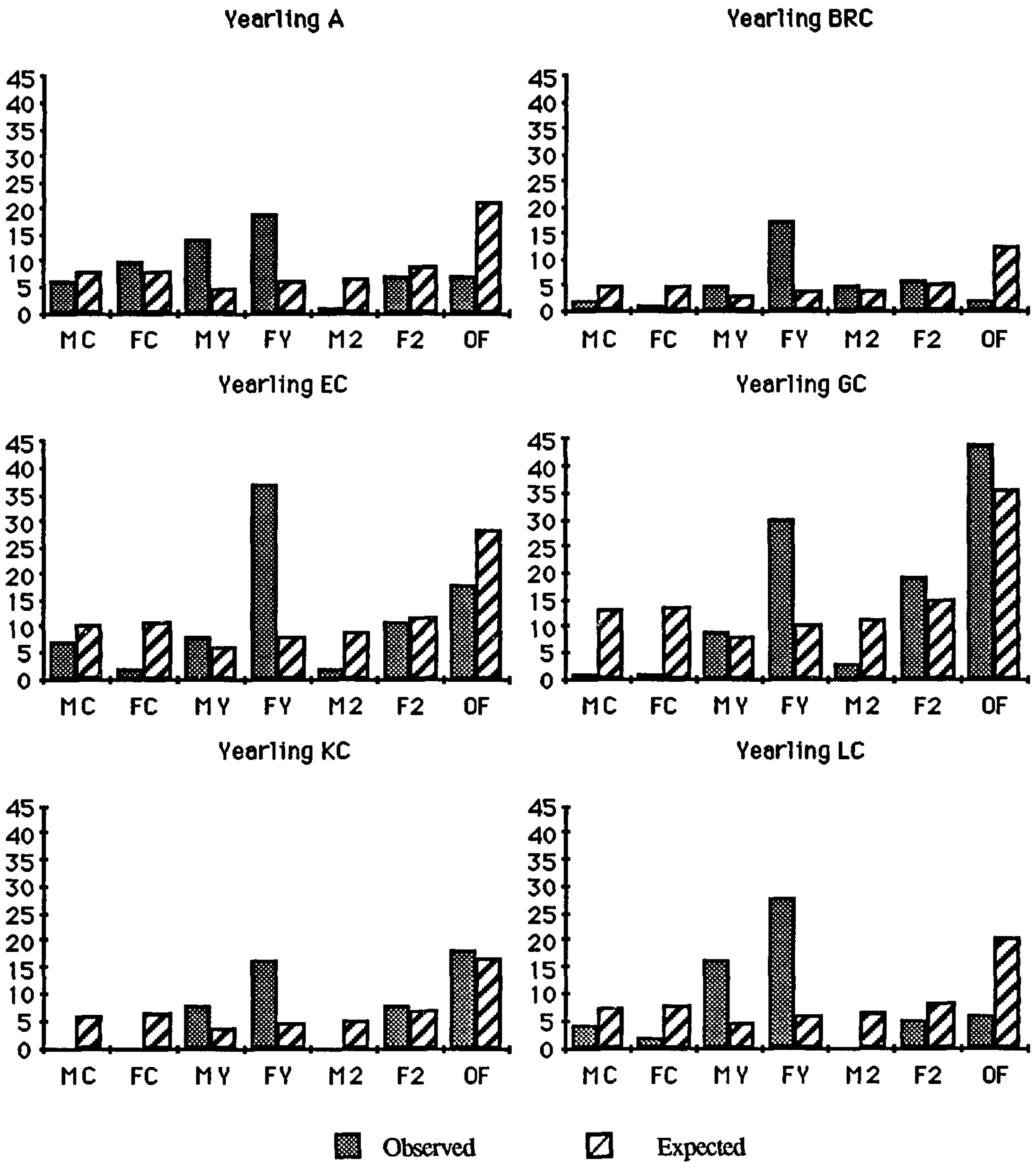
In ungulate species in which adult males and females live in separate social groups there is a general pattern of young males becoming more solitary as they develop. Water buffalo bulls in Australia are gregarious with other males when they are young, but become more solitary when they leave their natal group (Tulloch, 1978). Male white-tailed deer leave their maternal group at one or two years of age and become social "floaters" for a year, moving in and out of all-male groups. After this year, they join all-male groups that consist of two or three bucks that form a stable core and a shifting number of peripheral young males (Brown, 1974). Bison bulls in large groups (greater than 4 or 5 members) are usually all young; in larger mixed-age bull groups there is often a distinct sub-group of young males and a smaller sub-group of older males (Petersburg, 1973).

The dyadic associations between yearling bison bulls fit into the pattern of adult bull social grouping. When not solitary, older bulls are most often found in pairs (Petersburg, 1973). Petersburg states that pairs of adult bulls are more stable, in terms of group membership, than groups of larger size. This suggests that the dyadic relationships of the young bulls may continue as they mature, but I know of no concrete evidence on this point. In June of 1986, prior to the rut, I saw two groups of 3-year-old males (composed of some of my study animals born in 1983) that remained intact over a period of one week. One group had five 3-year-olds and one had three. The groups were occasionally joined by adult males for short periods. Future observations of these known subject animals, as they reach adulthood, will provide information on the stability of yearling associations.

In summary, young bulls form a sub-group within the herd. They interact with each other in ways that maximize their experience in intermale agonistic encounters and minimize the risks involved in serious fights. This picture of yearling bull social organization is consistent with the hypothesis that the pattern of male bison social development should reflect the social structure among adult bulls and not the structure of the cow/juvenile herd into which they are born.

APPENDIX

As mentioned in chapter 3, the twelve yearling males had significant individual variation in the proportion of interactions they initiated with partners of various sex/age classes. Figure A-1 presents the interaction data for each of the yearling bulls. The expected values are based on random interaction with respect to sex and age of partner (chapter 3). It is clear that yearlings differ in the frequency of interactions they initiate with older females, but each yearling interacted more than expected with other yearlings and 2-year-old females.



Yearling A

Yearling BRC

Yearling EC

Yearling GC

Yearling KC

Yearling LC

Figure A-1: Number of interactions initiated by 12 male yearlings with partners of different sex/age classes (see chapter 3). Sex is M or F for male or female. Age classes are as follows: C - calves, Y - yearlings, 2 - two year olds. OF represents older females. Ordinates are number of interactions observed and expected.

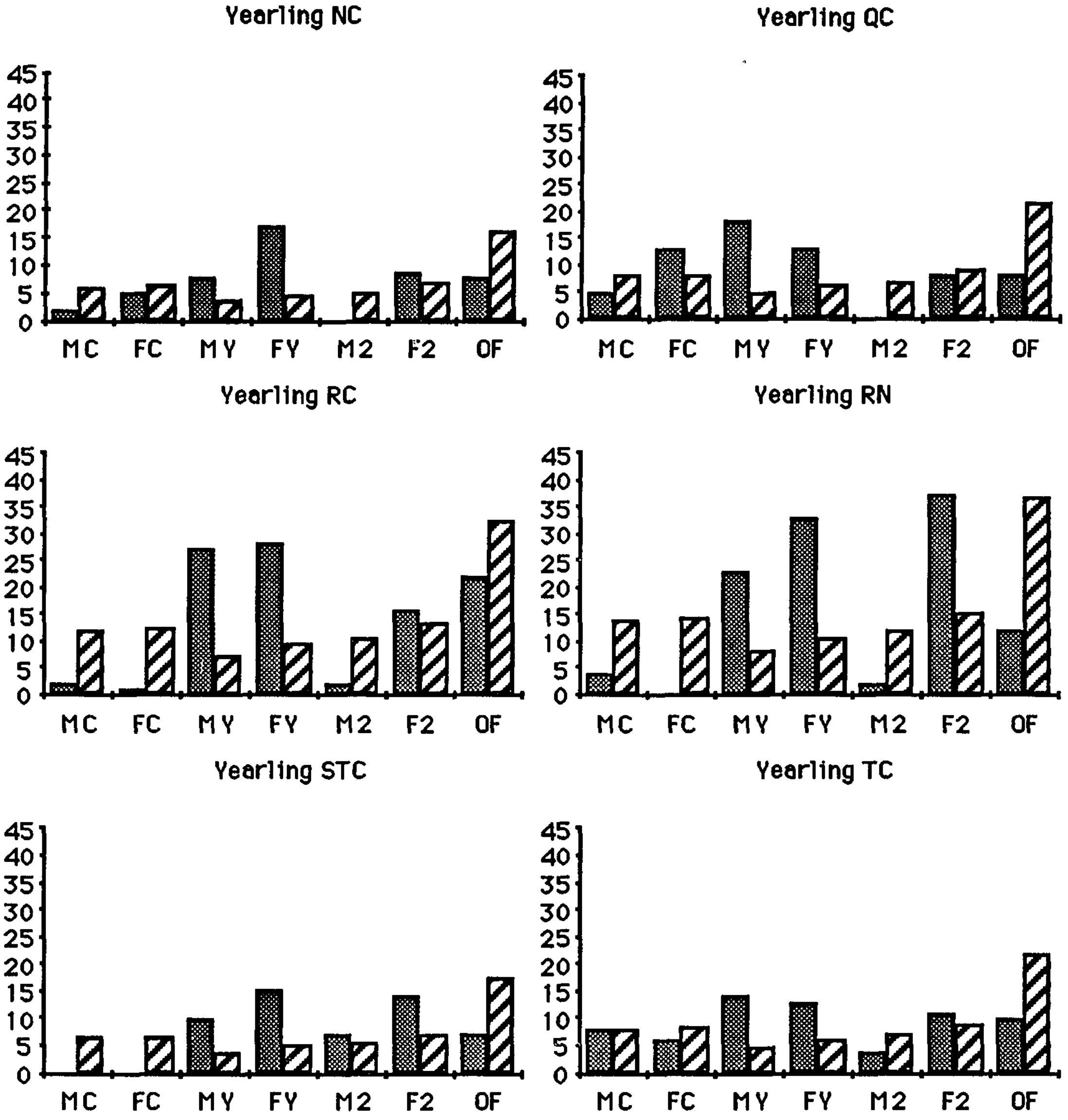


Figure A-1 (continued).

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