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Play behavior and dominance relationships of bighorn sheep on the National Bison Range

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Play Behavior and Dominance Relationships

of Bighorn Sheep on the National Bison Range.

by

Christine C. Hass

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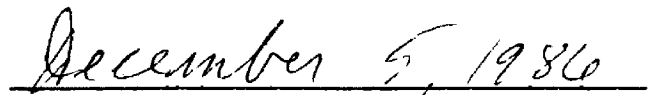for the Degree of Master of Arts

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Play Behavior and Dominance Relationships
of Bighorn Sheep on the National Bison Range. (96 pp.)

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   A 27-month study of bighorn sheep (Ovis canadensis)
on the National Bison Range, Montana, focused on two
aspects of social behavior: play behavior and dominance
relations. Data collected from the lambs supported the
Motor Training Hypothesis for the function of play
behavior, but not the Social Cohesion or Social
Competition Hypotheses. Male lambs played more than
female lambs, and lambs chose partners closest to them
in size and age. The most common components of play
were those patterns used in intraspecific conflict and
predator evasion. The number and sex of available play
partners influenced the amount of play more than did
maternal investment. Peak play periods coincided with
the period of most rapid growth. These data are
consistent with the hypothesis that play behavior,
under certain environmental and social constraints,
provides lambs with immediate, as well as delayed,
motor training benefits.
   Dominance relationships among bighorn rams and ewes
were examined to quantify structure, development, and
reproductive correlates of rank. Both rams and ewes
exhibited highly stable hierarchies that were strongly
correlated with age. Dominance relationships were not
evident until after the sheep were one year old.
Behavioral interactions, particularly among the rams,
were closely tied to dominance rank. Direct
reproductive benefits of high rank, in terms of more
breeding opportunities, were obvious for rams. No
reproductive benefits, in terms of lamb weight, lamb
sex, date of estrus or lambing, nor nursing duration or
rate, could be found for ewes.

ACKNOWLEDGEMENTS

TABLE OF CONTENTS

iv

LIST OF TABLES

v

LIST OF FIGURES

CHAPTER I

INTRODUCTION

The development of behavior in any given species is most often the result of two processes: learning and the maturation of innate behavior. Animals mature (physically and psychologically) at different rates; differential growth rates may have profound influences on behavior (Geist 1971, Clutton-Brock et al. 1982).

Bighorn sheep (Ovis canadensis) are intriguing animals for a study of development. They are social ungulates with pronounced sexual dimorphism; rams weigh up to twice as much as ewes and have much larger horns. Ewes and rams follow different developmental regimes. Ewes reach adult size and maturity at 1-3 years of age, whereas rams may reach sexual maturity at 1-2 years, but do not achieve full body size until 6-8 years of age (Blood et al. 1970, Geist 1971, Jorgenson and Wishart 1984). Growth rates differ not only between the sexes, but also among herds (Geist 1971, Shackleton 1973) and among years on the same herd, depending on the available forage (Horejsi 1976, Bunnell 1978).

Bighorns of all ages play; lambs, yearlings, rams and ewes exhibit both social and locomotor play (Geist 1971, Berger 1979). Lambs are born to females that differ in social rank, and live in groups of mixed age and sex that present a variety of partners (ewes and yearlings of both sexes, as well as other lambs) to play with. The amount of playing by lambs reportedly varies with physical environment

1

and group size (Berger 1979), population quality (Geist 1971, Shackleton 1973), and maternal investment (Horejsi 1976).

This study is not the first to address play in bighorns. Geist (1971), Shackleton (1973), Horejsi (1976) and Long (1980) used the amount of playing observed as relative measures of population vigor. Berger (1979, 1980) studied the structure and ecology of play in three different populations of bighorns. None of these studies focused on dyadic interactions between known individuals, however. In conjunction with other studies of bighorn behavior, access was obtained to a relatively small bighorn herd (50-60 animals) situated on the National Bison Range. These animals range within a fenced enclosure, but are not "captive". All individuals in the population were known, and could be closely monitored on a year-round basis, a pre-requisite for a detailed study of development.

Studies of play behavior continue to be plagued by problems of definition (Bekoff and Byers 1981, Fagen 1981). For the purposes of this study, I use Bekoff and Byers' (1981:300) definition: "Play is all motor activity performed post-natally that appears to be purposeless, in which motor patterns from other contexts may often be used in modified forms and altered temporal sequencing". Among ungulates, play is often divided into locomotor-rotational play, which includes running and jumping components; and social play, which includes all patterns which involve more than one

individual (Byers 1984). In this study, I focused on social play, particularly contact and display patterns performed among lambs.

Numerous hypotheses have been generated to explain the benefits of play behavior (see Fagen 1981 for a review and summary). Of these, many were not testable in field situations. I chose to test three of the hypotheses by observing a free-ranging herd, and by reviewing the literature concerning the natural history and ecology of other bighorn herds:

I. The Motor Training Hypothesis.

Repeated exercise has numerous beneficial, or potentially beneficial, effects, including thickening bones and strengthening muscles, increasing cardiopulmonary capacity and efficiency, and increasing the efficiency of actions performed (Bekoff and Byers 1981 and references therein). These physical and neurological processes have been lumped together under the term "motor training". Behaviors can thus be fine-tuned, so animals learn how and when to perform them in the correct environmental and social contexts (Fagen 1981, Bekoff 1984). If play provides motor training benefits, the following might be expected: (1) play behavior should occur in both sexes and appear early in life (during the most rapid growth phase); (2) social play patterns should resemble adult aggressive and sexual behaviors; and (3) male lambs (because rams show greater

variance in reproductive success than ewes (Geist 1971, Hogg 1984a)) should exhibit more social play than females, and choose partners that are closest to them in size or age to provide rigorous and challenging play.

II. The Social Cohesion Hypothesis.

Social attachments may be formed, and social bonds maintained or strengthened in play (Bekoff 1977). Play may act as "social glue" (Fagen 1981) by keeping groups cohesive and reducing the tendency to disperse (Bekoff 1977). It is not whether an animal plays, but the amount of play that may reduce its tendency to disperse (Bekoff 1984). Individuals that play together may be more inclined to remain with their playmates, and less likely to disperse. The following, therefore, might be expected: (1) female lambs should exhibit more social play than male lambs, because females tend to remain with the ewe group on their natal range, while males tend to disperse with the rams to separate ranges when 1-4 years old (Geist 1971); (2) lambs should play in same sex groups, because ram and ewe groups are separate for most of the year; and (3) play should be a cooperative venture in which all players benefit; dominance relationships need not be formed early and should not be evident in play bouts. Dominance reversals should be common and play should rarely, if ever, escalate into a fight.

III. The Social Competition Hypothesis.

"If a juvenile can reduce the body growth of his

'playmates' by gaining dominance, he inflicts upon them a permanent disadvantage" (Geist 1978 :3). In species characterized by dominance hierarchies, it might be beneficial to obtain dominance over one's peers early in ⟵ life, and to use that dominance, in play bouts, to inflict stress upon (potential) competitors and increase their "cost of living" (Geist 1978). To be consistent with this hypotheses, (1) dominance relationships should be formed early and dominant animals should use their rank to control interactions, (2) because rams and ewes are geographically separated for most of the year and the most intense competition for resources probably occurs within ram and ewe groups, lambs should play preferentially with lambs of the same sex, and (3) because rams may not only compete for forage and bedding sites, as ewes do, but they also compete for dominance positions and breeding opportunities (dominance may be more closely tied to reproductive success), male lambs should play more than female lambs.

The above hypotheses are not mutually exclusive and care must be taken in interpreting results. The predictions made are by no means the only implications of these hypotheses, but merely those I felt to be most tractable for this study. Because it is almost impossible to determine the evolutionary forces that shaped play behavior, the hypotheses may represent effects and not necessarily functions of play behavior. However, the study of the beneficial effects may

be one way to study function (Fagen 1981).

The Motor Training hypothesis is the most widely supported hypothesis to date, based on structure and behavioral sex differences in juvenile Canids (Bekoff 1974, Vincent and Bekoff 1977), Mustelids (Poole 1978, Biben 1982), Ungulates (Byers 1977, 1980; Berger 1979, 1980; Pfeiffer 1985), and Pinnepids (Gentry 1974), to name a few. Juvenile interactions of collared peccaries (Tayassu tajacu) may support the Social Cohesion hypothesis (Byers and Bekoff 1981, Byers 1983, 1984). Studies of young Columbian ground squirrels (Spermophilus columbianus, Steiner 1971) and Primates (Poirier and Smith 1974) indicate possible relationships between play and the establishment of dominance hierarchies, but no studies to date have shown that animals use their dominance status to inflict stress on their subordinates in play.

Data on three populations of bighorn sheep in British Columbia, Oregon and California provided evidence for the Motor Training hypothesis (Berger 1979, 1980). Berger also demonstrated pronounced interpopulation variability in bighorn behavior, showing the need for studies in different habitats and of different subspecies. Berger worked with each population for two to seven months and was often able to identify the sex of the lambs. However, perhaps because he did not know many individuals, he did not test the Social Cohesion or Social Competition hypotheses.

Because the amount of playing by bighorn lambs has been correlated to the amount of maternal investment (Shackleton 1973, Horejsi 1976), I also examined the relationship between maternal investment and play behavior.

This study began as an exploration of the structure of play in bighorns and tests of three hypotheses concerning the possible functions of play behavior. One of the hypotheses connected play behavior to the development of dominance relations. However, few studies concerned dominance relations in bighorn sheep, although the dramatic horn-to-horn clashes of the rams were well-documented and recognized as important in deciding breeding priviledges. The relationships between horn size, rank and breeding opportunities of free-ranging rams were well described (Geist 1971), but studies of ewes were short-term, under captive conditions (Eccles 1981, Bennett 1986). Data on dominance relations in free-ranging bighorns, particularly ewes, were sorely lacking.

Rams and ewes live on separate ranges for most of the year (Geist 1971), and essentially exist in two separate societies. Rams form bachelor herds composed of sexually mature animals ranging in age from 18 months to over 10 years (Geist 1971, pers. obs.). Bachelor herds are composed of individuals that vary considerably in body and horn size. No strong ties are apparent among the rams, and the society is characterized by strict protocol based on body and horn size

(Geist 1971).

Ewe society is focused on the nursery group, composed of lambs and lactating ewes, yearlings of both sexes, some 2-year-olds and other ewes who associated with the group for brief periods of time. Although ewes reach adult size and maturity at 1-3 years of age (Geist 1971, Jorgenson and Wishart 1984), sexually mature ewes show considerably less variation in size than the animals in the bachelor herd (Geist 1971, Jorgenson and Wishart 1984). Ewes have been considered paedomorphic in their behavior, with respect to rams; all members of ewe society (except lambs) may behave like juvenile males (Geist 1971). The two bighorn sheep societies theoretically consist of the behaviorally immature nursery group, and the maturing and mature bachelor herd.

Although the young rams leave the nursery groups when they are sexually mature and able to dominate the ewes (Geist 1971), when and how dominance relations develop among rams and ewes has not been reported. A free-ranging herd of bighorns was studied to determine how the different developmental regimes and social organizations of rams and ewes affect the structure and development of dominance relations, and to try to correlate rank with such variables as age and reproductive success.

CHAPTER II

MATERIALS AND METHODS

Study Area

The study was conducted on the National Bison Range (NBR), a 7504 ha. National Wildlife Refuge administered by the U.S. Fish and Wildlife Service. The NBR is located approximately 70 km north of Missoula in northwestern Montana. The vegetation is characterized by Palouse (Agropyron) Prairie, with thick patches of Douglas-fir (Pseudosuga menziesii) on the north slopes and scattered Ponderosa pines (Pinus ponderosa) on the south slopes. Elevations range from 788 to 1489 m. Bighorn sheep inhabit the southern half of the Refuge, an area of steep hillsides dissected by many small drainages. As with the Refuge as a whole, the sheep range is smoothly contoured, with only a few, small rock outcrops.

The NBR is surrounded by a 2.4-m game fence that prevents emigration or immigration of wild (and domestic) ungulates. Wild ungulates maintained on the Refuge include wapiti (Cervus elaphus), bison (Bison bison), pronghorns (Antilocapra americana), mountain goats (Oreamnos americanus), mule deer (Odocoileus hemionus), white-tailed deer (O. virginianus) and bighorns. The Refuge is divided into eight pastures by raised drift fences that restrict the movements of the bison, but allow smaller ungulates, including bighorns, to pass underneath. Careful management of all ungulates on the Refuge prevents overgrazing.

9

Study Population

The bighorns on the NBR were descendants of 12 animals that were brought to the Refuge in 1922, from Banff, Alberta (NBR Refuge Narrative Reports). During the course of my study, the number of sheep in the population ranged from 50 to 53 (Table 1).

The bighorns were habituated to people and could be approached to within less than 10 m. The sheep were observed from June 1979 through May 1982 by another observer (Hogg 1984a); my study began in June 1982 and terminated in September 1984.

All of the sheep were individually recognizable by horn characters, natural mutilations such as torn ears, or ear tags. To facilitate rapid identification, some adults and all lambs of 1983 and 1984 were splattered with sheep branding paint or Nyanzol A dye. Both the paint and the dye were squirted onto the animal's coat from a hypodermic syringe. This resulted in variable patterns, some of which were visible from more than one km through a spotting scope.

Ages of sheep were estimated initially by J. Hogg in 1980, by counting horn annuli. Because ages of ewes cannot be reliably determined in the field (Geist 1966), ewes five years or older were classified as "older" (Hogg 1983). Where ages were needed for calculation purposes, a mean age was calculated for members of the "older" ewe group by figuring a

Table 1. Age and sex composition of the NBR herd on
1 September 1982-4. Age is in years. L = lamb.
+ indicates ewes that were estimated to be at least five
years old in 1980.

	1982		1983		1984	
	Age	#	Age	#	Age	#
Rams	10	3	11	1	11	1
	9	1	10	1	10	1
	8	3	9	2	9	1
	7	1	8	1	8	3
	6	3	7	3	7	1
	5	2	6	2	5	1
	3	1	4	1	4	2
	2	2	3	2	3	5
	1	5	2	5	2	2
	L	2	1	2	1	2
			L	2		
Total		23		22		19
Ewes	7+	9	8+	9	9+	8
	6	3	7	3	8	3
	5	3	6	3	7	3
	4	1	5	1	6	1
	3	1	4	1	5	1
	2	5	3	5	4	5
	1	5	2	5	3	5
			L	4	1	4
					L	2
Total		27		31		32
Herd Total		50		53		51

yearly mortality rate of 11.7% (Geist 1971) and a maximum age of 12 years. Ages of sheep born in 1980 and later were known precisely.

"Lamb" refers to an animal that was less than 12 months old, "yearlings" were 12-23 months, and "adults" were two years and older.

Data Collection

Censuses

Censuses were conducted bi-weekly throughout the year, except for the rutting and lambing periods, when daily censuses were conducted. During a census, an attempt was made to find all of the sheep in the population, except during the lambing period, when a concerted effort was made to find only ewes and lambs. Censuses and observations conducted during the rut (November-December) yielded approximate estrous dates for most ewes. By adding the length of known gestation periods ($\bar{X}$ = 173.6 days, N = 16; Hogg 1984a), an approximate parturition date was obtained for almost every ewe. I made intensive efforts to keep track of each ewe around her parturition date, and attempted to capture lambs soon after birth. Domestic ewes reportedly establish discriminating behavior within the first 30 minutes after birth (Poindron and LeNeindre 1979), so I waited until lambs were at least one hour old before attempting to capture them. Lambs older than 24 hours were seldom catchable.

After capture, lambs were ear-tagged, and weight and sex were recorded. In 1984, radio-collars were also fitted on nine lambs. Individual ewes remained isolated from other ewes for 2-12 days following parturition. If the birth was not observed, a ewe observed in isolation with a lamb less than five days old was assumed to be the lamb's mother.

Censusues conducted throughout the lambing period (roughly 10 May-20 June) revealed which ewes were pregnant, and how many aborted or failed to conceive. Opportunistic observations of sheep social behaviors, particularly dominance interactions, play, and ewe-lamb interactions, were also noted during censuses.

Observations

Focal observations were conducted on the ram groups mainly during September through early November, but also occasionally throughout the rest of the year. Observations in 1982 were conducted on an ad libitum basis (Altmann 1974). During 1983 and 1984, all-occurences samples (Altmann 1974) of dominance interactions were recorded when group composition was relatively stable. Ad libitum samples were recorded when group composition changed rapidly during the observation periods, and during censuses.

Observations of the ewe groups were conducted in an opportunistic, hierarchical fashion. I attempted to keep as many lambs as possible in view, while I wandered with the

group. All-occurences samples of suckling bouts were recorded for all lambs in view: in-view and out-of-view times were recorded to the nearest minute, for each lamb. If at least two lambs were in view, and neither one suckling, then all-occurences samples of play were also recorded. If all members of a group, including adults, yearlings, and lambs could be consistently kept in sight (e.g., when bedded, or grazing in a bunched group in an open area), all-occurences samples of suckles, play, and dominance behaviors were recorded. Ad libitum samples of play and dominance behaviors were recorded when group composition was changing too quickly to record accurately. I attempted to stay as far from the group as possible, while still being close enough to identify accurately all focal animals, with the lambs having highest priority.

The duration of all interactions were recorded to the nearest minute. All sheep identities and behavioral acts were abbreviated, resulting in a form of shorthand that facilitated rapid note-taking. Group composition was noted at the beginning of each observation period and all animals entering and leaving the group (and times) were recorded. A hand-held digital stopwatch was used to keep track of elapsed time, as well as durations of selected behaviors.

Play bouts were recorded during focal observations during the summers of 1982-1984, and opportunistically throughout the year. In 1982, Mounts were recorded, as well

as the number and duration of play bouts. In 1983 and 1984, the following patterns comprising individual bouts were also recorded.

Ethogram

The following patterns were recorded in social interactions during the study:

Contact Patterns

Head Butt (HB): Forehead or horns are used to forcefully bump the head of another.

Butt (B): Forehead or horns are used to forcefully bump the body of another.

Clash (CL): A very forceful HB preceded by an SLR (see below) by one or both sheep.

Touch Heads (TH): a light forehead-to-forehead contact that is sustained for at least one second.

Shoulder-Push (SP): Shoulder-to-shoulder contact, in parallel position, in which two sheep push side-to-side or around in circles.

Neck Wrestle (NW): The head and neck are placed over the neck of another, in parallel or anti-parallel position, and used to press the opponents head toward the ground.

Face-rubbing (FR): Face or horns are slowly rubbed on the face or horns of another.

Front-leg kick (FK): A foreleg is raised and extended toward another, and contacts the opponents chest, belly or

legs.

Pawing (PW): A front hoof is used to scrape the back of a
reclining opponent.

Displays (non-contact patterns)

Straight-legged rear (SLR): A rear on extended hind legs,
with the forelegs straight or slightly bent at the
carpus, and head inclined toward another sheep.
Also referred to as a "threat jump" by Geist (1971).

Head Tip (HT): The horns (or forehead in young lambs) are
inclined toward another sheep while the chin is
tucked in toward the chest. The same pattern has
been called a "horn threat" by Geist (1971).

Low Stretch (LS): The head and neck are lowered and extended
on an even horizontal plane with the back.

Twist (T): A Low Stretch in which the lowered head is rotated
on its longitudinal axis.

Present (P): The head is raised, with the neck arched and the
rostrum oriented parallel to the ground.

Calculations and Statistics

Play Patterns and Rates

G-tests (Sokal and Rohlf 1981) were used to test for
significant differences in the proportion of patterns used by
different individuals and groups. Frequencies were adjusted
to account for differences in membership of different sex
classes.

Weekly play duration rates were obtained by dividing the

total number of minutes in which play was recorded by the total number of observation minutes on all lambs combined (lamb-minutes) for each week. Week 1 began on 23 June each year. Non-parametric ANOVAs (Sokal and Rohlf 1981) were used to assess differences among years.

Maternal Investment

Suckling rates were used to estimate post-natal maternal investment. All-instances samples of suckling bouts were obtained during almost daily observations of the nursery bands. A suckling bout began when the lamb was judged to have grasped a teat, and terminated when the lamb moved its head, voluntarily or otherwise, away from the udder. Weekly suckling rates were obtained by dividing the total duration of all observed suckles (in seconds) by the total number of observation minutes on all observed lambs (combined) for a week. Non-parametric ANOVAs were used to test differences among years; Pearson's coefficient, r, was calculated to examine the correlation between play rates and suckling rates.

Dominance Assessment

Dominance relations were assessed by assembling a win-loss matrix (Brown 1975) based on dominance interactions, for each sex. Within ram groups, I scored non-contact displacements, and courtship behaviors (Mounts, Front-leg Kicks, and Twists often accompanied by growling and tongue-flicking) as wins for the initiator, and Face-rubbing

as a win for the recipient. Prior to the onset of rut each year, subordinate rams were observed butting and pushing dominant rams out of bedding sites, before displaying subordinance by Face-rubbing (see also Geist 1971). During this pre-rut period, only non-contact displacements were recorded as wins for the initiator. For ewes, contact and non-contact displacements from bedding sites, foraging locations, mineral licks, horning posts, or other spatial locations were scored as wins for the initiator and, as with the rams, Face-rubbing was scored as a win for the recipient. In both sexes, the winner of a dominance fight was recorded as winning one interaction.

Many of the behaviors used in dominance-subordinance interactions were also used in playful contexts by lambs. To avoid circularity, wins and losses between lambs were only assigned for displacements, and only when not accompanied by any play signals. Play signals included the rotational patterns Gambol, Heel Kick, and Neck Twist (Berger 1979). Nods (see Berger 1979, Byers 1980) were also recorded as play signals. Yearlings and adults also used the above patterns in playful contexts; the presence of play signals was used to separate playful interactions from dominance interactions.

The results of the win-loss matrices were tested to determine if they differed significantly from random order (Appleby 1983). This consisted of counting the number of circular triads and unknown relationships in a group. For

known relationships, the winner of the majority of the
encounters wihtin that dyad was assigned a value of 1, and
the loser received a value of 0. Appleby's (1983) method of
assessing randomness was based on the assumption that
individuals who had not been observed interacting had equal
probabilities of winning an interaction. However, among rams
older individuals won 97% of the encounters with younger
rams. When two rams of disparate ages had not been observed
interacting, the older animal was assigned a 0.97 probability
of winning the interaction and the younger was assigned a
value of 0.03. For two rams of the same age whose
relationship was unknown, a 0.50 probability was assigned to
each (see also Rutberg 1986). Older ewes won in 88% of
interactions with younger ewes, therefore, when the
relationship was unknown, older ewes were assigned a 0.88
probability, and younger ewes a 0.12 probability. Ewes of
equal age were each assigned a 0.50. A chi-squared value was
used to assess the degree of randomness in the matrix. A
significant result indicates a non-random order and a
tendency toward transitivity (A > B, B > C, therefore A > C).
The degree of linearity of the hierarchy was calculated by
Kendall's coefficient K (Kendall 1962, Appleby 1983) which
ranges from 0 (non-linear) to 1.0 (completely linear). The
coefficient K was used in preference to Landau's index of
linearity, h, (Landau 1951), due to the lack of information
present in each of the matrices.

The probability of linearity within a group of more than 10 animals is low (Appleby 1983, see also Schjelderup-Ebbe 1975), so rather than assigning ordinal ranks to the sheep, I calculated Dominance Values for each sex in each year using the win-loss matrices based only on the results of recorded interactions (not including probabilities for unknown relationships). Dominance Values (Beilhartz et al. 1966, Eccles 1981) were used as relative measures of dominance, and were calculated as follows:

$$D.V. = \arcsin\sqrt{x_i};$$

where x_i is the proportion of opponents dominated. These D.V.s were normally distributed and permitted the application of parametric statistics. Dominance Values were calculated only for animals interacting with at least 10% (arbitrarily chosen) of the other herd members.

Interaction Rates

All-occurences samples collected in 1983 and 1984 were used to determine if sheep interacted at different rates according to their Dominance Values. For each year, both ewes and rams were divided into four equal groups comprising the lowest scoring 25% (group A), the second lowest scoring 25% (group B) et cetera. A computer program was written to compute expected rates of interaction based on the amount of time the animals in each rank-group were observed (Altmann and Altmann 1977), assuming each animal had an equal probability of interacting with any other in the group.

These expected rates were then compared to the observed values and a G-test was used to test for significance.

Dominance interaction rates were calculated by dividing the observed number of dominance behaviors in a rank-group by the total number of hours of observation on all members of each rank-group. These rates were comparable among rank-groups and, for each sex, among years. The sampling periods were biased toward times of the day and times of the year in which sheep were most likely to be interacting (e.g., summer afternoons for the ewes, and autumn mornings for the rams), and do not represent absolute rates of behavior.

Reproductive Correlates

Simple "reproductive performance" variables were calculated from observations conducted during the rutting and lambing periods. Focal animal sampling of estrous ewes and associated rams allowed assignment of estrous and birth dates for each ewe, whereas the number of copulations and the number of ewes bred (during observation periods) could be calculated for individual rams.

Lamb birth weights were used as estimates of pre-natal investment, while nursing durations and rates were used to estimate post-natal maternal investment. A nursing bout began when the lamb was judged to have grasped a teat, and terminated when the lamb moved its head away from the udder. Mean nursing duration was the mean of all recorded suckles for a ewe during the summer. Daily nursing rate was the

total nursing duration for each ewe divided by the number of minutes of continuous observation on that ewe in an observation period. Daily nursing rates were averaged over the summer to obtain mean nursing rates for each lactating ewe.

These "reproductive performance" variables were regressed against D.V.s and tested for correlation with rank.

CHAPTER III

STRUCTURE AND FUNCTIONS OF PLAY BEHAVIOR

Results

Survivorship

At the beginning of the study, mid-June 1982, two surviving lambs represented the entire surviving lamb crop for that year, out of 21 born (Hogg 1983). Both were males, and 111.4 hours of focal observations were obtained between 22 July and 7 September.

In 1983, 26 lambs were born; seven were alive at the end of June but one male disappeared on 17 or 18 July, so only six lambs (23%) survived until fall. Nine lambs were caught and weighed, but only one of those survived. Surviving lambs included two males and four females, and 247.2 hours of focal observation were completed between 25 June and 15 September.

In 1984, 23 lambs were born, but only two survived until the end of June. Both were females. Eleven lambs were caught and weighed, and nine of those were fitted with radio-collars in an effort to determine the cause of the high lamb mortality. Three radio-collars fell off the lambs when 10-14 days old and six were recovered from predator-killed lambs. Predation was probably the cause of most of the lamb mortality in this herd. Focal observation hours on the two lambs totaled 138.7 between 23 June and 4 September. No lambs that were handled survived until the end of the summer.

23

Structure of Play

In 1982, 40 play bouts, totaling 84 minutes were recorded. Bouts lasted up to 10 minutes, with a mean of 2.3 minutes. Because play was recorded to the nearest minute, the minimum bout was calculated as being one minute long, although the number of acts recorded in a minute ranged from 1 to 21. Most play occurred during late July with very few bouts being observed after mid-August (Fig. 1). Mounts were common between the two male lambs; JN mounted BS 41 times, and BS mounted JN 16 times. This difference was significant (G-test, $G = 11.25$, $p < 0.05$).

In 1983, 331 play bouts totaling 672 minutes were recorded. Play bouts lasted up to 22 minutes, with a mean of 2.2 minutes. As in 1982, most play occurred during July, with few bouts being observed after mid-August (Fig. 1). Play bouts involved 2-7 lambs.

In 1984, 70 play bouts were recorded, for a total of 107 minutes. Bouts ranged up to nine minutes long and averaged 1.5 minutes. Play was infrequent, and most play occured during early July (Fig. 1).

In 1983, the only year in which more than one dyad of lambs were present, the duration (number of play minutes per bout) was significantly correlated with the number of players ($r = 0.76$, $p < 0.01$; Fig. 2).

Because 1983 was also the only year in which both male and female lambs were present, only data from that year can
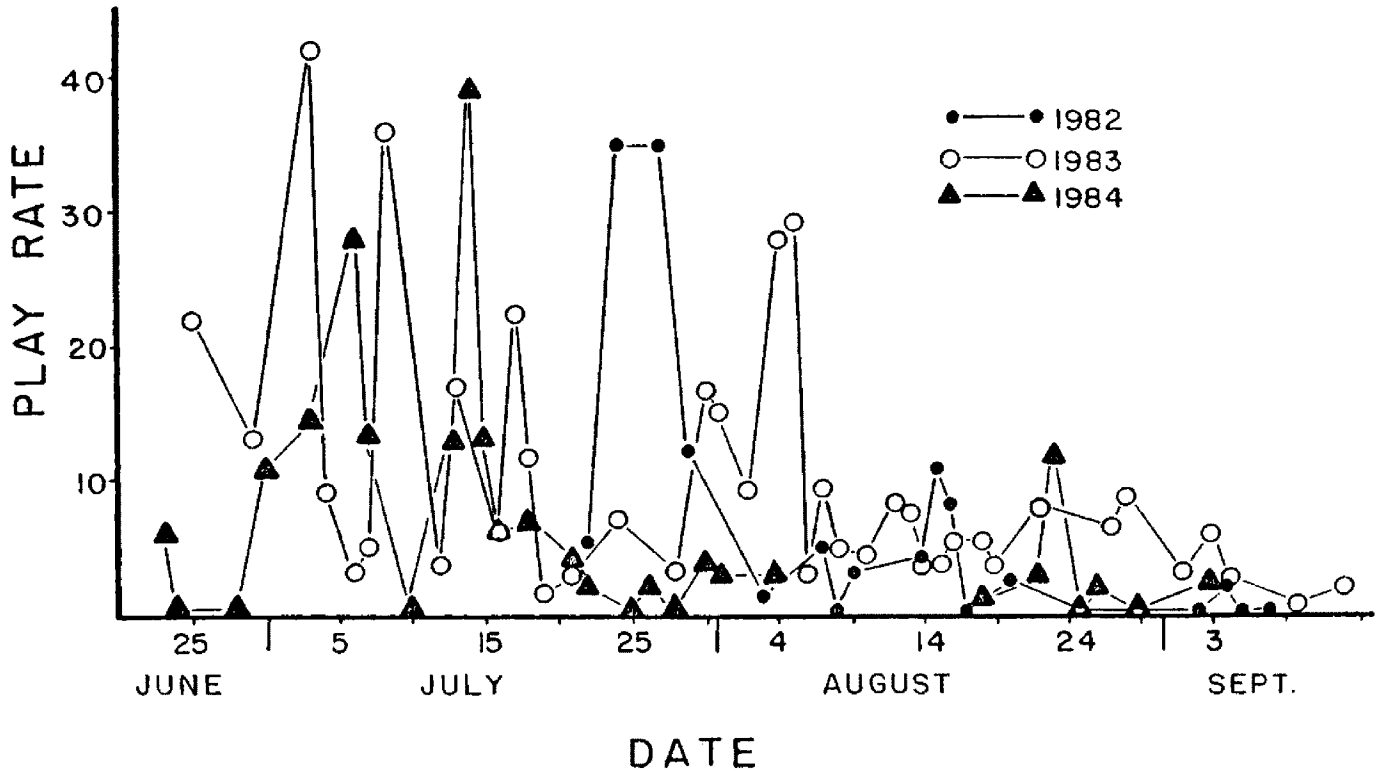
Figure 1. Distribution of play bouts (and their rates) during the summer observation periods. Note the decrease in play during August. Play rate = play minutes/lamb-minutes of observation.
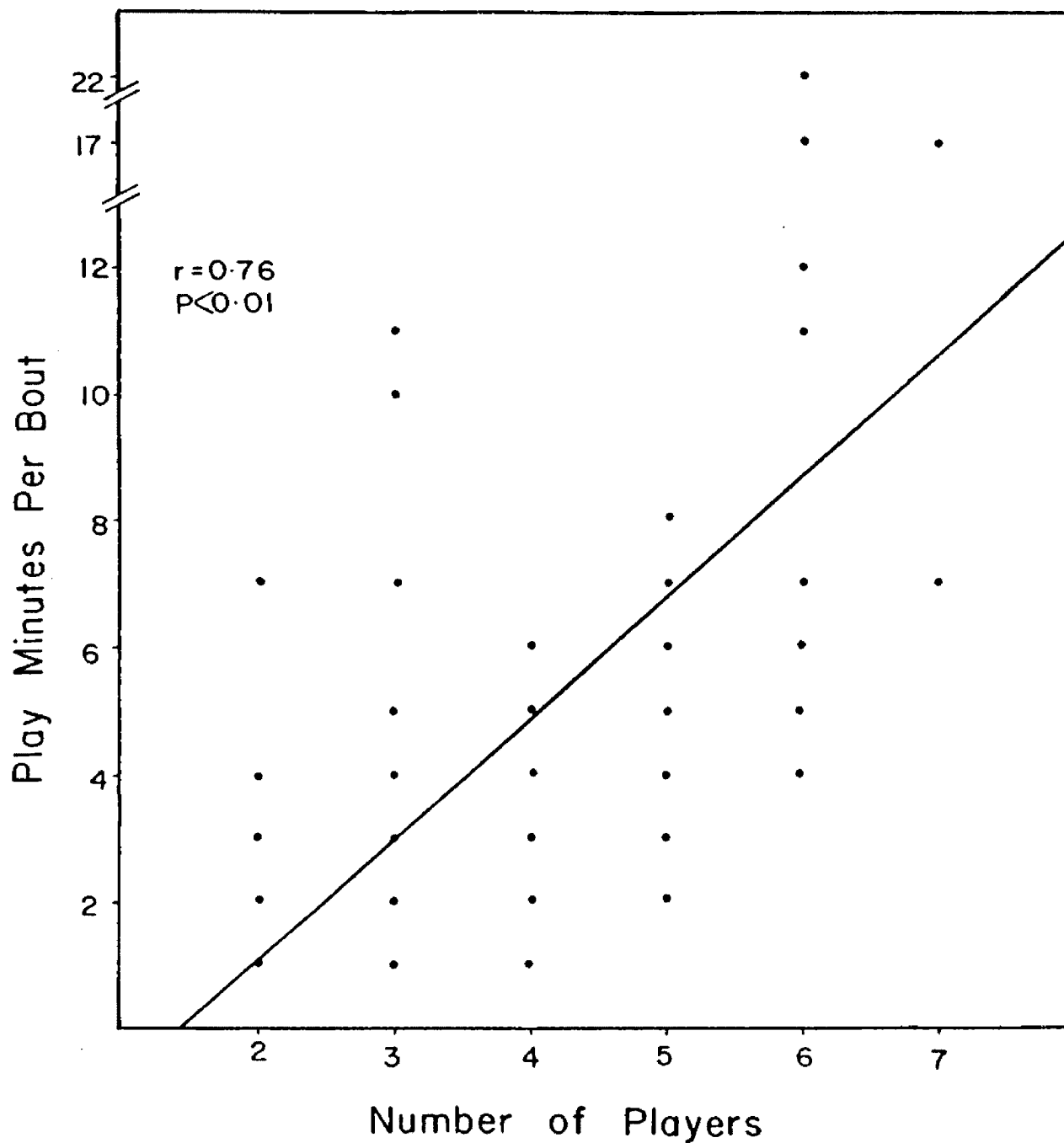
Figure 2. The duration of play bouts were significantly correlated with the number of players involved in 1983. Line drawn from regression equation.

be used to analyze differences in the amount and type of play between male and female lambs. Overall, males were involved in more play patterns than females and exhibited a larger repertoire. Males initiated more patterns than females ($G = 115.2$, $p < 0.001$), but either sex was about equally likely to receive play invitations ($G = 0.36$, $p > 0.10$).

For all patterns, except Mounts, males initiated more patterns to other males (per lamb) than females (Fig. 3); significant differences were found for Clashes and SLRs ($G = 10.9$, $p < 0.001$). Females initiated about the same number of patterns to either sex (Fig. 3); no significant differences were found for any pattern. Female lambs were never observed performing Mounts, Twists or Presents. Lambs initiated most contact patterns (TH, SP, NW, CL, BH, and B) with lambs of the same sex ($G = 4.7$, $p < 0.05$; Fig. 4). Males and females both initiated more displays (SLR, HT, T, and P combined) to males than females, with males initiating significantly more displays to males than females ($G = 12.9$, $p < 0.001$; Fig. 4). Lambs initiated almost three times more contact patterns (per lamb) than displays ($G = 159.3$, $p < 0.001$).

Of the 21 possible dyads that lambs could participate in, nine (43%) were same-sex dyads, whereas 44% of the 1441 play acts recorded (initiated and received) occurred in same-sex dyads. Overall, lambs in 1983 were not playing more with lambs of the same sex than would be expected by chance ($G = 1.26$, $p > 0.05$).
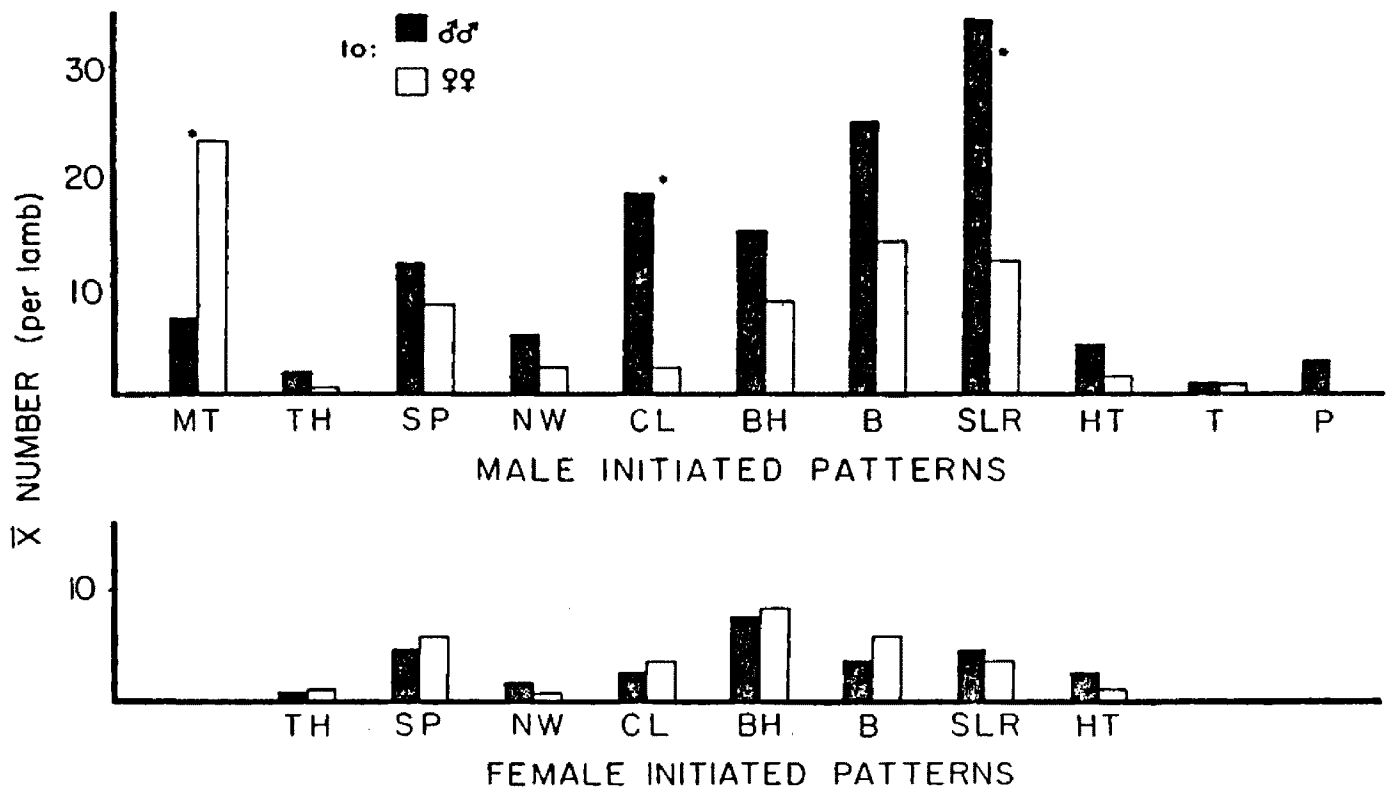
Figure 3. Number of male initiated patterns (top) and female initiated patterns (bottom) to male and female lambs, 1983. See Methods for a description of patterns. * = significant at p < 0.001.
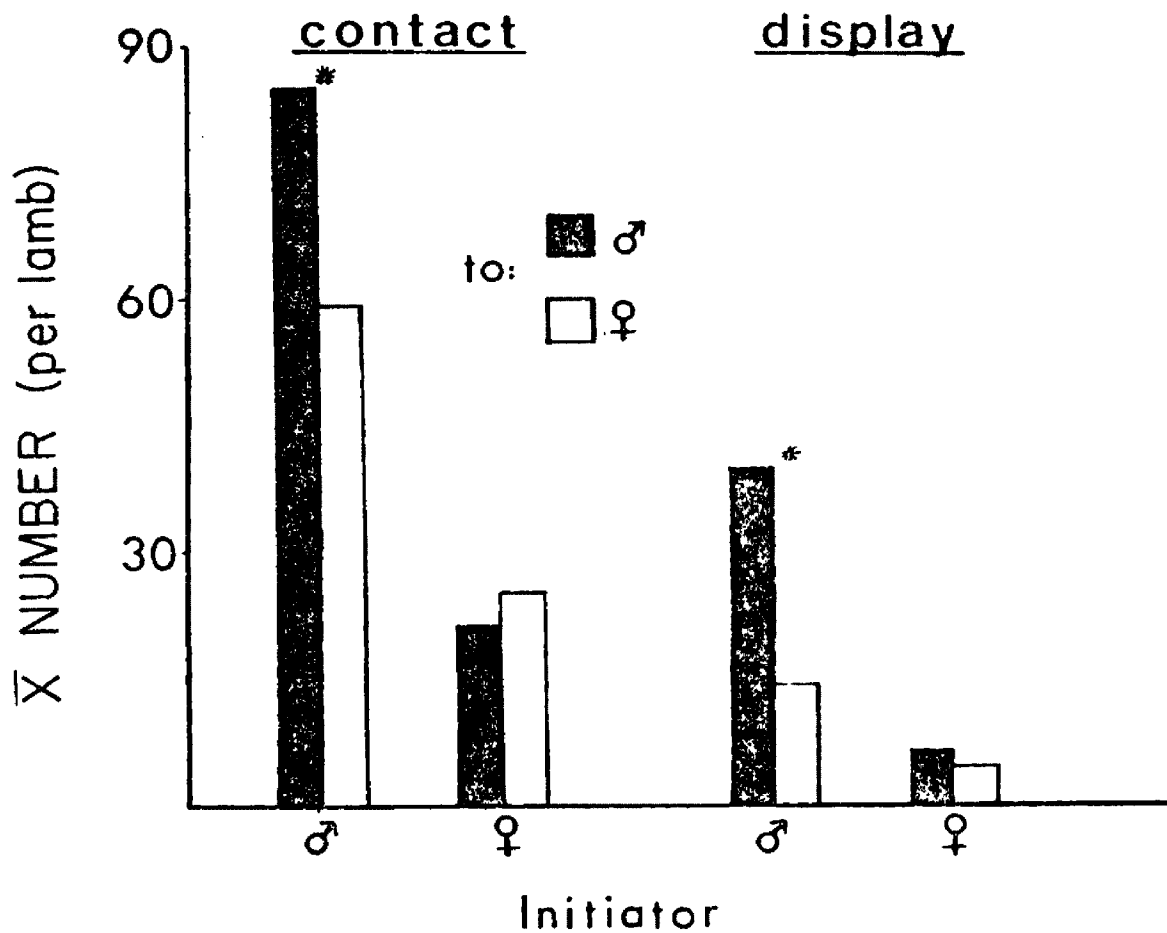
Figure 4. Summary of total contact patterns (MT, TH, SP, NW, CL, BH, and B) and display patterns (SLR, HT, T, and P) to male and female lambs. Lambs used significantly more contact than display patterns in play bouts. * = significant at p < 0.01.

A successful play initiation was followed by more play patterns between initiator and recipient. Males succeeded in initiating significantly more play bouts with males than females (G = 6.6, p < 0.01), and females also succeeded more often with males (G = 7.9, p < 0.01). Overall, although males initiated more bouts, females were successful in initiating bouts a higher proportion of the time, 34% vs. 23% for male success (G = 10.6, p < 0.01).

Lambs did not play equally with all other lambs (Table 2). Males selected among females (G = 79.3, p < 0.01), with EL receiving the most initiations. Females did not discriminate between the two male lambs (G = 1.3, p > 0.05), but only one female (DY) did not discriminate among the female lambs (EL: G = 10.1, p < 0.01; JL: G = 47.9, p < 0.001; JO: G = 18.3, p < 0.001: DY: G = 4.5, p > 0.05). Males initiated bouts with males or females closest to them in age. The two females that made the most pronounced choices for each other as play partners (JL and JO, see Table 2) were known to have a coefficient of relatedness ≥ 0.125 (their mothers were at least half-sisters, J. Hogg, pers. comm.). The relatedness of the other lambs, or their mothers, is not known.

Males mounted females more often than males, with the two oldest females receiving 78% of the observed Mounts (Table 3). Of the two male lambs that survived the summer, CA mounted SI 10 times, and SI mounted CA four times, this

Table 2. Total play patterns (MT, TH, SP, NW, CL, BH, SLR, HT, T, AND P) initiated and received for each lamb dyad in 1983. Lambs appear across the top of the table in birth order. * indicates the animal closest in age to the initiator.

		Recipient							
		EL ♀	CA ♂	SI ♂	JS ♂	JL ♀	DY ♀	JO ♀	Total
	EL	--	37*	35	2	9	22	27	132
	CA	145*	--	177	7	65	73	40	507
	SI	82	75*	--	6	48	38	44	293
Initiator	JS@	3	1	8*	--	4	6	7	29
	JL	12	33	17	2	--	21*	68	153
	DY	18	27	23	0	32	--	31*	131
	JO	22	29	34	8	64	39*	--	196
Total		282	202	294	25	222	199	217	1441

@ JS disappeared in mid-July.

Table 3. Distribution of Mounts by the two male lambs in 1983. Lambs appear across the top in birth order.

		Recipient						
		CA	SI	EL	JL	DY	JO	Total
Initiator	CA	--	10	114	4	7	8	149
	SI	4	--	24	22	3	4	60

difference was not significant (G = 2.6, p > 0.05).

In 1984, only female lambs were present, so sex differences could not be analyzed. The number of female-initiated patterns (to females) could be compared to those of 1983, however. In 1983, compared to 1984, females initiated more patterns (Wilcoxon rank sum T = 5.5, p < 0.05), including significantly more Clashes (G = 9.5, p < 0.05) and SLRs (G = 12.5, p < 0.001). The two females of 1984 initiated significantly more contact than display patterns (G = 75.4, p < 0.001).

Weekly play rates differed among the three years. In 1982 observations began on 22 July, so weekly play rates were compared for weeks 6-8 and 10-13 for the three years (no data were available for week 9, 1984). Differences among the three years were not significant for the last seven weeks (Friedman's randomized blocks x^2 = 4.07, p > 0.10). No significant differences were found when comparing 1982 to 1983 (Wilcoxon rank sum T = 13, p > 0.05) or 1982 to 1984 (T = 10, p > 0.05). Weekly play rates were higher in 1983 than 1984 (T = 12, p < 0.05; Fig. 5).

Play was infrequent in sheep other than lambs. A vigorous play bout involving at least eight rams, aged 23 months to almost four years, was observed in early April of 1983. Many SLRs and Clashes, as well as Gambols and Heel Kicks were observed. Because the young rams were not marked at that time and their rapid movements made identification by
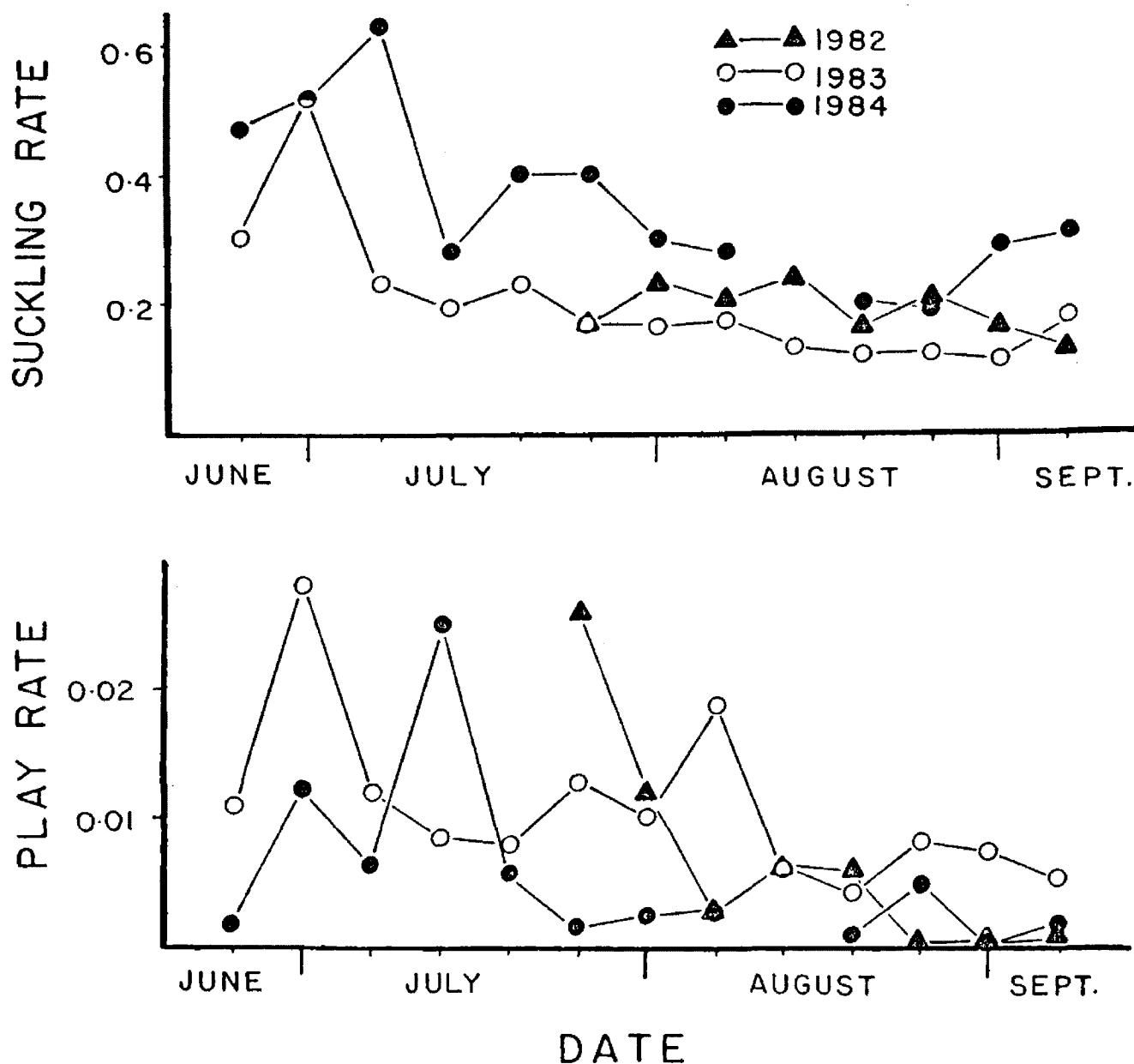
Figure 5. Bottom: weekly play rates (play minutes/lamb-minutes of observation) were highest in 1983, whereas, top, weekly suckling rates (minutes suckling/lamb-minutes of observation) were highest in 1984. Only in 1983 was a correlation found between suckling rate and play rate.

horn characters almost impossible, no quantitative data were recorded. In August of 1983, a nine minute locomotor bout involved 18 members of the nursery band, aged three months to more than eight years. The lambs, yearlings of both sexes, and adult ewes raced up and down a steep road-cut, executing many Heel Kicks, Gambols, Neck Twists, leaps and exaggerated Head Tips. During late December, 1983, a 2-year-old ram and a 3-year-old ram were observed engaging in a "mock-battle". They would Clash, stand back and Present, then Neck Twist and/or Gambol before Clashing again. I observed four Clashes in this manner before a 7-year-old ram approached and Clashed on the 3-year-old. The younger rams then ceased interacting and left the area.

Interactions among yearlings were infrequent, and usually reflected dominance relationships, with one animal using dominance patterns, and the other subordinance patterns. Play in yearlings ceased about the time when definitive dominance relations could be ascertained.

In 1982, the male lambs were observed on two occasions playing with ewe yearlings, and on two occasions playing with a small 2-year-old ewe. No lamb-yearling play was observed in 1983 or 1984.

Dominance interactions among the lambs were negligable, and in no year was it possible to assign any ranks to them. The sheep did not appear to be settling ranks until after one year of age.

Maternal Investment

Of the 20 lambs that were weighed in the course of the study, only one survived long enough to provide any play data, so no comparisons between weight and play could be made. However, weekly suckling rates could be compared among the years (Fig. 5). Significant differences were noted in weekly suckling rates for the three years (weeks 6-13, Freidman's randomized blocks, $x^2 = 10.3$, $p < 0.01$). For weeks 6-13, lambs in 1982 had higher suckling rates than lambs in 1983 (Wilcoxon signed ranks $T = 5$, $p < 0.05$), but lower than in 1984 ($T = 1$, $p < 0.05$). Lambs in 1984 had higher suckling rates than those in 1983 ($T = 0$, $p < 0.005$). The differences in suckling rates can be directly attributed to the number of lactating ewes each summer (see Hass 1984). The two lambs in 1982 were nursed by four ewes (two ewes/lamb), the six lambs in 1984 were nursed by eight ewes (1.3 ewes/lamb), and the two lambs in 1984 were nursed by six ewes (three ewes/lamb).

For 1982 and 1984, the correlations between weekly suckling rates and weekly play rates were not significant (1982: $r = 0.06$, $p > 0.05$; 1984, $r = 0.07$, $p > 0.05$), but in 1983 a strong positive correlation was found ($r = 0.78$, $p < 0.01$). Overall, the correlation of suckling rates to play rates for the three summers was not significant ($r = 0.11$, $p > 0.05$, Fig. 5).

Of the three hypotheses tested in this study, only the Motor Training Hypothesis was supported. The most commonly used patterns in social play bouts of lambs were patterns used by adults in courtship and intraspecific conflict. Males played significantly more than females, and exhibited significantly more of the two most common components of the male dominance fight; the Clash and the SLR (Geist 1971, pers. obs.). Less ritualized fights or brawls among rams also included Shoulder Pushes and Butts. Interactions around estrous ewes, among coursing rams (Hogg 1984a,b) and between tending and coursing rams, included Shoulder Pushes, Butt Heads, Butts, Clashes and Touch Heads (pers. obs.). Fights between ewes usually included SLRs, Clashes, and Presents, while Touch Heads, Shoulder Pushes, Butt Heads, Butts, Head Tips, Twists, and Presents were all used in dominance displays and displacements. During play, lambs used contact patterns more often than displays, whereas in dominance interactions, displays were used more often than contacts (Chapter IV). Although Geist (1971) refers to a sheep that rests his chin on the neck or back of another as performing a vestigal neck fight, the Neck-Wrestling observed in lamb play bouts was not observed in adult sheep (also noted by Shackleton 1973, Eccles 1981). The oldest sheep I saw performing this pattern were yearling rams. The large curled horns of the older rams may prevent the execution of the pattern, but it also appears absent in the ewes, who are less

restricted morhologically.

Males exhibit a greater variance in reproductive success than females (as estimated by the number of copulations (Geist 1971, Hogg 1984b)); if play has any influence on the subsequent development of skills influential in reproductive success, males might be expected to play more than females, especially in the performance of patterns relating to rank acquisition. The data presented here support this idea, as do data presented by Berger (1979, 1980) for other populations of bighorns, Byers (1977, 1980) for Siberian ibex (Capra ibex), and Pfeiffer (1985) for scimitar-horned oryx (Oryx dammah). A correlation between sexual dimorphism in adults and sexual dimorphism in play appears to be widespread (Bekoff 1974, Gentry 1974, Sachs and Harris, Symons 1978, Biben 1982, to name a few), but sexually dimorphic play was also evident in scimitar-horned oryx, which are sexually monomorphic (Pfeiffer 1985), suggesting that variance in reproductive success may influence play more than differences in adult size or growth rates.

Lambs appeared to choose partners that would provide the most challenging play, usually those closest in age. The lambs did not show a significant preference to play with lambs of the same sex. The two female lambs in 1984 played less than the two male lambs in 1982, although not significantly, and my overall impression was that female lambs were less motivated to play than were males (see Meaney

et al. 1985). This lower level of motivation might explain why play rates in 1984 were so low, in spite of greater maternal investment (as estimated by suckling rates). Males were less successful in initiating play with females than with males, which might have encouraged them to play with other males, as Byers (1980) suggests. Although my sample sizes are small, these data, for the most part, concur with other studies of closely related bovids (Byers 1977, 1980; Berger 1979, 1980). Unlike the other researchers, I found that males mounted females more than males; the majority of Mounts were performed on one female lamb (EL), who was closest in age and size to the two male lambs in 1983 (Table 3).

The year-to-year variation in the amount of play observed was probably more a function of the number, and sex, of available play partners, than in the amount of maternal investment. This is contrary to the findings of Shackleton (1973) who found a direct relationship between maternal investment (total suckling time) and the amount of play observed. There may be a maternal investment "threshold", below which lambs are inadequately nourished, resulting in a decrease in the amount of playing (Muller-Schwarze et al. 1982). The NBR lambs, with more than one ewe nursing for each lamb, were probably well above this threshold. The importance of the number of play partners was recognized by Berger (1979) who found that desert lambs, which occur in

smaller nursery groups, played much less than mountain lambs, in spite of greater maternal investment. Although Berger also found a significant correlation between group size and the number of acts performed in play sequences of mountain lambs, he attributed much of the restriction of playing by desert lambs to a hazardous environment. If play serves to "program" lambs about the vagaries of the environment (Geist 1971), then lambs should use play as a means of learning how to deal with hazardous environments for times of emergency (i.e., when escaping from predators). Small groups sizes may adequately explain the relative infrequency of play behavior in desert bighorn lambs.

The importance of exercise early in the life of a mammal has been recognized (see Bekoff and Byers 1981, Fagen 1981, for reviews). Although I was unable to weigh lambs older than two days of age, growth data are available from other herds of Rocky Mountain bighorns. The peak play periods of NBR lambs coincided with the peak growth period of lambs from Ram Mountain, Alberta (Jorgenson and Wishart 1984, Fig. 6), which suggests that play may be occuring at a time for optimal physical development in lambs.

Most of the benefits of play are speculated to accrue at later developmental stages (Fagen 1981). However, play in lambs may also have immediate benefits (see Martin and Caro 1985). Young lambs spent a considerable amount of time engaging in locomotor play: stotting rapidly through rocky
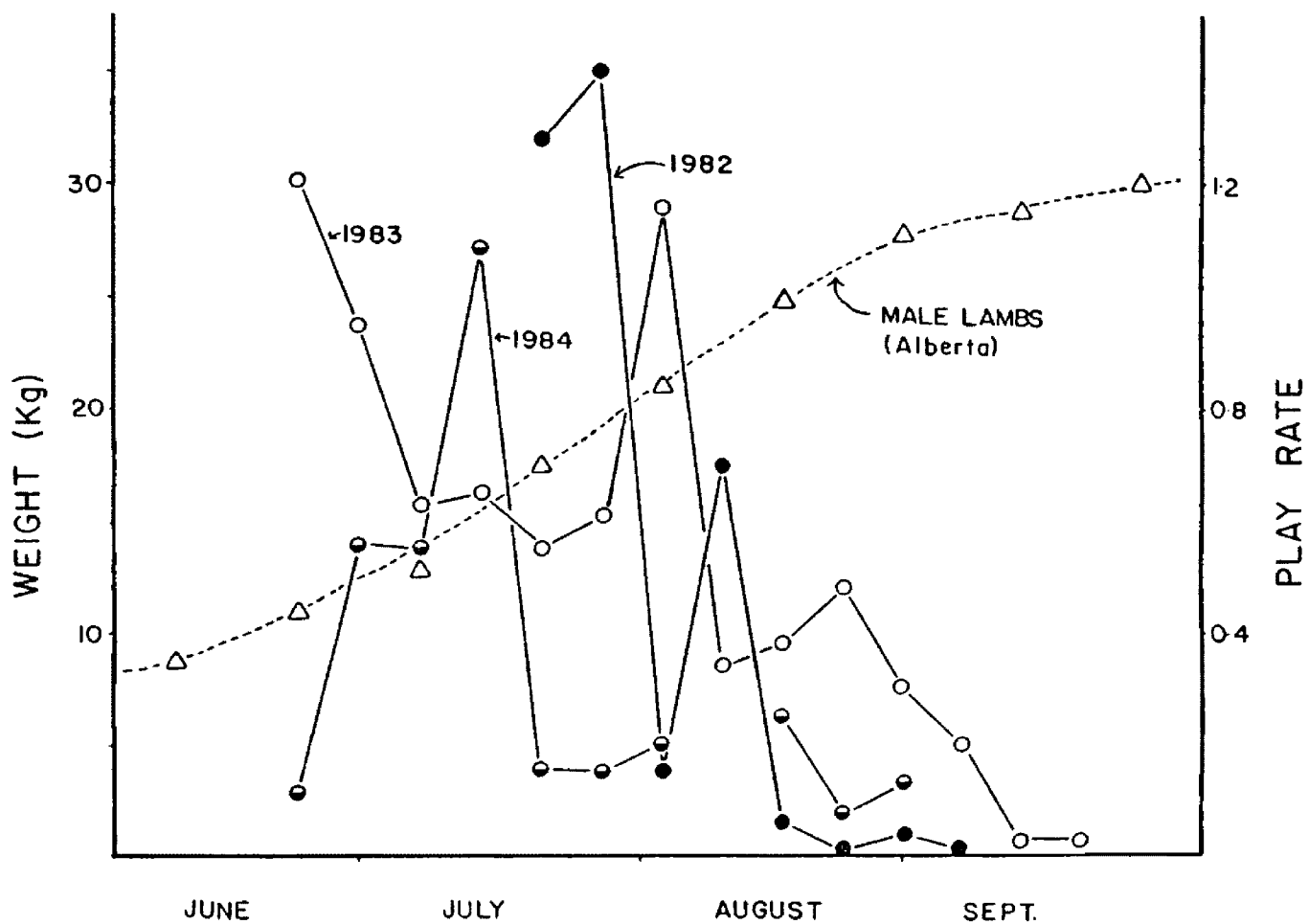
Figure 6. Peak play periods occured during peak growth periods for lambs. Growth curve from Jorgenson and Wishart (1984). Play rates recalculated on a biweekly basis.

outcrops and up and down steep roadcuts. Stotting was the form of locomotion used by older sheep when alarmed. Stotting probably served to audibly and visually signal conspecifics, and possibly distract or confuse predators (see also Caro 1986). Lambs may be developing skills necessary for predator evasion, during a period when they are highly vulnerable.

Lambs are strongly attracted to other lambs (see also Geist 1971). This may promote social play; likewise, social play may be an attracting force among lambs. Social groupings of lambs and their mothers may, therefore, reduce predation by facilitating detection of predators, and possibly confuse predators. If social play is an attracting force among lambs, then besides immediate anti-predation benefits, play may indirectly promote social development by simply bringing lambs together to interact (Meaney et al. 1985).

Although play appears to be a cooperative venture, as suggested by Bekoff (1977, 1978, 1984) and Fagen (1981), it appears to have little role in the development of social bonds among adult bighorns. Groups of ewes are more cohesive than groups of rams. There is ample evidence that ewes rarely leave their natal groups (Geist 1971, Thorne et al. 1979), yet the male lambs exhibited more play behavior, and lambs did not show a significant preference for lambs of the same sex. Rams usually leave the ewe groups to join ram

groups, often far from their maternal ranges, when they succeed in dominating the ewes (Geist 1971, pers. obs.). In the NBR herd, rams over two years of age were seldom seen with the ewes outside of the breeding season. Interestingly enough, in two reported instances of ewes leaving their maternal groups, both came from expanding (high quality) populations (Geist 1971, Keating 1982). It also appears that lambs from high quality populations play more (Geist 1971, Shackleton 1973). Play may promote behavioral flexibility, possibly preparing an animal to be a successful disperser (Geist 1971), but the relationship between play and dispersal should not be looked at too simplistically (Fagen 1981). Regardless, play does not appear responsible for the establishment of any strong ties within groups of Rocky Mountain bighorns.

Dominance relationships were not evident in the behavior of lambs, and were often hard to distinguish in yearlings (Eccles 1981). A relationship was found between Mounts and dominance in two bison calves studied during their first six months (Lumia 1972). In 1982, JN mounted BS significantly more than the reverse, and JN eventually became dominant to BS. BS was older, and larger than JN throughout their first summer, but by fall BS appeared smaller, with a poorer quality coat, indicating he may have been under some physiological stress. In 1983, CA mounted SI more than the reverse, but SI eventually became dominant. Again, although

SI was younger, he eventually became the larger individual.

Among adult rams, Mounts were an indication of dominance; when a subordinate attempted to mount a dominant, he would suffer swift retaliation in the the form of Butts and Clashes. If dominance relations had formed in play, and were used to impose stress on subordinates, I would not expect to see the dominance-reversals observed between the male lambs in play (see also Bekoff 1978). During spring play bouts among adult rams in Upper Rock Creek (Montana), I observed class I (1/4 horn curl; after Geist 1971) and class II rams (1/2 curl) mounting class III (3/4 curl) rams with no retaliation (also reported by Geist 1971). Because horn size is usually a good relative indicator of rank (Geist 1971, Chapter IV), the assumption was made that class III rams were dominant to class II rams, et cetera.

I rejected the hypothesis that play may be a means of competing with one's peers based on my observations that 1) dominance hierarchies were not evident among the lambs, and 2) among ranked adults, no relationship was apparent between rank and exhibited play behaviors. Hogg (1984a Tables 2-6) provides additional evidence that a young ram's rank is not necessarily the rank he maintains within his cohort with advancing age, even among a group as stable as the NBR herd (without emigration or immigration). In other words, the advantages of obtaining dominance over one's peers early in life may be short-lived (Smith 1982). Among yearlings,

dominance-reversals were observed in play until dominance relations appeared to be established; no play was observed in the yearlings during 1984 (my largest sample size of yearlings) after 10 July. Play may have some role in settling dominance relations among yearlings, as Steiner (1971) suggests for ground squirrels, but among older animals, dominance relations were not reflected in play.

Play may promote behavioral flexibility and creativity (reviewed in Fagen 1981). Although bighorn rams may create breeding opportunities (Hogg 1984b), the role of play, if any, in the development and use of creative mating strategies has yet to be explored.

In play, bighorns lambs can experiment with their environment and conspecifics. Behaviors are tested and refined, so the lambs may learn when and how to perform them in correct social and environmental contexts (Geist 1971, Fagen 1981, Smith 1982, Bekoff 1984). The lambs may be developing fighting skills to be used later in life (Symons 1978), or perhaps learning how to get along better in groups (Poirier and Smith 1974). At the same time they are receiving the benefits of repeated exercise. The high frequency of broken legs among a low-quality population of bighorns may be the result of a weaker skeleton resulting from infrequent play (Geist 1971), but cause-and-effect are hard to separate here. Detailed, long-term studies relating play, population quality, dispersal, and reproductive success are needed.

CHAPTER IV

STRUCTURE AND DEVELOPMENT

OF THE DOMINANCE HIERARCHIES

Results

Rams

During the course of the 27-month study, 699 interactions between rams were recorded, including 367 interactions obtained during almost 40 hours of all-occurences sampling.

Interactions between all possible dyads were never observed during any year. Only rams interacting with at least 10% of the bachelor herd were included in the win-loss matrices (Tables 4-6). The maximum percent of possible dyads that was actually observed in any year was 53% (72 of 136 possible pairs) in 1983. A significant trend toward linearity was found in the matrices each year (1982: x^2 = 46.96, p < 0.001; 1983: x^2 = 107.93, p < 0.001; 1984: x^2 = 109.62, p < 0.001). The K values also indicated a high degree of linearity in the hierarchies (1982: K = 0.94; 1983: K = 0.93; 1984: K = 0.94), indicating that the ram hierarchies were highly transitive.

During each year, yearling rams remained with the nursery group and were not included in the ram hierarchies. Only Dominance Values (D.V.s) from individuals interacting with at least 25% of the herd were used to correlate with other variables. For rams aged two and older, D.V.s were significantly correlated with age (1982: r = 0.76, p < 0.05;

46

Table 4.   Win-loss matrix for rams in 1982, based on dyadic interactions.   xi = proportion of opponents dominated. N = 253.

	L O S E R										
WINNER	CC	TP	SE	BD	BY	ST	GE	3B	ML	MG	xi
CC	--	21	51	7	4	3		3		10	1.00
TP		--	12	6	4					1	0.80
SE	2		--	23	9			4		24	0.67
BD				--	8			19	1	7	0.57
BY					--	1		16	6	2	0.50
ST						--	4			2	0.50
GE							--			2	0.50
3B								--	1		0.17
ML									--		0
MG										--	0

Table 5. Win-loss matrix for rams in 1983. Xi=proportion of opponents dominated. N = 290.

<u>L o s e r</u>

Winner

	CC	SE	TP	MC	ST	BD	BY	3B	GE	ML	MG	PY	HK	SR	RH	SK	Xi
CC	--	1	5			6	1		1								1.00
SE		--	11			9	1	9	1	4	5	2	2		2		0.91
TP			--	1		12	3		2	3	1		1		1		0.80
MC				--	4		1			4			1				0.80
ST					--		2			4	15	6			1		0.71
BD						--	37	2	5	6	5	3			1		0.70
BY							--	2	21	1		2			1		0.56
3B					4			--	1		2	2	1				0.56
GE									--	1	2	1	4			2	0.45
ML									5	--	14	1			1		0.44
MG											--	3	4	2	4	3	0.38
PY												--	1		3	1	0.33
HK												4	--		8	2	0.20
SR														--			0
RH															--		0
SK																--	0

Table 6. Win-loss matrix for rams in 1984. xi = proportion of opponents dominated. N = 162.

L O S E R

WINNER	SE	TP	BD	MG	BY	GE	ST	HK	SK	PY	SR	RH	JN	BS	xi
SE	--		6	1	1	5				3	1		3		1.00
TP		--	2		1		1						1		1.00
BD			--	1	8	11	5				1	1	1	1	0.80
MG				--			2			2		1	1		0.67
BY					--	6				1	1	2	1	2	0.66
GE						--	5	2	4	1	2	2	1		0.64
ST						2	--	7	4	2	3	7	4	1	0.58
HK								--		3	1	3	1		0.50
SK									--				1		0.33
PY										--		2	2		0.29
SR									1		--		1		0.14
RH									1			--	1		0.14
JN													--	5	0.08
BS														--	0

1983: r = 0.83, p < 0.01; 1984: r = 0.86, p < 0.001; Fig. 7),
and any ram's D.V. one year was significantly correlated with
his D.V. the next year (r = 0.86, p < 0.01; Fig.8).
Significant differences were found between mean D.V.s of rams
within different horn size classes (after Geist 1971); class
II rams had lower D.V.s than class III rams who had lower
D.V.s than class IV rams (t = 3.67, p < 0.01, Table 7).

The number of copulations per 100 observation hours was
not correlated with a ram's D.V. (r = 0.15, p > 0.05; Fig.
9), D.V. was, however, significantly correlated with the
number of different ewes each ram was observed copulating
with (r = 0.48, p < 0.05; Fig. 9).

Rams with higher D.V.s initiated more displays of
dominance (displacements, courtship) than did rams with lower
D.V.s (1983: G = 47.87, p < 0.001; 1984: G = 7.16, p > 0.05;
Fig. 10), while the individuals with the lower D.V.s received
more dominance displays than expected based on group
composition (1983: G = 51.53, p < 0.001; 1984: G = 7.00, p >
0.05; Fig. 10). Although rates varied significantly with
D.V.s in 1983, but not in 1984, differences between years
were not significant (Wilcoxon signed ranks T = 15, p >
0.05). To see if individuals with higher D.V.s were
interacting at higher rates because they had more
subordinates available to interact with, I adjusted the
expected values to take into account the number of
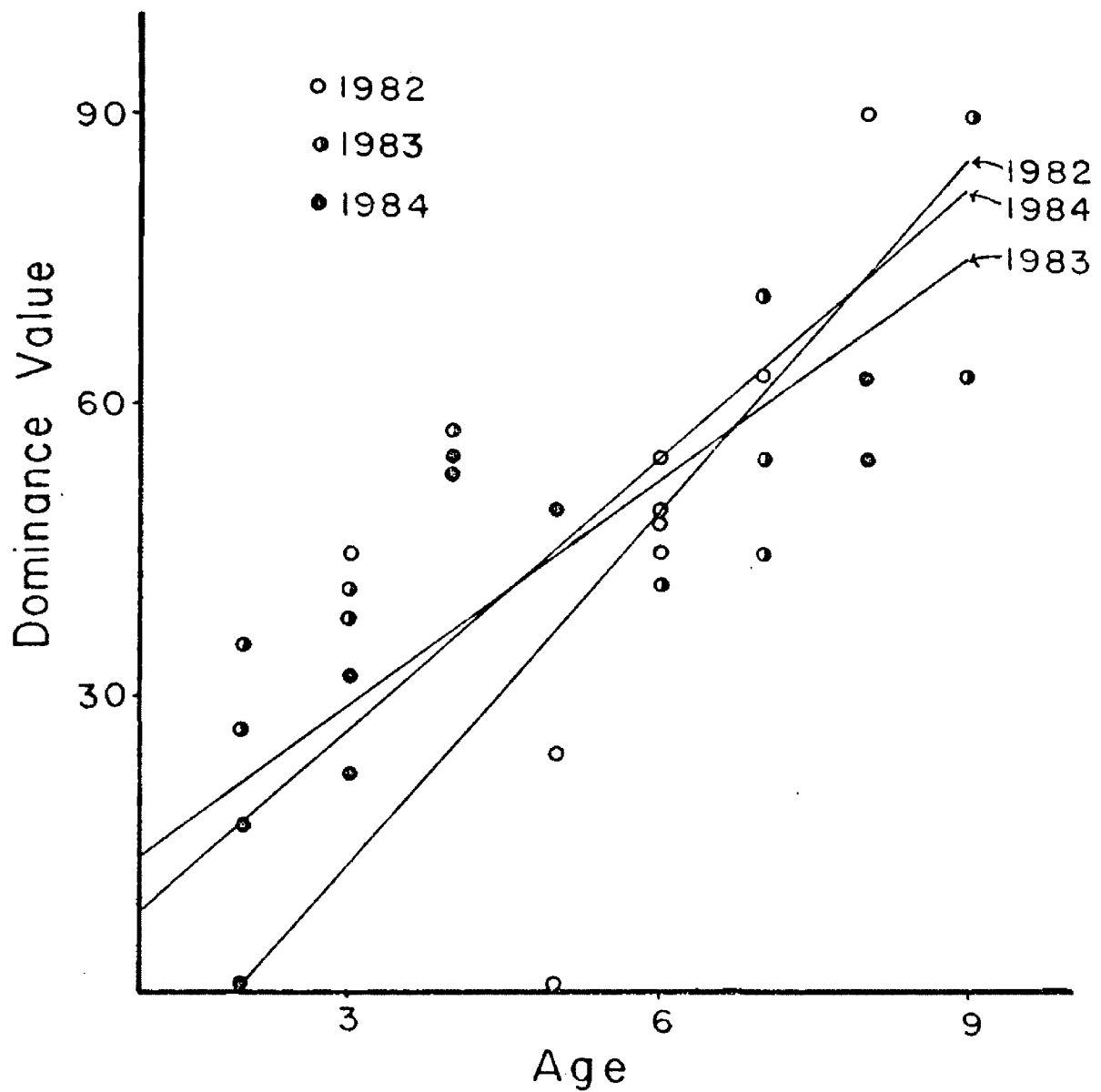
Figure 7. Ram Dominance Values were significantly correlated with age during all three years (1982: r = 0.76; 1983: r = 0.83; 1984: r = 0.86). Lines drawn from regression equations.
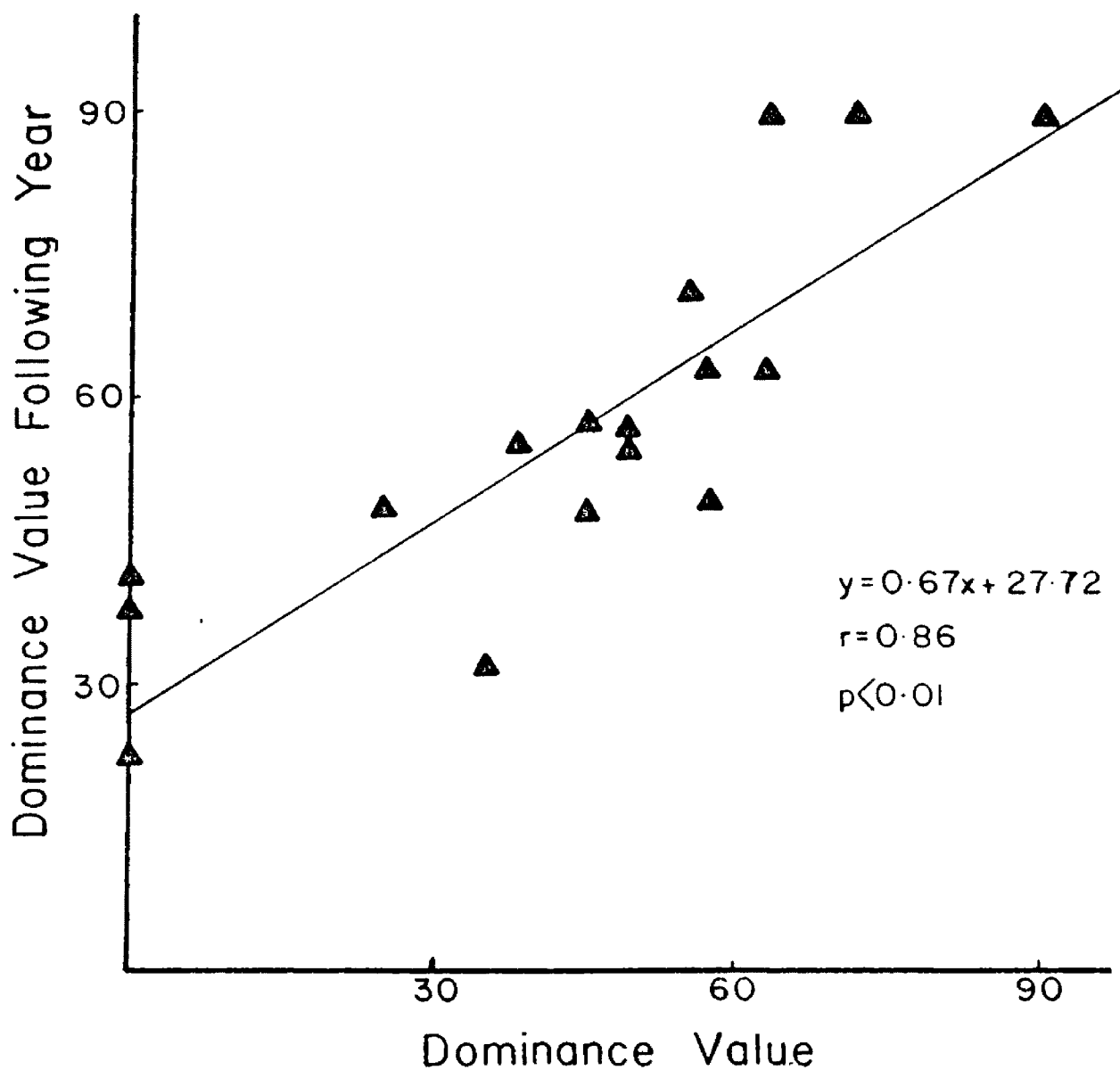
Figure 8. Ram's Dominance Values in one year were significantly correlated with their Dominance Values the following year. Line drawn from regression equation.

Table 7. Comparison of mean Dominance Values for ranked class II, III, and IV rams (after Geist 1971). Class I rams remained with the ewes and were not ranked. All three years combined.

	Horn Class		
	II	III	IV
Mean Age	2.0	3.8	7.4
Total N	9	15	16
Mean D.V.	13.72	37.57	65.15
Student's t	3.50	4.99	
p-value	<0.01	<0.001	
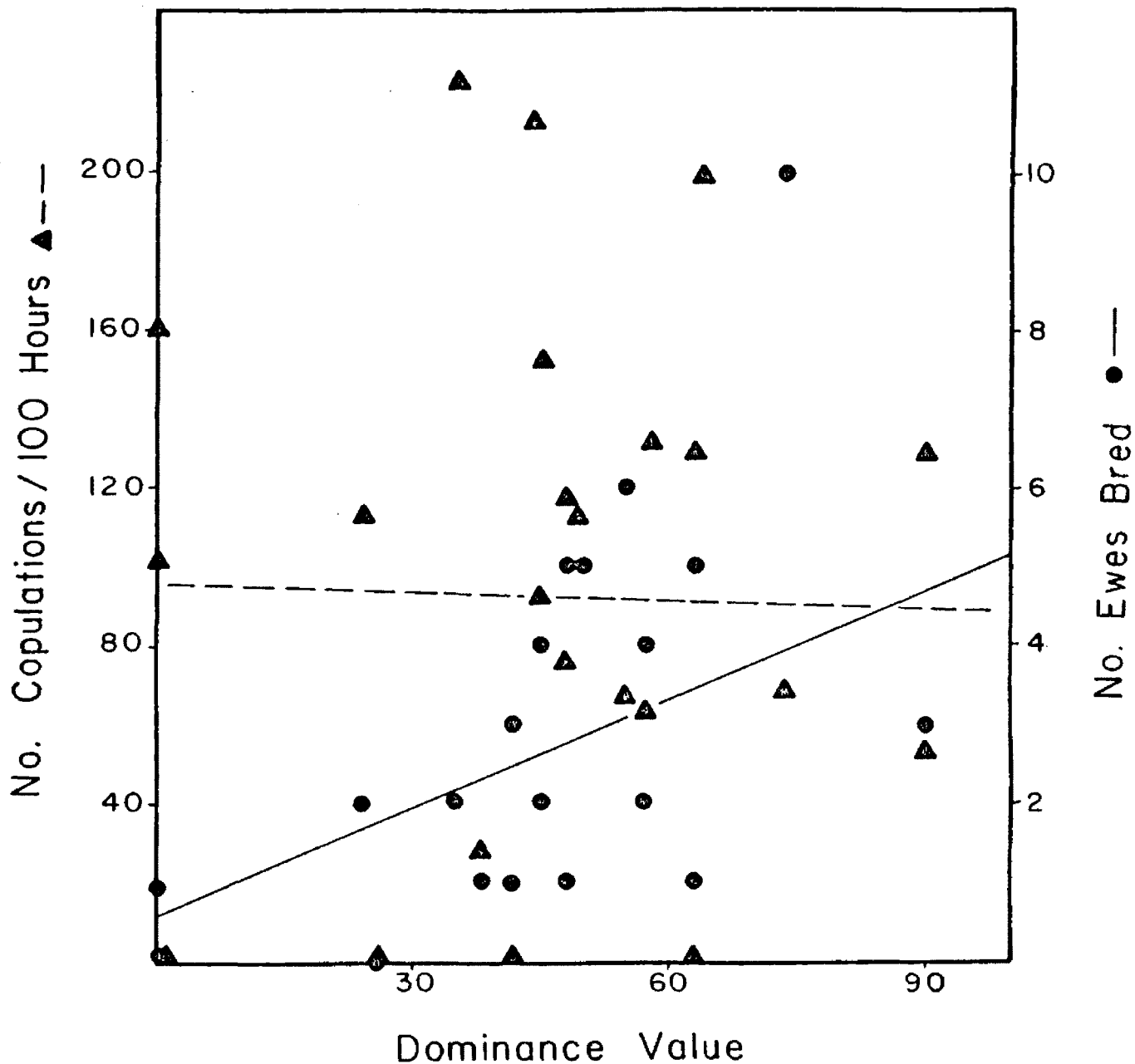
Figure 9. Dominance Values of rams were not correlated with the number of copulations per 100 observation hours (triangles, broken line; r = 0.15, p > 0.05), but were significantly correlated with the number of different ewes individual rams were observed breeding (circles, continuous line; r = 0.48, p < 0.05). Lines drawn from regression equations.
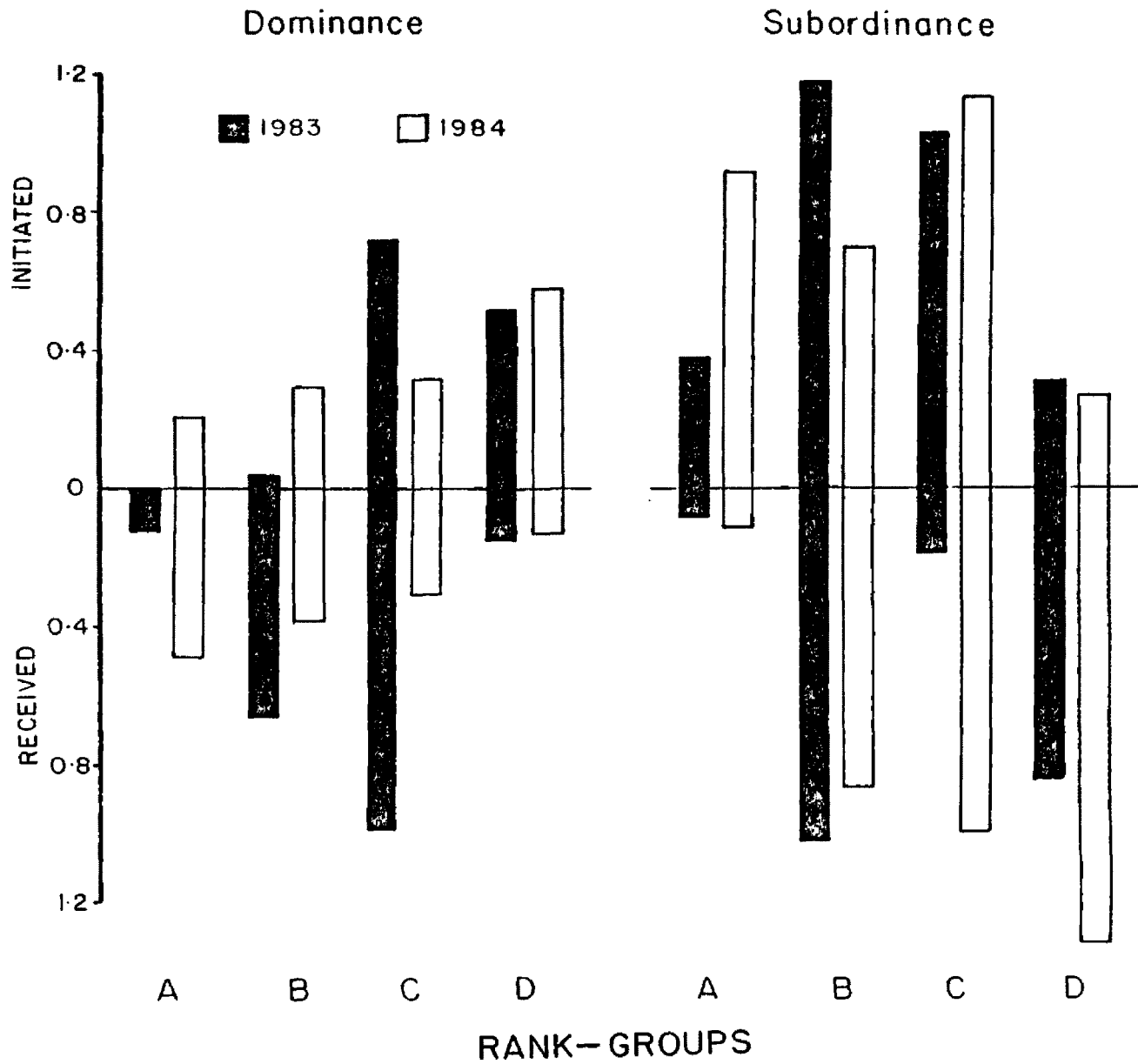
Figure 10. Rates of dominance and subordinance displays for rams in 1983 and 1984. Rank-groups: A = lowest 25% of ranks, B = second lowest 25%, C = second highest 25%, D = highest 25% of ranks.

subordinates each group had available to it. These "rank-specific" values were tested against the observed values, and again, high ranking rams initiated more patterns, and low ranking rams fewer than expected (1983: G = 29.47, p < 0.001; 1984: G = 10.62, p < 0.05), indicating that animals with higher D.V.s were indeed initating patterns at a higher rate than were lower ranking animals.

Rams with lower D.V.s initiated more subordinance displays than did higher ranking rams (1983: G = 38.60, p < 0.001; 1984: G = 19.76, p < 0.001). Higher ranking animals received more subordinance displays (1983: G = 46.02, p < 0.001; 1984: G = 47.94; p < 0.001; Fig. 10). These differences were independent of the number of dominants (potential interactants) available to each group (1983: G = 114.08, p < 0.001; 1984: G = 19.10, p < 0.001).

The differences apparent in the rates of dominance and subordinance displays were also readily visible when broken down by pattern. As might be expected, rams with higher D.V.s performed a higher percentage of displacements and courtship behaviors, while lower ranking rams initiated mostly Face-Rubbing; the reverse was true for patterns received (Fig. 11). The behavior of rams toward other rams was clearly linked to their relative rank in the group.

Five dominance fights were observed between rams during the course of the study. Three of these resulted in absolute changes in rank, whereas two of the fights were between
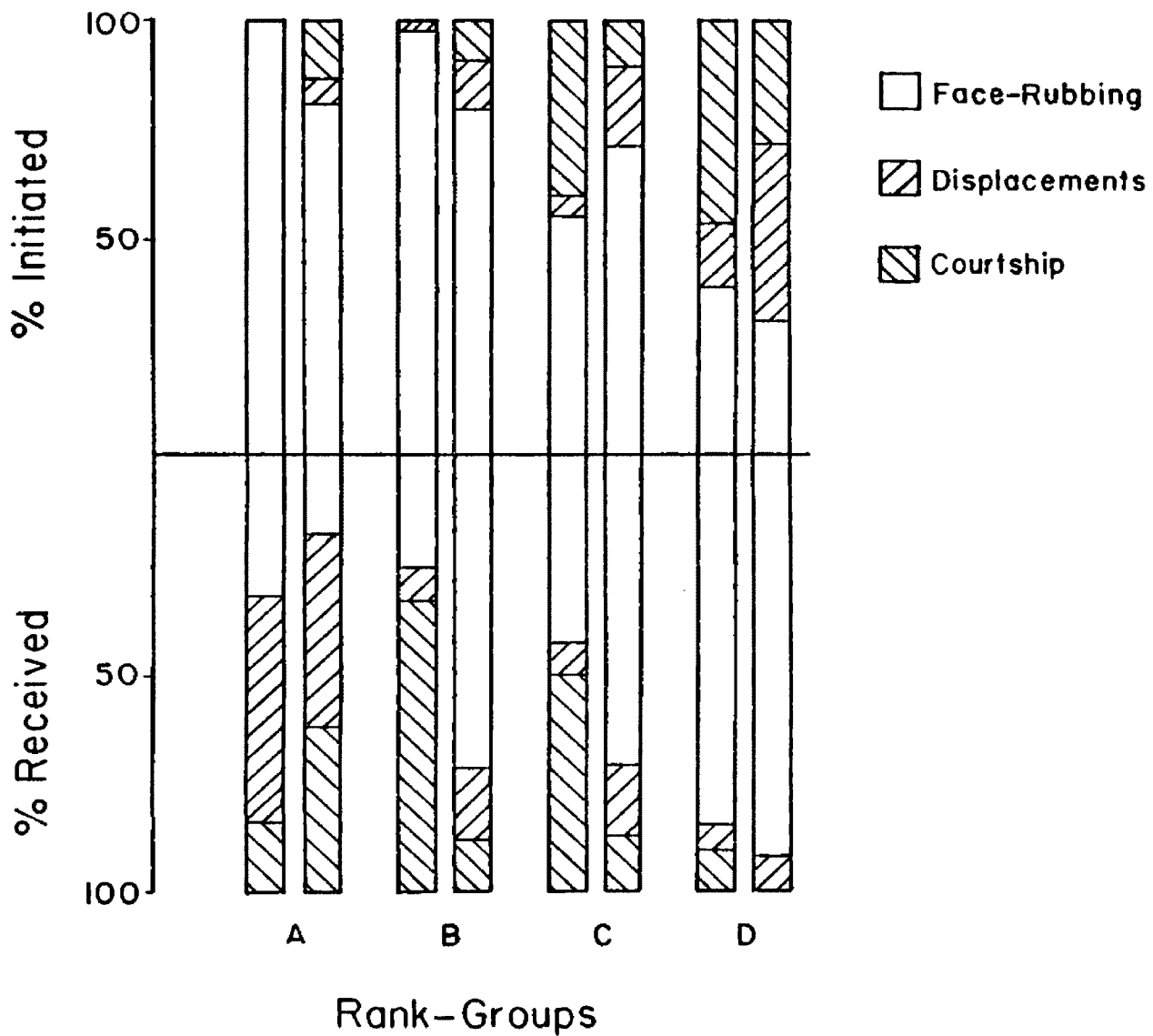
Figure 11. Patterns used in dominance interactions of rams were reflective of dominance rank. Rank-groups: A = lowest 25% of ranks, B = second lowest 25%, C = second highest 25%, D = highest 25% of ranks. First column in each group from 1983, second column from 1984.

yearlings whose rank was previously undetermined. Six other rank changes were also detected, although fights or turnovers were not seen. In some cases, (e.g., MG, BY, and GE, Table 8), a subordinate ram obtained a higher D.V. than his previous dominant, but the dyads were not observed interacting to determine if an actual turnover had taken place.

Interactions among yearlings and among 2-year olds were infrequent. In 1982, the five yearlings could not be ranked within the cohort with certainty, and a year later, as 2-year-olds, relationships among three of them still could not be ascertained (note SR, RH, and SK in Table 8). During early 1983, interactions between the two yearlings began to appear one-sided, with JN exhibiting courtship behavior to, and mounting BS, with no dominance reversals apparent. No dominance fight was ever observed between the two, and JN continued acting as the dominant until the end of the study when they were 28 months old (Table 8).

Play bouts involving the two male yearlings in the summer of 1984 were also one-sided, with SI exhibiting dominance displays, and CA subordinance displays. No dominance reversals were apparent, even though play signals (Neck Twists, Gambols, etc.) were often present. On 21 July, what appeared to be a long (3+ hours) dominance fight between CA and SI was also accompanied by occasional play signals. No change in relationship was evident after this lengthy

Table 8. Dominance Values and ages for those rams in 1982-4 that interacted with at least 10% of the bachelor herd. D.V.s prior to rut each year. *indicates those who were discarded from calculations due to the small number of observed interactions. Arrows indicate instances when one ram dominated another with a higher Dominance Value.

Ram	1982 D.V.	Age	Ram	1983 D.V.	Age	Ram	1984 D.V.	Age
CC	90.0	8	CC	90.0	9	SE	90.0	8
TP	63.4	7	SE	72.5	7	TP	90.0	9
SE	54.7	6	TP	63.4	8	BD	63.4	8
BD	49.1	6	MC	63.4	9	MG	54.7	4
BY	45.0	6	ST	57.7	4	BY	54.3	8
ST	45.0	3	BD	56.8	7	GE	52.9	4
*GE	45.0	2	BY	48.2	7	ST	49.8	5
3B	24.1	5	3B	48.2	6	HK	45.0	3
ML	0	5	GE	42.4	3	*SK	35.3	3
MG	0	2	ML	41.8	6	PY	32.3	3
			MG	38.3	3	SR	22.2	3
			PY	35.1	2	RH	22.2	3
			HK	26.6	2	JN	16.8	2
			SR	0	2	BG	0	2
			RH	0	2			
			*SK	0	2			

interaction.

Rams appeared to advance in the hierarchy either by default, as younger rams joined the bottom of the hierarchy, or by actively fighting their way up the ranks. For instance, the ram SE, was ranked 3rd in the fall of 1982. He had achieved that position not only by default, along with his cohort, but also advancing over the members of his cohort by fighting (Hogg 1984a). The other 6-year-olds were ranked 4th and 5th. During late December 1982, SE battled with and defeated TP for the second place spot. Shortly after the onset of rut in November 1983, he battled CC and became the alpha ram, at the age of seven (Table 8).

Ewes

During the study period, I recorded 1425 displacements and subordinance displays between ewes, including 466 interactions recorded during almost 100 hours of all-occurence sampling. All interactions were used to compile win-loss matrices for each year.

As with the rams, the win-loss matrices for the ewes were incomplete. Five of the 27 ewes present in 1982 were never observed interacting with any other ewes and were excluded from analyses. Only 100 pairs were observed interacting, or 28% of the 351 potentially interacting dyads (Table 9). Between 22 July and 7 September 1982, 174 interactions were recorded between ewes in the nursery band. The mean group size of the nursery band was 19.3 ± 4.8, which

Table 9. Win-loss matrix for ewes in 1982. xi = proportion of opponents dominated. N = 174.

	AL	R5	OH	LB	DB	DE	TY	TT	HE	HT	MY	RC	SH	BR	UB	UI	SS	EY	BN	LL	BE	UM	xi
AL	—	4	7					1	1			3		4	1	1	2	2	9	2		5	1.00
R5		—	1				1	1	1			2		5	1	1			2	1		1	1.00
OH	3		—	2		1	1	1	1		1	1	1	1	3	2	1	3	1	2		1	0.88
LB			—	—	1			1					1	3	1				1	1			0.86
DB		1	—	1	—	—	1	2	2	3	1	—	1	1	1	2	2	2	6	4			0.77
DE			—	—	—	—			3							1		1		1	1		0.67
TY				—	—	—	—	2			2	2		1	2				1				0.67
TT					—	—	1	—	2	1	2	2		1	1	1			1	2		3	0.67
HE	1						—	2	—		1	1	2	1	4	1							0.64
HT								—	—	—	1			1	1	1	1		1	1		1	0.62
MY										—	—	—											0.50
RC											—	—	—	1	2	1	1	1	2		1	1	0.38
SH												—	—	—	1		1						0.33
BR											2	—	—	—	1	1	1	1	1	1			0.33
UB														—	—	1	1			1			0.29
UI															—	—	1	1		1		1	0.27
SS																—	—	1		1			0.12
EY																	—	—	1	1			0.12
BN																		—	—	1		1	0.08
LL																			—	—	1	3	0.08
BE																				—	—		0
UM																					—	—	0

Winner

included two (male) lambs, lactating ewes, yearlings of both sexes, some 2-year-old ewes, and assorted non-lactating ewes that associated with the group for variable periods of time.

Of the 166 displacements recorded in 1982, 113 (68%) were from bedding sites, two (1%) were from horning posts and mineral licks (one each), and the remaining 51 (31%) were from spatial positions (e.g., one ewe displaced another from the spot where she was standing, or from the path along which she was walking; Table 10).

In 1983, 596 displacements and subordinance displays were recorded. The nursery group averaged 22.2 ± 5.7 (including 6-7 lambs). Four ewes, as well as the female lambs, were observed interacting too few times to include in the hierarchy. Displacements of lambs by ewes were not recorded; the win-loss matrix included 23 ewes. Interactions were recorded between 50% (175) of the 351 possible dyads (Table 11). Of 569 displacements, 64% were from bedding sites, 36% were from spatial positions, and the remaining 2% were from mineral licks, horning posts and foraging positions (Table 10). In 69% (244) of the displacements from bedding sites, the displacing ewe did not recline in the newly vacated bed.

In 1984, 655 displacements and subordinance displays were recorded. During the summer, the nursery group averaged 18.4 ± 3.8, including two lambs. Four ewes and the two female lambs were not included in the matrix (Table 12).

Table 10. Locations of displacements by ewes during the summers of 1982-4. Percent of total in parentheses.

	Bedding Sites	Spatial Positions	Mineral Licks	Horning Posts	Forage	Total
			Locations			
1982	113 (68)	51 (31)	1 (<1)	1 (<1)	0	166
1983	355 (64)	201 (36)	3 (<1)	8 (1)	2 (<1)	569
1984	308 (59)	198 (38)	13 (2)	4 (<1)	3 (<1)	526

Table 11. Win-loss matrix for ewes in 1983. xi = proportion of opponents dominated. N = 596.

												L o s e r											
	AL	FS	HT	HE	R5	OH	LE	DE	DB	LB	BE	TY	SH	UB	BR	UI	RC	SS	BN	EY	TT	UM	LL	xi
AL	—			11		13		7	2	1	1	3	1	1	2	2	2	1	7	2	2	3	3	0.95
FS	3	—		8		12		4		1	4	1	2	1	3	1			4	1	10	6	1	0.94
HT	—	—	—	1		4		10	4		3	1	1	2	1				1	1	1		2	0.89
HE	4	4		—	2	4				1	3			2		2			4	8	1	1	1	0.85
R5				2	—	2			1	1		1		2		1								0.83
OH						—		7	1	1	1	1	1	1	5	2		1	1	2	1	1		0.76
LE			1			—	—	3	2		2	5	2	4	1	2	2	1	3	3		3	3	0.76
DE	4		3	16		—		—	1	2	2	2	2	2	3	4		1	7	2	10	4	1	0.74
DB			5			—		—	—			2			6	2	2		10		1		1	0.69
LB									—	—		2	2	2		1		1						0.60
BE		4								—	—	5		1		2		5	3	3		4		0.56
TY											—	—	1	1	2	1			7	2		4	1	0.44
SH											—	—	—			1								0.38
UB												2	2	—	2	1			2			1	1	0.36
BR												1	1	2	—	—	1	1	1			2	0	0.35
UI												2		2	2	—					2		10	0.33
RC																	—							0.30
SS																	—	—			1		1	0.27
BN																			—		1		1	0.23
EY																				—	1		1	0.17
TT																				—	—	1		0.07
UM																					—	—	—	0.06
LL																					7		—	0.06

Table 12 Win-loss matrix for ewes in 1984. Xi = proportion of opponents dominated. N = 655.

Winner (rows) × Loser (columns). Diagonal cells are marked `--`.

Winner	AL	DB	LE	OH	HT	DE	R5	UI	UB	LB	HE	BE	SS	BR	TY	TT	SH	LL	EY	UM	BN	EL	RC	DY	JO	JL	Xi
AL	--								1	1			1													1	1.00
DB		--			5	2		2	1	1	4	4	2	3	4		1	1			7			1	4		0.94
LE			--		7	4	1				12	2	2	2		12		2	4	2	6	1	1		4	3	0.89
OH		8		--				1	1	1	3				1	2	1			2	2	3	1	1	3	2	0.82
HT					--	1	3				10	5		4	1	7	1	1	5		8	6			3	1	0.82
DE				7		--	3	2			2	4	1	2	3	2	3	3	4	9				2	1	4	0.76
R5	1	1	4	5	3		--	1		1	2			1		2			3		5	2		4			0.72
UI				1				--	1	1	2			2	1	1		1	3	2	2	2	1	1	1	1	0.68
UB									--	1	2			1	2	2	1			1	1	2		1			0.67
LB						1	2			--						5						1		2	1		0.67
HE				1	1	7	1	1			--			7	5	2	8	3	2	3	5	4		6	1	5	0.64
BE							2				5	--	2	2	2	1	1	3	2	3	1	1		2		3	0.60
SS								2	1		3		--			7		3	3	4	3			3	1	1	0.58
BR													2	--		6	1	2	1		3	3	1	2	2	1	0.55
TY							4							2	--	1	2				2	1		2	1	2	0.53
TT														1		--	1	1			1	2	2	3	4	2	0.43
SH														1	1		--	1			2	1		1		1	0.40
LL								1								10		--	1	1	3	4	3	2	4	6	0.40
EY																1		3	--		7			3	4	11	0.33
UM													2					3	8	--	8				2	2	0.31
BN																		1	5	1	--	2	1	1		5	0.30
EL																						--		5	1	2	0.14
RC																						1	--				0.10
DY																						1		--	3		0.05
JO																									--	10	0.05
JL																										--	0

99

Only 230 of the 435 potential dyads (53%) were observed interacting. Fifty-nine percent of the 526 recorded displacements were from bedding sites, 38% were from spatial positions, and the remaining 4% were from mineral licks, horning posts and foraging positions (Table 10). Of the 308 displacements from bedding sites, 24% resulted in the displacing ewe occupying the just vacated site.

During all three years, the hierarchies were significantly non-random (1982: x^2 = 147.4, p < 0.001; 1983: x^2 = 171.7, p < 0.001; 1984: x^2 = 192.7, p < 0.001). The ewe hierarchies did not demonstrate the linearity of the ram hierarchies (1982: K = 0.73; 1983: K = 0.79; 1984: K = 0.71). Unlike the ram hierarchies, the more complete the win-loss matrix, the greater number of triangles present in the ewe hierarchy (for example, see Table 12). An ordinal ranking system would probably underestimate the complexity of the relationships among the ewes; Dominance Values were felt to be more representative of the ewe's ranks relative to the other ewes.

Dominance Values were significantly correlated with age (1982: r = 0.93, p < 0.01; 1983: r = 0.73, p < 0.01; 1984: r = 0.78, p < 0.01). Among ewes less than 4 years of age, D.V. was significantly more closely related to age (r = 0.81), than among ewes 4 years and older (r = 0.50; t = 2.27, p < 0.05; all three years combined, Fig. 12). A ewe's D.V. in one year was significantly correlated with her D.V. the
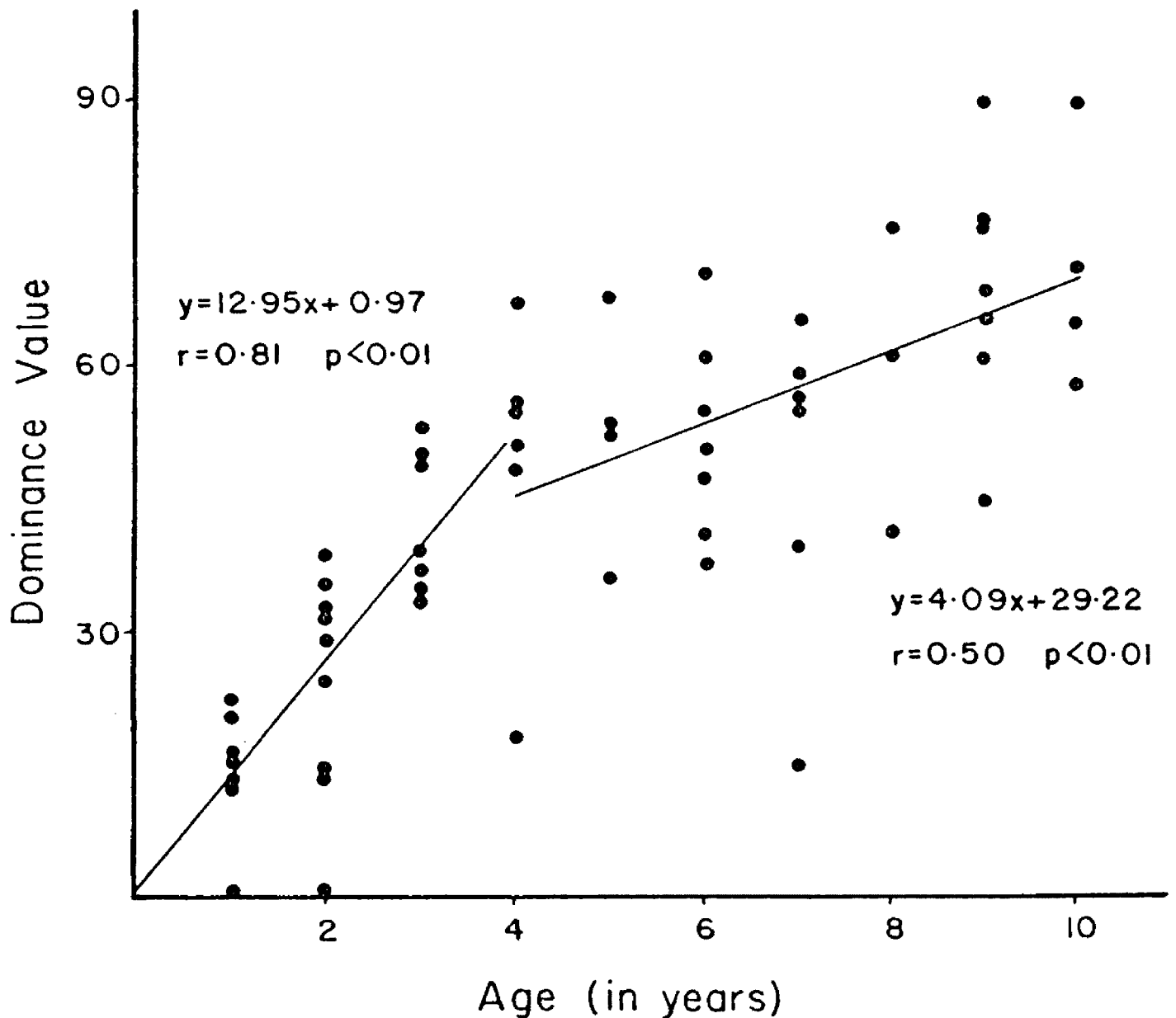
Figure 12. Ewe Dominance Values were significantly correlated with age. All three years combined. Correlation coefficients significantly different between ewes less than four years old, and those four years and older (t = 2.27, p < 0.05).

following year (r = 0.75, p < 0.01). The correlation was greater for ewes less than 4 years of age (r = 0.71) than among older ewes (r = 0.53; Fig. 13), but the difference in correlation coefficients was not significant.

A ewe's D.V. was not related to her estrous date, whether measured from the onset of rut (r = -0.23, p > 0.05) or from the median date (r = -0.19, p > 0.05). Consequently, D.V.s and birth dates of lambs the following summers were not correlated, whether measured from the first birth of the season (r = 0.02, p > 0.05) or from the median date (r = 0.09, p > 0.05). D.V.s of ewes the previous summer, which might have affected the ewe's condition at conception, had no relationship to the sex of lambs (T-test, t = 0.08, p > 0.05). A ewe's D.V. the previous summer was significantly, negatively correlated with the weight of her male lamb (r = -0.78, p < 0.01), but not with the weight of her female lamb (r = 0.21, p > 0.05; Fig. 14). I also examined the influence of a ewe.'s age the previous year on the weight of her lamb. The weights of male lambs were negatively correlated with ewe age (r = -0.87, p < 0.01) but female weights were not (r = 0.03, p > 0.05). Dominance Values of lactating ewes were not related to mean nursing durations (r = 0.06) or mean nursing rates (r = 0.06).

During an earlier study of mother-young relationships of the Bison Range bighorns (Hass 1984), I identified three classes of lactating ewes: those that nursed only their own
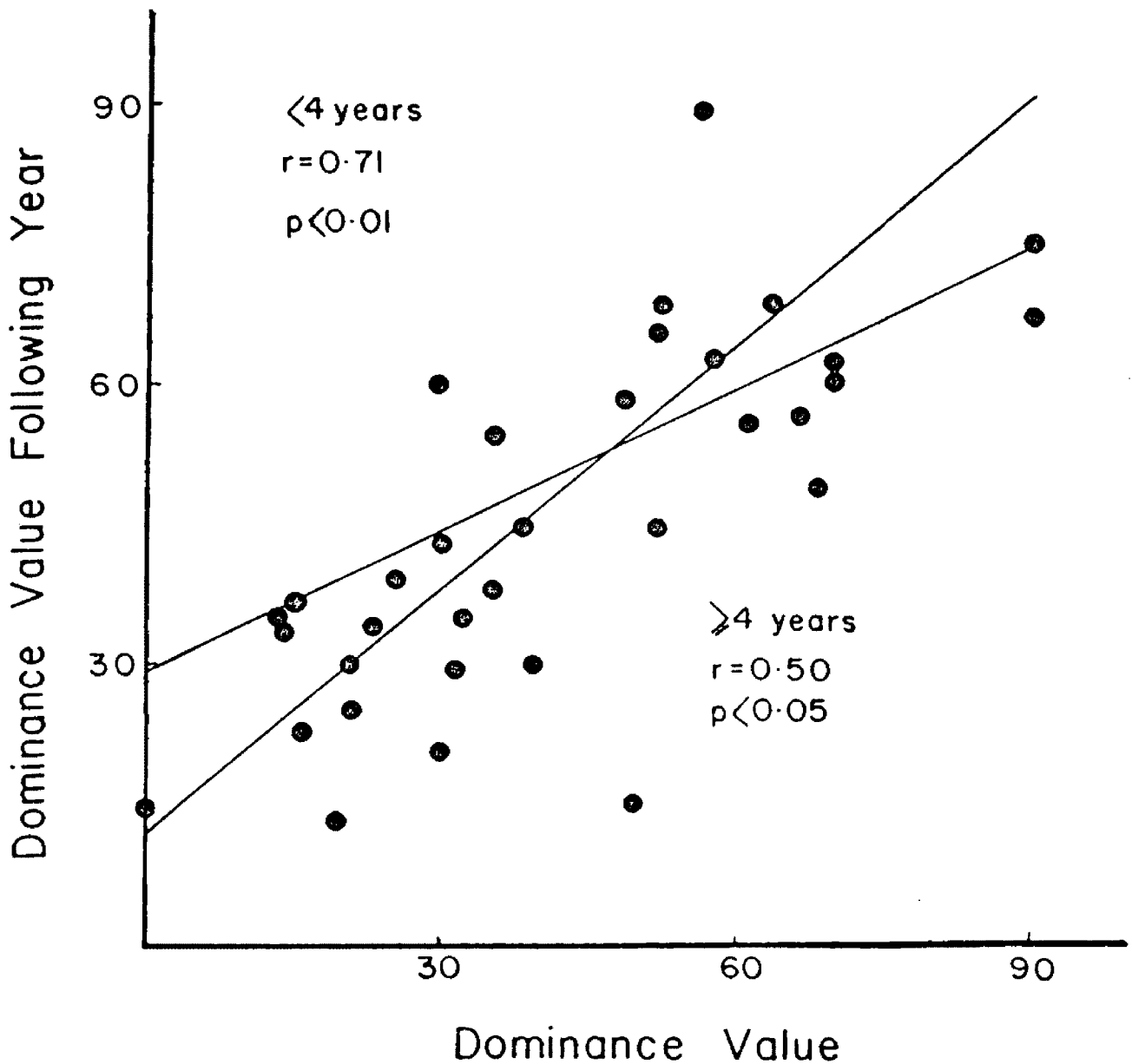
Figure 13. Ewe's Dominance Values one year were significantly correlated with their Dominance Values the following year. Correlation coefficients between age groups not significant. Lines drawn from regression equations.
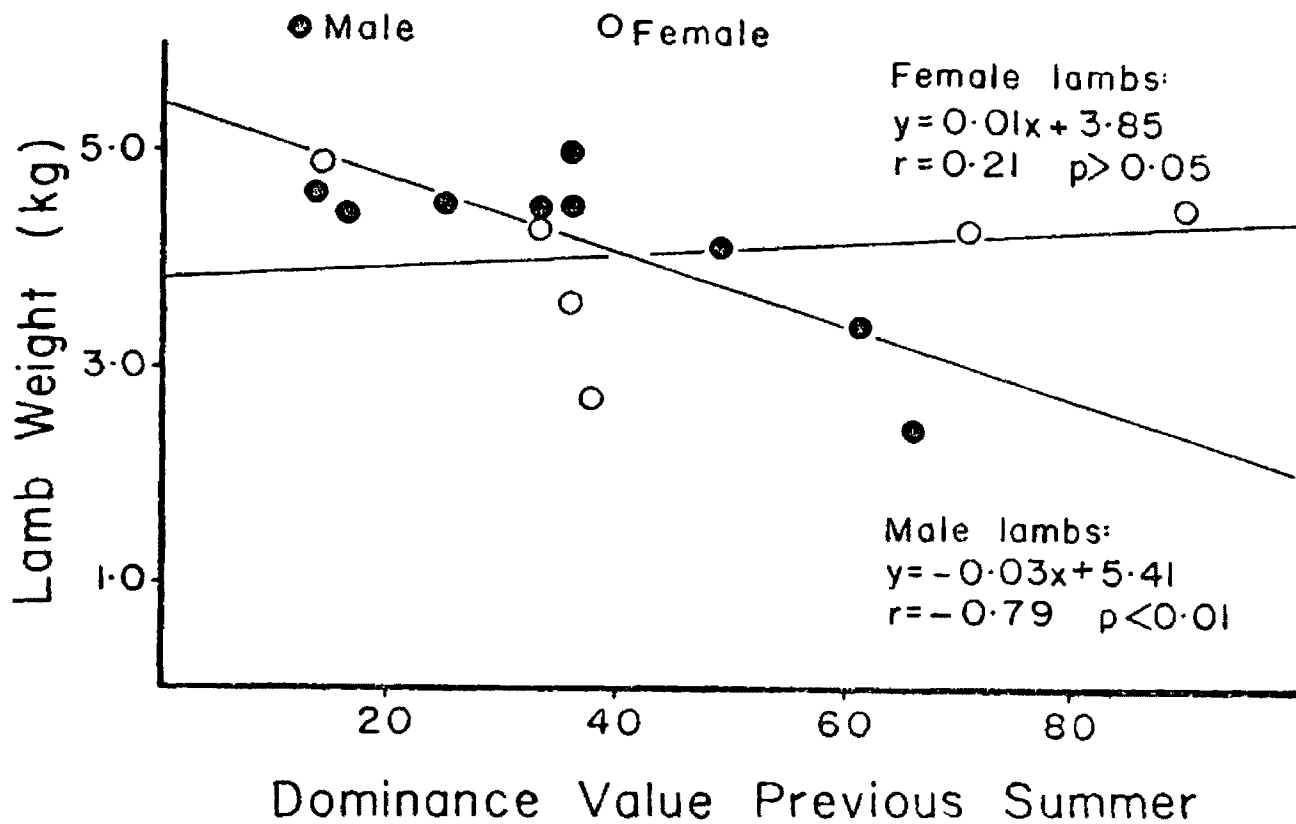
Figure 14. Ewe's Dominance Values were not related to the weight of their female lambs, but were negatively correlated with the weight of their male lambs. All three years combined.

lambs (OO ewes), those that nursed their own and other lambs (O+ ewes), and ewes that had lost their lambs to predation, but continued to nurse the surviving lambs (Helpers). Helpers had the highest D.V.s ($\overline{X}$ = 69.3), OO ewes had the lowest mean values ($\overline{X}$ = 42.4), and O+ ewes were in between ($\overline{X}$ = 49.0). The differences were significant (One-way ANOVA, F = 5.08, p < 0.03).

Ewes with high D.V.s initiated more displacements than lower ranking ewes (1983: G = 185.72, p < 0.001; 1984: G = 85.54, p < 0.001), while individuals with lower D.V.s were displaced more frequently than expected, based on group composition (1983: G = 54.66, p < 0.001; 1984: G = 14.87, p < 0.05; Fig. 15). In 1983, this difference was independent of the number of subordinates available to each group (G = 39.58, p < 0.001), but in 1984, no differences were found between observed displacement rates and those expected based on the number of subordinates available to each group (G = 0.57, p > 0.05).

In 1984, I recorded the patterns used to displace other ewes. These were lumped into "contacts" (Butt, Paw, Touch Heads) and "displays" (Low Stretch, Head Tip, SLR), and interaction rates were calculated for the four rank groups (Fig. 16). Displays were recorded more than twice as often as contacts. All rank-groups used more displays than contact patterns. Higher ranking ewes initiated more contacts (G = 25.85, p < 0.001) and displays (G = 84.30, p < 0.001) than

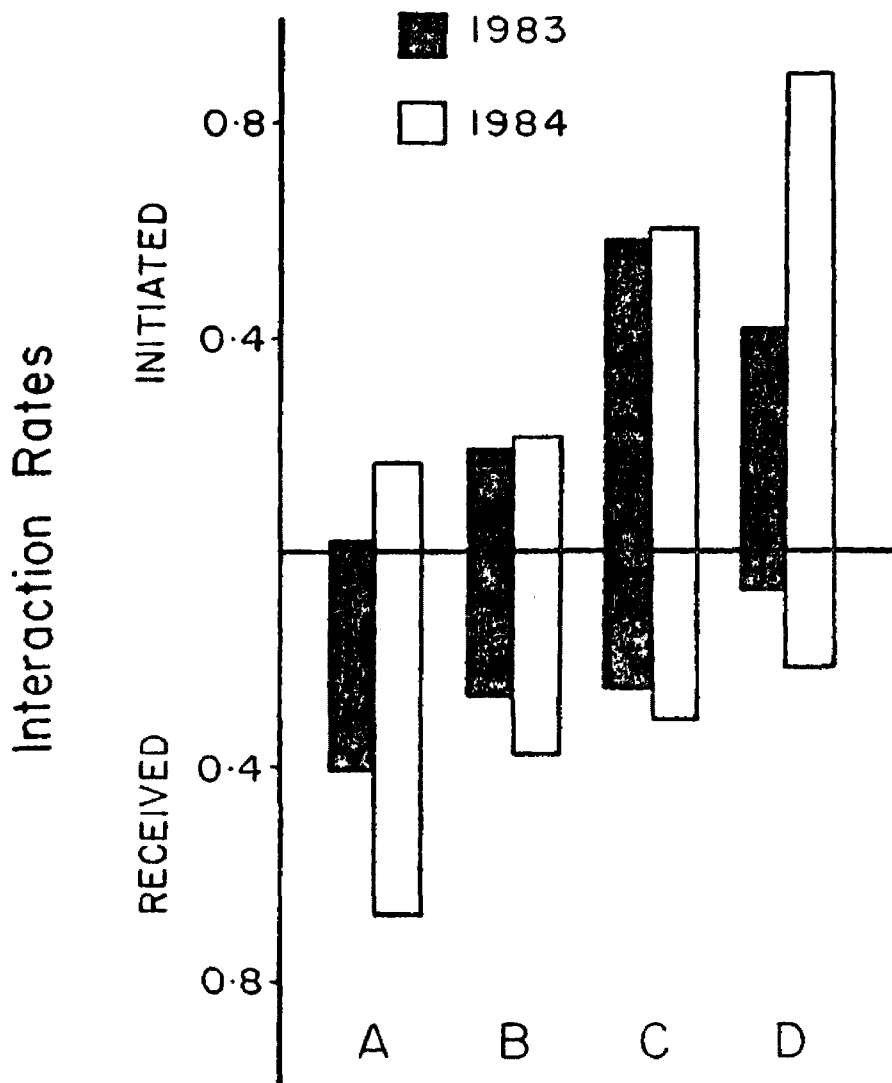Figure 15. Rates of displacements for ewes, 1983 and 1984. Rank-groups: A = lowest 25% of ranks, B = second lowest 25%, C = second highest 25%, D = highest 25% of ranks.
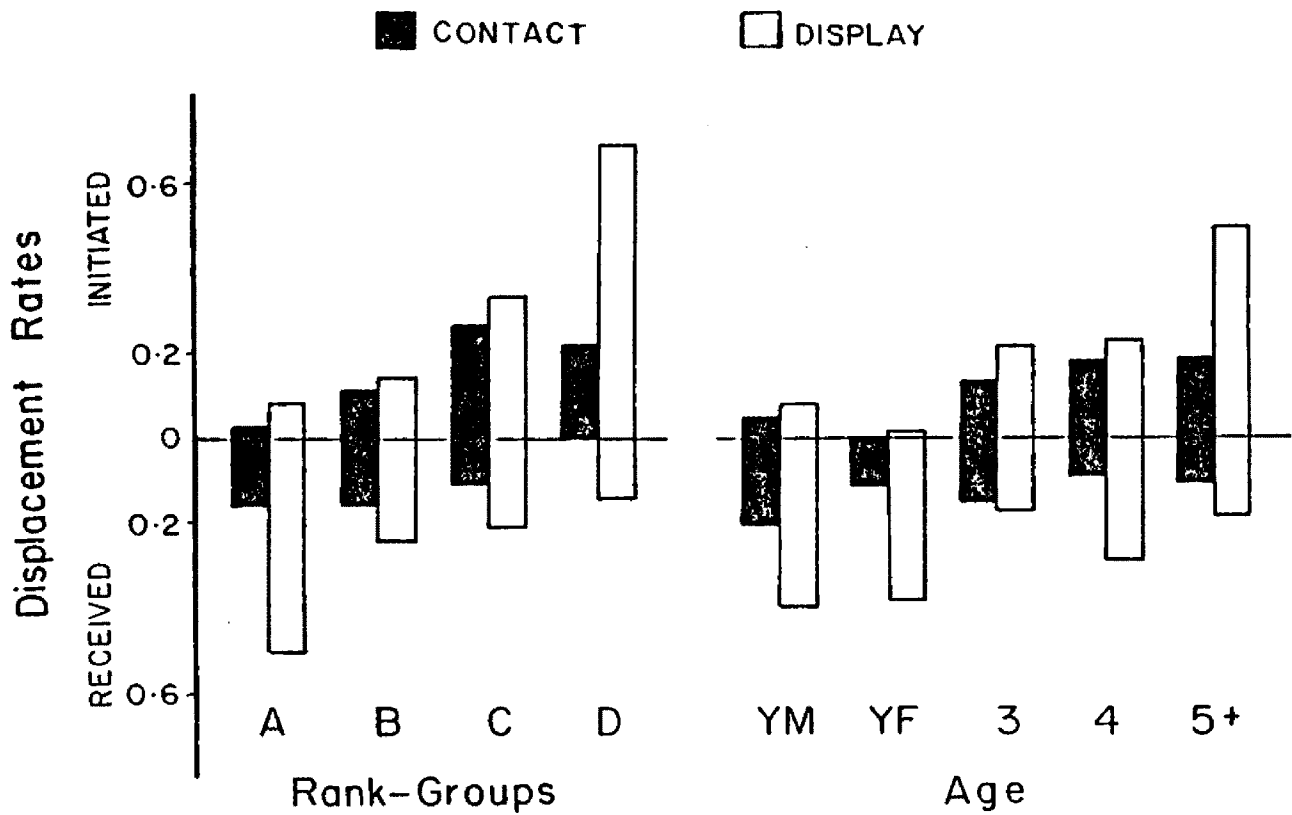
Figure 16. Rates of display and contact displacements for ewes, 1984. Rates were dependent on both rank and age. Rank-group: A = lowest 25% of ranks, B = second lowest 25%, C = second highest 25%, D = highest 25% of ranks. YM = yearling males, YF = yearling females.

expected based on group composition. However, observed values did not differ significantly from those expected based on the number of subordinates available (contacts: G = 1.68, p > 0.50, displays: G = 5.13, p > 0.10). All rank-groups were equally likely to receive displays, based on group composition (G = 2.58, p > 0.50), but lower ranks received more contacts, and higher ranks fewer than expected based on group composition (G = 9.94, p < 0.05; Fig. 16).

Because the rank-groupings might be masking some age-related differences, particularly among the younger sheep, rates of display and contact displacements were recalculated for yearling ewes, and ewes aged 3, 4, and 5 and older (there were no 2-year-old ewes in 1984). I also calculated rates for the yearling rams (Fig. 16). Again, all groups performed more displays than contacts, and there was a significant increase with age for both contacts (G = 29.31, p < 0.001) and display rates (G = 92.07, p < 0.001). Yearling rams initiated more of both contacts and displays than yearling females. Yearlings of both sexes received more than 1/3 of the contact displacements, although they made up only 19% of the ewe group; the differences between observed and expected values were not significant (G = 5.02, p > 0.10). Yearlings (both sexes) did, however, receive a higher proportion than expected of displays: 72 of 147 displays (G = 29.87, p < 0.001; Fig. 16).

Daily interaction rates were significantly correlated

with the maximum daily temperatures (r = 0.48, p < 0.05), but not with minumum daily temperatures (r = 0.23, p > 0.05; temperatures recorded at NBR headquarters, about 10 km from sheep range, and obtained from NBR Narrative Reports). Although locations of interactions were not recorded, most consisted of ewes displacing each other from bedding sites in the shade, which might account for the relationship between maximum temperature and interaction rates.

During the study, nine dominance fights were observed, of which five resulted in changes in rank. An additional 21 rank changes were detected by the results of dominance interactions. Most of the rank changes were the results of 3- and 4-year-olds advancing in the hierarchy. The lowest ranking ewes were generally the yearlings and 2-year-olds (Table 13). Yearlings seldom interacted among themselves, and dominance relationships among them were sometimes difficult to determine. By two years of age, clear-cut dominance relationships were evident. By three to four years of age, ewes actively fought their way up the hierarchy, making it possible for a 4-year-old to be quite high ranked. Although variability in the Dominance Values increased in the older ewes, they did not appear to lose rank with increasing age (Table 13).

Lambs

Displacements, either from bedding sites, spatial positions or forage were extremely rare in lambs. During

Table 13. Dominance Values and ages for those ewes in 1982-1984 that interacted with at least 10% of the nursery group. * indicates those discarded from further calculations due to the small number of observed interactions. Arrows indicate instances when one ewe dominated another with a higher D.V.

| | 1982 | | | 1983 | | | 1984 | |
Ewe	D.V.	Age	Ewe	D.V.	Age	Ewe	D.V.	Age
AL	90.0	7+	AL	76.7	8+	*AL	90.0	9+
R5	90.0	7+	FS	76.0	8+	DB	75.9	8
OH	69.3	7+	HT	70.5	6	LE	70.5	9+
LB	67.8	5	HE	67.2	4	OH	65.2	9+
DB	61.0	6	R5	65.9	8+	HT	65.2	7
DE	54.7	6	OH	61.0	8+	DE	60.8	8
TY	54.7	4	LE	61.0	8+	R5	58.2	9+
TT	54.7	6	DE	59.1	7	UI	55.7	4
HE	52.9	3	DB	56.3	7	UB	54.7	4
HT	52.2	5	LB	50.8	6	LB	54.7	7
*MY	45.0	7+	BE	48.2	3	HE	52.9	5
RC	38.3	2	TY	41.4	5	BE	50.8	4
*SH	35.3	5	SH	37.8	6	SS	49.5	3
BR	35.3	2	UB	36.7	3	BR	47.9	4
UB	32.3	2	BR	36.7	3	TY	46.9	6
UI	31.5	2	UI	35.3	3	TT	40.9	8
SS	20.7	1	RC	33.2	3	SH	39.2	7
EY	20.7	1	SS	31.5	2	LI	39.2	3
BN	16.8	1	BN	28.7	2	EY	35.3	3
LL	16.1	1	EY	24.1	2	UM	34.0	3
*BE	0	2	TT	14.9	7	BN	33.2	3
UM	0	1	UM	14.0	2	EL	21.7	1
			LL	13.6	2	RC	18.4	4
						DY	12.9	1
						JO	12.6	1
						JL	0	1

1983, five displacements were recorded in more than 1200 lamb-hours (rate = 0.0041 displacements/hour), and in 1984 only one displacement was recorded in almost 280 lamb-hours (rate = 0.0036 displacements/hour). These rates were considerably lower than those found for yearlings in 1984 (Fig. 16). Before lambs were a year old, males were considerably larger than females, and evidently dominant, as dominance displays from male to female were recorded, as well as female-to-male subordinance displays with no dominance reversals observed between the sexes. Yearling rams usually became dominant to the adult ewes when 13-18 months old, after which they dissociated with the nursery groups and joined the bachelor herd.

Discussion

Well-defined, stable hierarchies existed for both sexes of bighorns on the NBR. Ram hierarchies were strongly linear, but ewe hierarchies were not. The hierarchies for both sexes were absolute (Wilson 1975), and rank did not change with situation or location.

Other studies have assumed bighorn ram hierarchies to be linear (Geist 1971, Hogg 1984a), but provide little data to support that assumption. The probability of a linear hierarchy occuring by chance in a group of more than 10

animals is remote (p « 0.001, Appleby 1983), but dominance relations probably do not develop by chance (Chase 1982). Indeed, the strength of the linearity of the ram hierarchy suggests that rams are behaving in such a way as to minimize deviation from linearity.

Rams, and to a lesser extent ewes, are polymorphic. Rank is correlated with age, which in rams is related to body size and horn size-two important aspects of fighting ability (Geist 1971, Hogg 1983, Table 7). Strange rams are probably capable of estimating relative rank by horn size (Geist 1971), so it is possible that few reversals would show up until more than 10 animals were present in each horn size class (see Schjelderup-Ebbe 1975, Chase 1982, and Appleby 1983 for discussions of the magic number 10). Among horn size classes, "recognition" of gross morphological characters is probably all that is necessary, while recognition of finer details within horn classes, perhaps approaching individual recognition (Barnard and Burk 1979), may promote the appearance of dominance reversals, or triangles, in groups of more than 10. Among the bighorn rams of the NBR, no horn size class (of animals which were observed interacting) ever numbered more than 10. Groups this small may indeed be transitive.

The behavior of rams was shown to be linked to their rank in the group, although age effects are hard to separate here. Not only do rams gain in rank, and priority of access,

with age, but as a result of this advancement in the hierarchy, the rams switch from acting aggressively subordinate to acting aggressively dominant; interacting at rates greater than expected based on group composition or the number of available interactants.

As the close relationship between age and rank indicates, rams may advance in the hierarchy simply by getting larger and growing more horn, while smaller rams join the hierarchy at the bottom. Definitive dominance relationships first appeared (were observed) between one and two years of age. During this time the young rams were also settling dominance relationships with the ewes; first the yearling ewes, then moving up the ranks to the bigger, older ewes. They appeared to test each ewe in the group, performing the typical ram dominance patterns-courtship and non-contact displacements. Some ewes appeared to concede right away, while others rebuked the young rams until the rams became large and strong enough to physically overpower them. By the time rut began, the yearling rams appeared dominant to all the ewes. At this time, they began to interact with the big rams as they joined the ewes on the rutting area. Following the rut, the yearling rams usually left with the bachelor herd, although they might be observed with the ewes for brief periods of time during the next year.

Once the young rams joined the bachelor herd, they still appeared to be settling dominance relations among themselves.

Within a cohort, even among a group as stable as that on the NBR, fights and upsets continued to occur until at least six years of age. Upsets also occured between cohorts. After nine or 10 years of age, rams declined rapidly in condition. On occasion, younger rams (5-6 years) were observed fighting and beating these old rams (although they were not always successful). Usually, however, the old rams became solitary and were not observed interacting with the other rams; Dominance Values could not be calculated for them. The switch from the nursery group to the bachelor herd was accompanied by a change in the ratio of contact-to-display patterns. Interactions among lambs were characterized by more contact than display patterns (Chapter III), whereas once dominance relations developed, displays became much more common than contacts (see also Geist 1971, p. 170).

The rams on the NBR are prevented from emigrating, likewise, no strange rams were added to the group during this study. The developmental changes of dominance relations of the young rams have been reported elsewhere (Blood 1963, Geist 1971), but the development of rank relations, and the switch from the ewe group to the ram group, appears to correspond more with sexual development than age, per se. Among a herd of Dall's sheep in Alaska, 2-year-old rams were not yet dominant to ewes (S. Brainerd, pers. comm.), and among bighorns of the Pecos Wilderness of New Mexico, 2-year-old rams still associated with the ewes and were

observed going through the same behavioral changes observed in yearling rams on the NBR (pers. obs.). Among high quality bighorns of upper Rock Creek, Montana, large male lambs (10-11 months old) were seen switching back and forth from ewe groups to ram groups, although interactions between the male lambs and ewes were not observed (pers. obs.). At any rate, bighorn herds exhibit profound differences in growth rates (Buechner 1960, Geist 1971, and others), and these differences may have dramatic effects on the development of dominance relations. Likewise, it is not unusual for rams to join and leave different bachelor herds in their lifetime (Geist 1971). What effects these changes in group composition have on the development and stability of dominance ranks within groups are unknown.

One of the hypothesized benefits of high rank is an increase in the number of breeding opportunities, which is supported by this study and others (Geist 1971, Hogg 1984a,b). Copulation rate varies slightly with the mating strategy utilized (tending, coursing or blocking) the choice of which may be dependant on rank (Hogg 1984a,b). Whether or not a copulation was successful was not possible to determine in the field. Ewes are bred repeatedly throughout their 1-2 day estrus, often by many different rams of disparate ranks. Although a high ranking ram may have more breeding opportunities, much more needs to be known about sperm competition before the relationship between rank and

reproductive success in bighorn rams is understood (Hogg 1984a,b).

Ewes are less polymorphic than rams, reaching most of their body and horn size by ages 2-3 (Blood et al. 1970, Jorgenson and Wishart 1984). Rank was significantly correlated with age, as has been found with other female ungulates: red deer (Cervus elaphus; Hall 1983); dairy cows (Bos taurus; Reinhardt and Reinhardt 1975); Chillingham cows (B. taurus; Hall 1986), Pere David's deer (Elaphurus davidianus; P. Schoknecht, pers. comm.); white-tailed deer (Townsend and Bailey 1981); ponies (Equus caballus; Clutton-Brock et al. 1976); reindeer (Rangifer tarandus; Espmark 1964), roe deer (Capreolus capreolus; Espmark 1974); bison (Rutberg 1983, 1986); and a small captive group of bighorn ewes (Bennett 1986). During each year, at least 12 ranked ewes were three years and older, and the more ewes in this catagory, the more triangles apparent in the ranks. Other studies of ungulates have found similar results: numerous triangles in isomorphic groups of more than 10 animals (Beilharz and Mylrea 1963, Espmark 1964, Clutton-Brock et al. 1976, Collis 1976, Hall 1986, Rutberg 1986).

While high dominance rank may provide rams with more breeding opportunities, the benefits of high rank to ewes are less clear. Presumably, high rank would allow a ewe access to limited resources and possibly reduce stress (Cherkovich

and Tatoyan 1973), allowing a ewe to maintain a better body condition, the benefits of which could be passed on to her offspring.

Among red deer hinds (Clutton-Brock et al. 1984, 1986), dominant hinds conceived earlier, bore a higher percentage of males than females and affected the breeding success of their sons more than their daughters. The body size of males (an important factor in breeding success) was related to growth and nutrition during the first 18 months of life (Clutton-Brock et al. 1984, 1986), a factor greatly influenced by the amount of maternal investment (Clutton-Brock et al. 1982). The body condition of Dall's ewes (O. dalli) may affect horn growth of their ram lambs for up to five years following birth, but appears to affect their ewe lambs to a lesser extent (Bunnell 1978). Horn size is an important component of fighting ability and rank among both bighorn and thinhorn rams (Geist 1971, but not the only component, J. Hogg, pers. comm.), leading to the possibility that the body condition of a ewe during gestation and lactation may influence her son's reproductive success, perhaps more than that of her daughters (as hypothesized by Trivers and Willard 1973).

In a study of dominance relations in a captive group of California bighorn ewes, Eccles (1981) found a stable, age-related hierarchy. However, horn lengths and body weights were not strongly correlated with Dominance Values,

and dominants did not have higher quality diets or different activity budgets than subordinates. The prime breeding age for bighorn ewes is reported to be from five to seven years (Geist 1971). In the NBR ewes, the mean Dominance Value for this age group was 54.08 ± 9.57, slightly above the median. Weights of ewes were not measured during this study, but among ewe six years old and older, body condition deteriorated obviously with age, although rank did not. Younger ewes invested more, pre-natally, in their male lambs, while older, and/or higher ranking ewes appeared to invest more in their female lambs. Variance in reproductive success is greater among males and is probably more closely related to early growth and parental investment than among females (see Clutton-Brock et al. 1982, Bunnell 1978). Overall, ewes invested more in male lambs, both pre- and post-natally, than in female lambs (Hogg and Hass, in prep.), and male lambs apparently cost more for a ewe to produce than female lambs. Therefore, ewes might be producing heavier (male) lambs when they are in better condition and can afford the added cost. As a ewe's reproductive potential declines with age, she might invest more in her female offspring and increase her "reproductive value" (Clutton-Brock et al. 1982).

Because body condition declined with age, although rank did not, little relationship was seen between rank and maternal investment. However, the sheep on the NBR are generally in excellent condition, and are not limited by

forage. In other habitats, where seasons are more severe, the access (to forage, water, bedding sites) obtainable by high rank may indeed make the difference between good and poor body condition, which, if not only affecting ewe survival, may affect the reproductive success of offspring born to ewes of differential rank. Ewes on the NBR seldom used their rank to obtain access to some limited resource, but more often appeared to be either maintaining a minimum personal distance or reinforcing rank relations. The rates of displacements appeared to be more a function of the number of subordinates available to each ewe, than an increase in aggressiveness with rank, as was found among the different ranks of the rams. These findings differed from those of Eccles (1981), who found a significant correlation between aggressiveness and Dominance Value of bighorn ewes. However, he measured aggressiveness by counting the number of aggressive encounters initated by each ewe, and did not adjust for group composition or the number of possible interactants. The advantages, to ewes, of obtaining and maintaining high dominance ranks (on the NBR) remain unclear.

Displays are physiologically less costly to bighorns than contact patterns (MacAurthur et al. 1981). As expected then, ewes used displays over twice as often as contact patterns to displace other ewes. Again, these results differ from those of Eccles (1981) who found contacts more frequently used than displays. In a small captive group,

high ranking bighorn ewes utilized displays more often than did low-ranking ewes (Bennett 1986). The displays used by ewes are more subtle than those of rams (Geist 1971, Eccles 1981, pers. obs.), and ratios of display-to-contact patterns used may be biased by conditions and observer ability.

For the first few years, ewes advanced in the hierarchy by default as younger ewes joined the bottom of the hierarchy, after which they fought their way up the ranks. Variability in Dominance Values increased with age, but the factors involved are unknown. Ewes usually associated with the nursery band for their first few years. Barren ewes four years old or older tended to associate in unstable groups of 2-5 animals. These ewes occasionally joined the nursery group for short periods of time. Barren ewes older than seven years seldom joined the nursery groups; they spent much of their time alone. All of the ewes not included in the hierarchy fell into this "older" catagory.

I found little evidence that ewes, as a group, were behaving like juvenile males. Ewes, like rams, exhibited rank/age-specific behaviors, and ewes did not appear behaviorally mature until around 5 years of age. Sexually mature ewes did not behave aggressively subordinate, as did young rams. The dramatic horn displays of the rams appeared as graded signals among the ewes; indeed, communication in general occured at a much more subtle level than among the rams (Hass, unpub. data). This is not suprising, as ewes do

not have large, curled horns to hide facial expression. Unlike previous studies of captive ewes (Eccles 1981, Bennett 1986), the ewes on the NBR interacted frequently, and I observed numerous dominance fights. Ewes rarely disperse from their natal ranges and form a matrilineal society composed of mothers, daughters, aunts, sisters, etc. (Hass 1984). Rams, on the other hand, often disperse far from their natal ranges, and may belong to several different bachelor herds in their lifetime (Geist 1971).

Bighorn rams and ewes form two separate societies that are not only geographically separated for most of the year, but are distinct in their group structure, relatedness of group members, communication, and structure and development of their dominance hierarchies.

SUMMARY

The ontogeny of behavior, whether it involves learning or the maturation of innate behavioral processes, has been a sadly neglected area of bighorn research. Considering the tremendous variability in organizational, developmental, and reproductive strategies used by bighorns in different habitats, the ontogeny of these strategies should be a fruitful area of research.

Because of this variability evident in different herds, to make statements about the function or benefits of play behavior or dominance relations, in bighorn sheep as a species, could be misleading if not patently false. On the NBR, the play of bighorn lambs appeared to provide motor training benefits, but did not appear to affect subsequent social structure or dominance relations of the herd. However, lambs probably learn, in play, how to get along in groups, how to fight, and how to deal with the environment. Lambs may be developing physical, as well as social, skills necessary for predator evasion during a period when they are highly vulnerable. But exactly what is learned could not be tested in this study. Due to the current lack of comparative data on inter- and intra-sexual play behavior, and development of dominance relations under different growth regimes, the effects of the relatively lush habitat and high lamb mortality are unknown.

Dominance relationships did not develop until after the sheep were one year old. This is probably a maturation response, dependent on the growth/physical development of the

89

young sheep. In extremely high quality herds, like the Upper Rock Creek herd, dominance relations may be developing in the lambs before they are a year old. Maternal influence and subsequent reproductive success of herds with different growth rates could vary dramatically from that observed on the NBR.

Both rams and ewes exhibited very stable hierarchies that were strongly correlated with age. Social behavior, particularly among rams, appeared dependent on rank, manifested primarily through dominance and subordinance displays. Rates of rank-related behaviors were reflective of the separate ram and ewe societies. Direct reproductive benefits, in terms of more breeding opportunities, were obvious for high-ranking rams. Reproductive benefits of high rank for ewes, in this study, remain obscure.

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