RUTTING BEHAVIOR IN MULE DEER: THE SIGNIFICANCE OF ANTLER SIZE IN MALE COMPETITION AND FEMALE CHOICE

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Thesis directed by Associate Professor Diana F. Tomback

Quantitative data on Rocky Mountain mule deer (Odocoileus hemionus hemionus) rutting behavior were obtained in Boulder, Colorado during the 1984 and 1985 breeding seasons in order to determine the significance of antler point number and size in both male competition (intrasexual selection) and female choice (intersexual selection). Specifically, I investigated the relationship between antler point number and size and male aggressive behavior rates, sparring rates, reproductive behavior rates, and dominance. During the 1984 breeding season, 229 sparring matches and 5 fights were observed. Throughout the 1985 breeding season, 33 bucks were individually identified and the following behaviors recorded: 279 aggressive behaviors, 192 sparring matches, 5 fights, and 255 reproductive behaviors. Data analysis indicated that 1) reproductive behavior rates, and 2) dominance correlated with both antler point number and antler size, 4) aggressive behavior rates correlated with reproductive behavior rates, and 5) aggressive behavior rates correlated with dominance. Additional results included: 6) females tolerated males with the greatest antler point numbers, 7) weekly reproductive behavior rates were highest when weekly sparring rates were lowest, and 8) daily sparring rates correlated

significantly with the number of males, females, and total number of deer present each day.

DEDICATION

For my mother and father who have always supported me and to Terry, for making it easier.

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I especially owe my thanks to my advisor Diana Tomback, and my other committee members, Jan Driscoll, and Marc Bekoff for their invaluable advice. My thanks also to Alan Brockway for his help with computer analysis and Lynn Hoffman for her field assistance

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CHAPTER I

INTRODUCTION

Certain physical and behaviorial traits may evolve by means of sexual selection. These traits may be the consequence of either intrasexual (i.e., male-male competition) and/or intersexual selection (i.e., female preferences). It still remains unclear whether the antlers of cervids are the selected product of intrasexual selection only or of both kinds of sexual selection. The recent "truth in advertising" hypothesis suggests that traits such as antlers are honest displays of a male's genetic quality and convey information to males and females alike (Kodrik-Brown and Brown, 1984). In fact, researchers have found that in mule deer (Odocoileus hemionus) antler point number and size are generally, but not strictly, correlated with age (Linsdale and Tomich, 1953; Anderson and Medin, 1969), supporting this idea. Most previous studies have discussed only the importance of antlers in male competition (Koutnik, 1981; Koutnik, 1983; Kucera, 1978; Wachtel et al., 1978; Bowyer, 1986). Little information is available on their relationship to female mating preferences.

Discussion of female attraction to large antlers dates back to Darwin (Clutton-Brock et al., 1982), but few quantitative studies have supported this idea. In red deer stags (Cervus

elaphus L.) there is little evidence that during the breeding season hinds prefer stags with the largest antlers (Clutton-Brock et al., 1979). However, in mountain sheep (Ovis canadensis and O. dalli estrous females accepted mounts most frequently from rams with the largest horns (Geist, 1971).

Aggressive and reproductive behaviors have been thoroughly described in the genus Odocoileus (Michael, 1968; Ozoga, 1972; Linsdale and Tomich, 1953; Geist, 1981; Cowan and Geist, 1961; Hirth, 1977; deVos et al., 1967; Dasman and Tabor, 1956), and there have been several quantitative field studies concerned with mule deer rutting behavior, particularly in relation to antler size (Kucera, 1978; Koutnik, 1983; Weinberg, 1985; Wachtel et al., 1978; Bowyer, 1986). Results suggest that high levels of aggression, reproductive success, and dominance are correlated with large antler size in mule deer and that females may prefer these large-antlered bucks for mating. In contrast, some observations in the genus Odocoileus have suggested that females have no preference for particular males (Michael, 1968; Linsdale and Tomich, 1953).

Quantitative data, however, are lacking on whether or not the most aggressive and/or dominant bucks have the greatest reproductive success. Even though reproductive success is difficult to assess in mule deer, it has been assumed that the most dominant bucks gain access to the greatest number of females (Koutnik, 1983; Kucera, 1978; Robinette, 1977; Geist, 1981; Linsdale and Tomich, 1953; Muller-Schwarze, 1972; Dorrance, 1966;

Wachtel et al., 1978).

The above predictions have not been adequately tested, nor have previous studies been based on a number of marked or known individuals to correlate dominance and reproductive success. Other studies of free-ranging mule deer bucks either investigated antler point and size correlations within a small, young population of identified California mule deer (O. h. californicus) (N = 13) (Koutnik, 1983) or else within a large population of unidentified desert mule deer (O. h. crooki) and southern mule deer (O. h. fuliginatus) (Kucera, 1978; Bowyer, 1986). Here, I report the results of an investigation designed to address the key questions. During the 1985 rutting season thirty three Rocky Mountain mule deer bucks (O. h. hemionus) were individually identified, categorized as to antler point number and antler size, and observed to determine the relationships among aggression, dominance, and reproductive success.

In addition, an important question to behavioral biologists is whether rates of aggressive behaviors, sparring, and reproductive behaviors produce identical male hierarchies. Researchers have used one or more of the above behaviors in various ways to establish dominance ranks for their animals. Clearly, the hierarchy may vary depending on the behavior(s) used; and, thus, conclusions based on different definitions of dominance may have limited application. I used the 1985 data to compare hierarchies based on aggressive behavior, sparring, and

reproductive behavior rates to study this problem.

Specific Hypotheses

Based on a review of the current literature, along with previous behaviorial observations of mule deer (Wachtel et al., 1978) the following hypotheses were formulated.

(1) Antler point number and size will predict male: (a) aggressive behavior rates, (b) sparring rates, (c) reproductive behavior rates, and (d) dominance rank (defined by Clutton-Brock et al., 1979).

(2) Females prefer males with the largest antler point number and size.

(3) Hierarchies based on aggressive behavior rates, sparring rates, reproductive behavior rates, and dominance (defined by Clutton-Brock et al., 1979) are not the same, i.e., do not show identical ranks for the same male.

Mule Deer Biology

Mule deer are generally gregarious (Geist, 1981; Kucera, 1978; Dorrance, 1966) and have a social organization consisting of family groups, buck groups, and feeding groups. Family groups include milk groups (a doe with her new fawns) and maternal groups (a doe and yearlings) (Linsdale and Tomich, 1953). Members within family groups are therefore genetically related (sometimes including three or four generations), representing a matriarchal organization (Hawkins and Klimstra,

1970).

A family comprises the most common social group remaining intact during summer and fall (Dasman and Tabor, 1956; Hawkins and Klimstra, 1970; Dorrance, 1966). During the winter and spring, a partial breakup occurs when male yearlings either leave to join buck groups (Dasman and Tabor, 1956) or associate with other social groups (Brown, 1974). Klimstra and Hawkins (1970) reported that 80% of the yearling white-tail bucks (Odocoileus virginianus) emigrated from their mother, whereas 87% of the yearling females remained. Family groups also disband during the fawning period (May and June), when females become intolerant (Miller, 1974) and highly aggressive towards other group members (Koutnik, 1981). Following parturition (June-August), maternal does reassociate with those from the previous winter group but remain antagonistic towards male yearlings (Miller, 1974).

Buck groups, also called fraternal groups (Linsdale and Tomich, 1953), form from February-August (Hawkins and Klimstra, 1970), after antlers are shed (November 15-February 7). Antler growth occurs between early March and late October. Abnormalities in antler morphology occasionally result, depending on age, diet, physical condition, injury (Anderson and Medin, 1971), and heredity (Rue, 1978). In white-tail deer, males within buck groups (consisting of 2-17 mature males) form true social bonds, although some of the very large bucks also associate with other buck groups (Brown, 1974). These groups disband at the beginning

of the rutting season (September-December) (Anderson and Medin, 1967), when antler velvet shedding results in higher androgen levels and thus increased aggression among males (Thomas et al., 1965). Other characteristics of the rut include bucks associating with does and active courtship (Dasman and Tabor, 1956). Actual breeding occurs from mid-November through early December (Anderson and Medin, 1967).

Feeding groups are temporary associations of large family groups (25-30 deer) and buck groups. These occur during late morning and late afternoon hours when feeding is most common (Linsdale and Tomich, 1953).

The mating system witnin the genus Odocoileus involves serial polygyny, not harem formation (Geist, 1981). True harem formation (males herding and defending groups of females) has not been observed (Kucera, 1978; Dorrance, 1966), but see Robinette (1977) and Hirth (1977). Of the two kinds of courtship strategies that have been described, the most common strategy involves a buck forming a tending bond with an estrus female until she is bred (Geist, 1981) or he is displaced by a more dominant buck (Kucera, 1978). The much rarer rush-courtship strategy is used by older bucks who "roar" while chasing females, and usually results in immediate copulation (Geist, 1981).

CHAPTER II

METHODS

Study Area

Data were collected in the foothills of the Rocky Mountains in Boulder, Colorado, near the National Center for Atmospheric Research (NCAR), at an elevation of approximately 1800 m. The terrain consists of gulleys, open fields, and a steep north-facing slope. This location was used by bucks for establishing dominance relations. Data were occasionally gathered in the adjacent Kohler Mesa-Skunk Creek area (elevation approximately 1710-1810 m) and in a residential portion located to the south. Observations of known bucks verified movements between these two areas (from NCAR to Kohler Mesa), especially during inclement weather. Some bucks were found exclusively in each area and others moved around to different locations.

Both NCAR and Kohler Mesa are located within the grassland-lower montane ecotone regions where vegetation consists predominantly of shrubs, grasses, herbs, and ponderosa pine (Pinus ponderosa) (Marr, 1967). These areas are also located within the City of Boulder Mountain Parks and Open Space region.

The area surrounding NCAR is protected from hunting and therefore simulates a wildlife sanctuary. Nevertheless, certain problems with data collection were encountered. Due to an

accessible location, large numbers of people often gathered there and sometimes disturbed normal deer activities. In addition, construction of an underground cable disrupted deer movements between these areas and may have resulted in occasional low population counts. Coyote (Canis latrans) and possibly cougar (Felis concolor) predation (evidenced by predator observations and bone remains), along with deaths from bullets and vehicles, contributed to deer mortality. Additional stress may have been caused by domestic dogs (Canis familiaris) chasing deer.

Deer Population

Herd population counts made during the 1984 and 1985 rutting seasons showed that there were approximately 63 deer in 1984 (31 males, 32 females and young) and 59 deer in 1985 (33 males, 26 females and young) indicating some stability in population size. The greatest number of males was present during the first sparring peak (see Results). Afterwards, bucks dispersed throughout their home range.

Ear tags and/or collars were placed on approximately 90 deer between 1982 and 1984 by Western Resource Development Corporation (WRDC) consultants and the Colorado Division of Wildlife. In the spring of 1984, the total deer population within a 16 square mile radius of Boulder was estimated at 888 ± 217 deer (WRDC, 1984).

There were six yellow tagged bucks observed in my study area in 1985. Four were tagged previously (Tag #'s 11, 12, 36,

37), and two more were tagged during the 1985 rutting season (Tag #'s 135 and 133). Observations of these tagged deer suggest that bucks return to the same breeding ground each year.

Observational Methods

A total of 97 hours of observation was logged over two rutting seasons: 25 hours during 9 September to 14 November 1984; 72 hours during 3 September to 30 December 1985. Data were dictated into a cassette recorder and collected with the aid of 7X binoculars, a 400 mm telephoto lens, and a stopwatch. Observations on deer herd composition were made at least three times a week in the afternoon, when deer gathered for feeding.

During 1984, sparring bucks were observed in order to determine seasonal sparring patterns. Other aggressive and reproductive behaviors were also recorded and described. Identification of individual bucks was uncertain from one observation period to the next except when ear tags or other distinguishing antler characteristics were present.

In 1985, 33 bucks were individually identified according to antler point number and antler size along with other distinguishing facial and body markings. Each new buck encountered was photographed and given an identification number. Photographs were taken each observational period until buck identification was certain. These photographs, carried in the field, were particularly useful for identifying individual bucks within the 8 point antler class, which accounted for 39% of the total bucks

observed. Figure 1 illustrates the differences and similiarities among four 8 point bucks. The antler shapes of bucks with I.D. #'s 2 and 3 are similiar, except for the shape of their left front fork, whereas forehead markings between bucks #1 and #4 are distinguishable.

Below, all buck I.D. numbers will be preceeded by the symbol # without the word I.D. Bucks were placed into antler point classes based on the total number of points present on both racks but excluding the brow tines. The antler point class distribution was as follows: 10 point (N = 1), 9 point (N = 1), 8 point (N = 13), 7 point (N = 5), 6 point (N = 5), 5 point (N = 1), 4 point (N = 6), and 2 point (N = 1). Bucks with abnormal antlers (Figure 2) were placed into the appropriate antler point class based on the number of points present on their normal rack. Buck #19 was in the 10 point antler class, and bucks #10, #11, and #27 were in the 8 point antler class. Information from direct observations along with photographic comparisons enabled all bucks to be placed into one of four antler size classes: small (= 1), medium (= 2), large (= 3) or very large (= 4). The antler size distribution was as follows: very large (N = 4), large (N = 11), medium (N = 11), and small (N = 7). Buck antler descriptions are found in Table 1. As in 1984, sparring, aggressive, and reproductive behaviors were noted for all bucks in the study areas in 1985, but with the benefit of individual recognition.

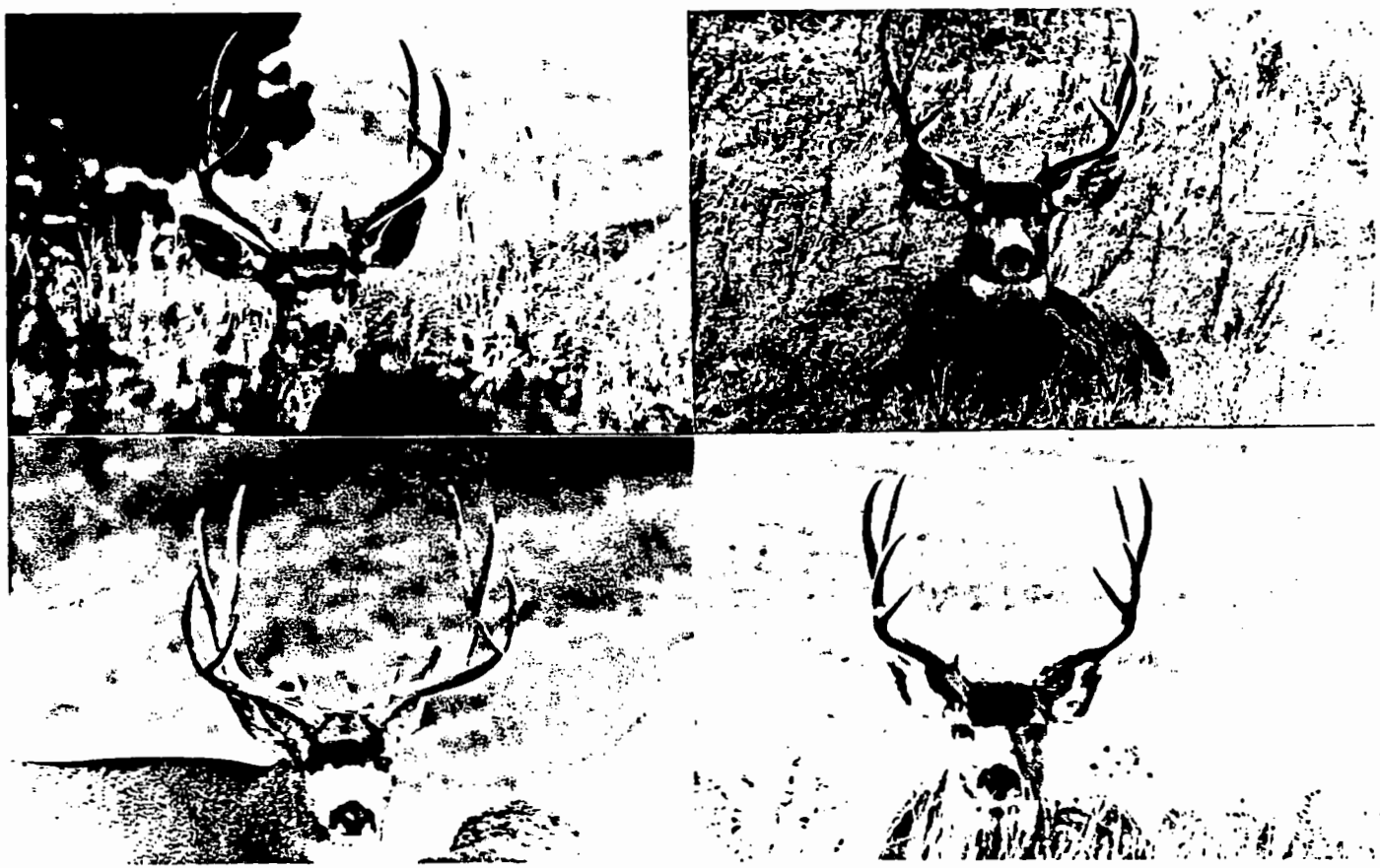

Figure 1. Antler symmetry comparison among four bucks in the 8 point antler class: (clockwise starting at top left) #1, #3, #2, and #4.

Figure 2. Antler abnormalities in four bucks: (clockwise starting at top left) #10, #19, #27, and #11.

Table 1. Antler characteristics of 33 bucks observed during the 1985 rutting season: Antler Size (AS), Point Number (PN), Left Rack (LR), and Right Rack (RR).

I.D.#	AS	PN	LR	RR	Notes
1	3	8	4	4	Limp left front leg
2	3	8	4	4	
3	3	8	4	4	
4	4	8	4	4	Largest antler spread
5	4	8	4	4	Limp right rear leg (Tag #135)
6	3	8	4	4	Velvet on right rear fork
7	3	8	4	4	
8	3	8	4	4	
9	2	5	3	2	Large body
10	3	8*	2	4	Tag #133
11	3	8*	4	?	Right rack broken
12	2	6	3	3	
13	2	6	3	3	Tag #11
14	3	8	5	3	Tag #12
15	2	7	4	3	
16	2	7	3	4	
17	2	7	4	3	Large old buck
18	2	7	4	3	Tag #36
19	3	10*	5	2	Large old buck
20	1	2	1	1	Spike

Table 1. (continued).

I.D.#	AS	PN	LR	RR	Notes
21	1	4	2	2	
22	1	4*	0	2	No left rack
23	1	4	2	2	
24	1	4	2	2	
25	1	4	2	2	
26	4	8	5	3	Loudest vocal hiss
27	3	8*	4	4	Broken right front leg
28	4	9	4	5	Largest antler spread
29	2	6	3	3	
30	2	7	4	3	
31	2	6	3	3	
32	2	6	3	3	
33	1	4	2	2	Tail not black-tipped

* = abnormal antlers

Data Analysis

For the 1985 data, rates of aggressive behaviors, sparring, and reproductive behaviors were calculated on a per-hour basis for each buck as follows. The total number of behaviors recorded was divided by the total amount of time the buck was observed. Behaviors used to calculate these rates are described in the Results. Since I defined fights as intense sparring matches, individual sparring rates, seasonal sparring rates, and dominance scores were calculated with fights (N = 5) included. Any reference to sparring below includes these fights. Individual rates for all 33 bucks were rank-ordered to produce three hierarchies. Since hierarchies for aggressive behaviors and sparring did not significantly correlate (see Results) they were treated separately. Overall frequencies for each of the 15 aggressive and 9 reproductive behaviors observed were calculated as follows. The number of observations for each behavior was divided by the total aggressive (N = 279) or reproductive behaviors (N = 255) recorded (see Results).

Dominance scores were calculated according to the definition by Clutton-Brock et al. (1979), which weights an individual's rank according to the rank of his contestants. The equation for the index is as follows:

$$\frac{B + \Sigma b + 1}{L + \Sigma l + 1}$$

For a given buck, B equals the number of bucks he defeated, and Σb equals the total number of bucks that they defeated (excluding the subject). L equals the number of bucks to which he lost, and Σl equals the total number of bucks to which they lost (excluding the subject). The 1 added to each ratio accounts for individuals never observed to defeat or lose to other animals. The larger the score the higher the dominance rank position.

Clutton-Brock et al. (1979) used the outcomes of fights to calculate dominance scores. I calculated dominance scores by combining aggressive behaviors with sparring (which includes fights) because hierarchies determined separately for each were significantly correlated (see p.23). When several displays were involved in an interaction, only the final outcome was scored. Dominance scores were based on a total of 124 aggressive interactions and 181 sparring matches. Seventeen sparring matches were excluded, because it was difficult to determine the winner.

Dominance scores were not calculated for the 7 yearlings, who are characterized by small antlers and body size, for the following reasons: (1) yearlings rarely beat older bucks in aggressive interactions, (2) based on the literature, females are not bred by yearlings, and (3) dominance scores calculated for yearlings revealed inaccurate hierarchy positions. Consequently, a fourth hierarchy was constructed using the dominance scores of the 26 older bucks. All raw data serving as the basis of the hierarchies formed for this study are reported in Appendix A.

The six resulting hierarchies, based on antler point number, antler size, aggressive behaviors, sparring, reproductive behaviors, and dominance, were compared to each other using Spearman's rank correlation coeficient (r_s) (Sokal and Rohlf, 1981). Individuals tied for the same rank were assigned the average value of those ranks. The Spearman correlation coefficients (r_s) were converted to t scores in order to determine their significance values (Siegel, 1956). A correlation was significant if $P \leq 0.05$. Because the considered hypotheses were directional, 1-tail critical values were used.

Female responses to male approaches and female behaviors indicating interest in certain males were also recorded. These behaviors are described in the Results. Observed and expected frequencies for avoid and tolerate behaviors by females in respect to numbers of males in the 2-7 and 8-10 antler point categories were analyzed by Chi-square tests (Siegel, 1956).

Daily rates for aggressive and reproductive behaviors, and sparring, were calculated for the population on a per-hour basis and reported weekly (see Results). These rates were also correlated with the daily herd composition using the Pearson's correlation coefficient (r) (Sokal and Rohlf, 1981). All statistical tests were conducted on IBM-compatible PCs using Microstat (Ecosoft, Inc.).

CHAPTER III

RESULTS

Aggressive Behaviors

Fifteen aggressive behaviors observed between bucks and sparring matches were used to calculate individual aggressive behavior and sparring rates, respectively, in 1985 (Table 2). These behaviors have been previously described for the genus Odocoileus (Linsdale and Tomich, 1953; Cowan and Geist, 1961; Thomas et al., 1965; Koutnik, 1981; Koutnik, 1983; Kucera, 1978; Hirth, 1977).

Of the total aggressive interactions observed in 1985, aggressive behaviors (N = 297) accounted for 60% and sparring (N = 197) accounted for 40%. Frequencies for each behavior (Figure 3) show that approach occurred most often (23% of total), followed by antler threat (13% of total), and antler thrash (10% of total). The antler lunge was observed most infrequently (1% of total).

In 1984, 234 sparring matches and 5 fights (2.1% of total) were recorded. In 1985, 197 sparring matches and 5 fights (2.5% of total) were recorded. Fights occurred most frequently during the time of peak sparring in 1984 and 1985 (see Aggressive and Reproductive patterns). Bucks in all antler point classes were

Table 2. Ethogram of mule deer aggressive and reproductive behaviors (Linsdale and Tomich, 1953; Thomas, et al., 1965; Koutnik, 1981).

Behavior	Descriptions
Male Aggressive Behaviors (N = 496)	
Approach (AP)	A buck walks towards another buck and may sometimes displace the opponent. Can occur in combination with eardrop, vocalizations, or with tail and hair raised.
Antler Thrash (ATH)	Buck swings antlers from side to side on trees or bushes which may result in forehead rubbing for scent marking.
Antler Threat (AT)	Antlers are pointed at an opponent. Used to solicit a spar contest.
Eardrop (ED)	With head erect, ears are dropped along the neck. Occurs with either the approach, hardlook, or crouch.
Antler Thrust (TH)	Antlers are rammed into opponent's rump or side.
Hardlook (HL)	Buck stares at opponent with head either raised or lowered. Occurs with eardrop and sometimes hair raise, tail raise, or vocalizations.
Crouch (CR)	Dominance display where a buck is hunched over with ears back, tail raised, and snorting or hissing vocalizations.
Rub-Urinate (RU)	Buck urinates on rear legs while rubbing them together. Used most frequently by dominant males.
Pursue (PU)	Buck persistently follows another trying to solicit a spar match or escort a buck away from females.

Table 2. (continued).

Behavior	Descriptions
Chase (CH)	A dominant buck charges at another buck in order to maintain access to an estrus doe.
Headshake (HS)	Dominance display where a buck shakes his antlers from side to side either after winning a spar contest, at an approaching male, after a flehmen, or while watching an opponent pursue does.
Antler Lunge (L)	Noncontact threat where a buck jumps towards another with antlers lowered, followed by a quick retreat.
Circle (CL)	Dominance display used in combination with a parallel walk. Opponents circle each other in a crouched position and may vocalize.
Parallel Walk (PW)	Broadside dominance display involving two opponents walking stiff-legged with hair raised and ears back.
Vocalizations (VO)	Hissing and snorting sounds which sometimes occur with the chase, rub-urinate, hardlook, or crouch.
Sparring (SP)	Direct contact involving two opponents using antler pushing and twisting. A contest ends when an opponent disengages his antlers and either walks, jumps, or runs away. Distinguishable from fights which are intense matches.

Table 2. (continued).

Behavior	Description
Male Reproductive Behaviors (N = 259)	
Approach (AP)	Buck walks towards a doe resting or feeding. Females often avoid buck advances but sometimes tolerate them.
Sniff (SN)	Buck investigates a doe's reproductive condition by smelling her perineal region.
Tend (TD)	Buck courts an estrus doe. Neck is extended as buck trots behind the female, periodically sniffing and vocalizing.
Flehmen (FL)	Buck stands open-mouthed with head extended and elevated. With upper lip retracted he tests a doe's reproductive status by using scent analysis.
Pursue (PU)	Buck persistently follows a doe walking away at a fast pace in retreat.
Vocalizations (VO)	Bleating courtship vocalization used by dominant bucks while tending does.
Chase (CH)	A buck runs after a doe that is avoiding his courtship attempts.
Lick (LK)	A buck licks a doe's perineal region which is followed by the contact display.
Contact (CT)	A buck places his chin on doe's rump prior to copulation.

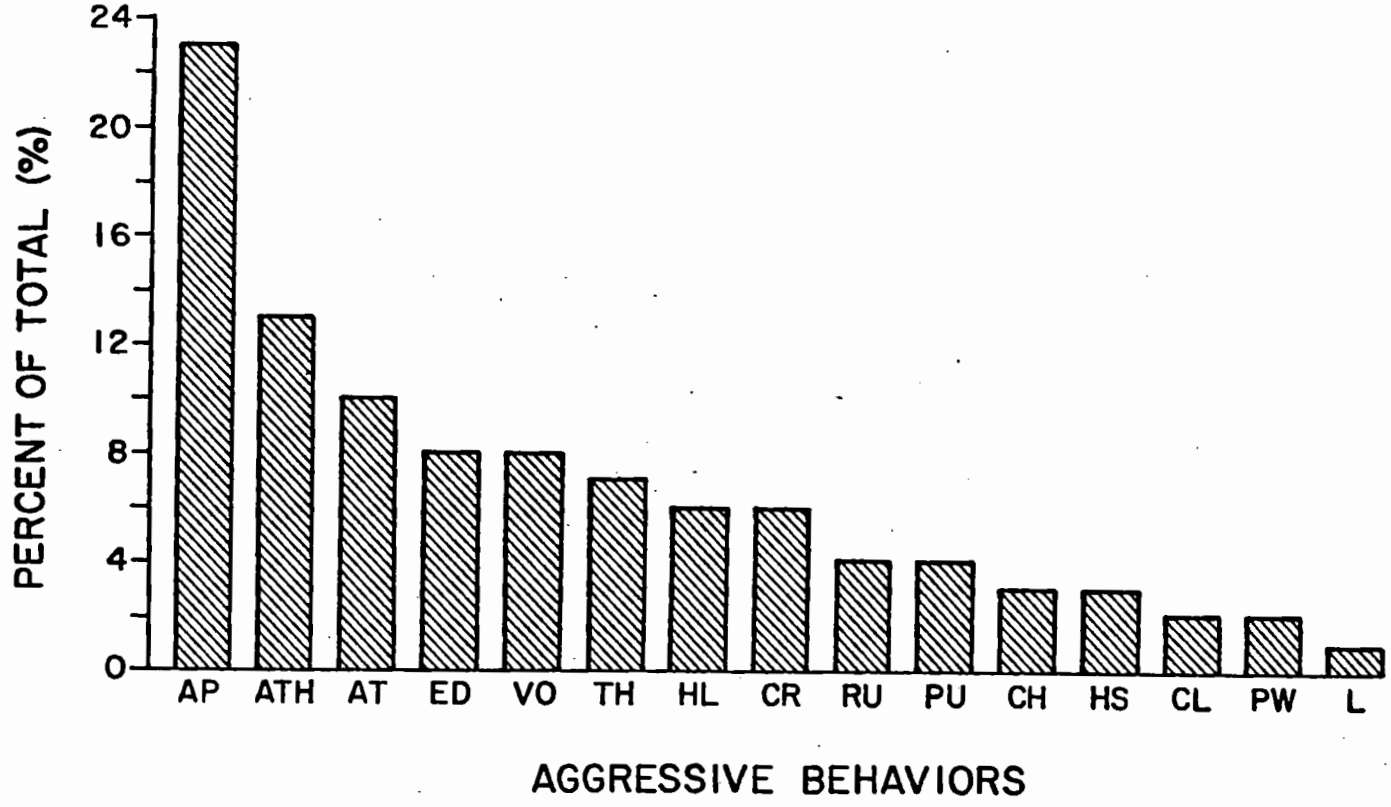

Figure 3. Histogram of 15 aggressive behaviors observed during the 1985 rutting season. See Table 2 for behavior abbreviations.

observed sparring, whereas bucks with the largest antler size class (4) were not.

For aggressive behaviors (Table 3), rates were highest for bucks #33 (6.00 behaviors/hr.) and #28 (3.90 behaviors/hr.) and represented the top two hierarchy positions. The lowest rates (0 behaviors/hr.) were recorded for bucks #17, #25, #26, #29, and #32. Buck #32 had the highest rate of sparring (6.79 matches/hr.), and bucks #4, #6, #13, #17, #25, #26, #27, #28, and #31 (0 matches/hr.) had the lowest (Appendix A).

Separate dominance scores using the index of Clutton-Brock et al. (1979) were calculated for aggressive behavior and sparring. Hierarchies based on each of these two categories correlated significantly (r_s = 0.43, d.f. = 24, 0.025 > P > 0.01), so a single dominance score was calculated combining aggressive behavior and sparring for each buck (N = 26). Dominance scores (Table 3), based on a combination of both aggressive behaviors and sparring, were highest for bucks #28 (26.00) and #4 (14.00) and lowest for buck #27 (0) (Appendix A).

Male Reproductive Behaviors

Nine male reproductive behaviors were recorded (Table2) and used to calculate individual reproductive behavior rates. These behaviors have also been previously described (Linsdale and Tomich, 1953; Cowan and Geist, 1961; Kucera, 1978; Walther, 1984; Weinberg, 1985). Frequencies for each behavior (Figure 4)

Table 3. Six hierarchies for 33 bucks observed during the 1985 rutting season: Point Number (PN), Antler Size (AS), Sparring (SP), Aggressive Behavior (AB), Reproductive Behavior (RB), and Dominance (D).

I.D.#	PN	AS	SP	AB	RB	D
1	3	2	4	9	15	11
2	3	2	21	22	24	23
3	3	2	19	16	19	15
4	3	1	25	4	4	2
5	3	1	10	11	25	5
6	3	2	25	25	28	9
7	3	2	13	24	14	6
8	3	2	14	12	7	16
9	6	3	17	13	27	8
10	3	2	7	15	9	19
11	3	2	18	6	3	14
12	5	3	22	17	22	17
13	5	3	25	8	30	12
14	3	2	5	5	5	3
15	4	3	11	14	23	22
16	4	3	2	10	18	13
17	4	3	25	28	11	12
18	4	3	9	3	10	10
19	1	2	24	27	17	7
20	8	4	6	23	16	-

Table 3. (continued).

I.D.#	PN	AS	SP	AB	RB	D
21	7	4	8	20	30	-
22	8	4	23	28	30	-
23	7	4	16	26	30	-
24	7	4	15	21	29	-
25	7	4	25	28	26	-
26	3	1	25	7	13	4
27	3	2	25	18	8	25
28	2	1	25	2	2	1
29	5	3	12	19	6	21
30	4	3	20	23	20	18
31	5	3	25	28	1	20
32	5	3	1	28	21	24
33	7	4	3	1	12	-

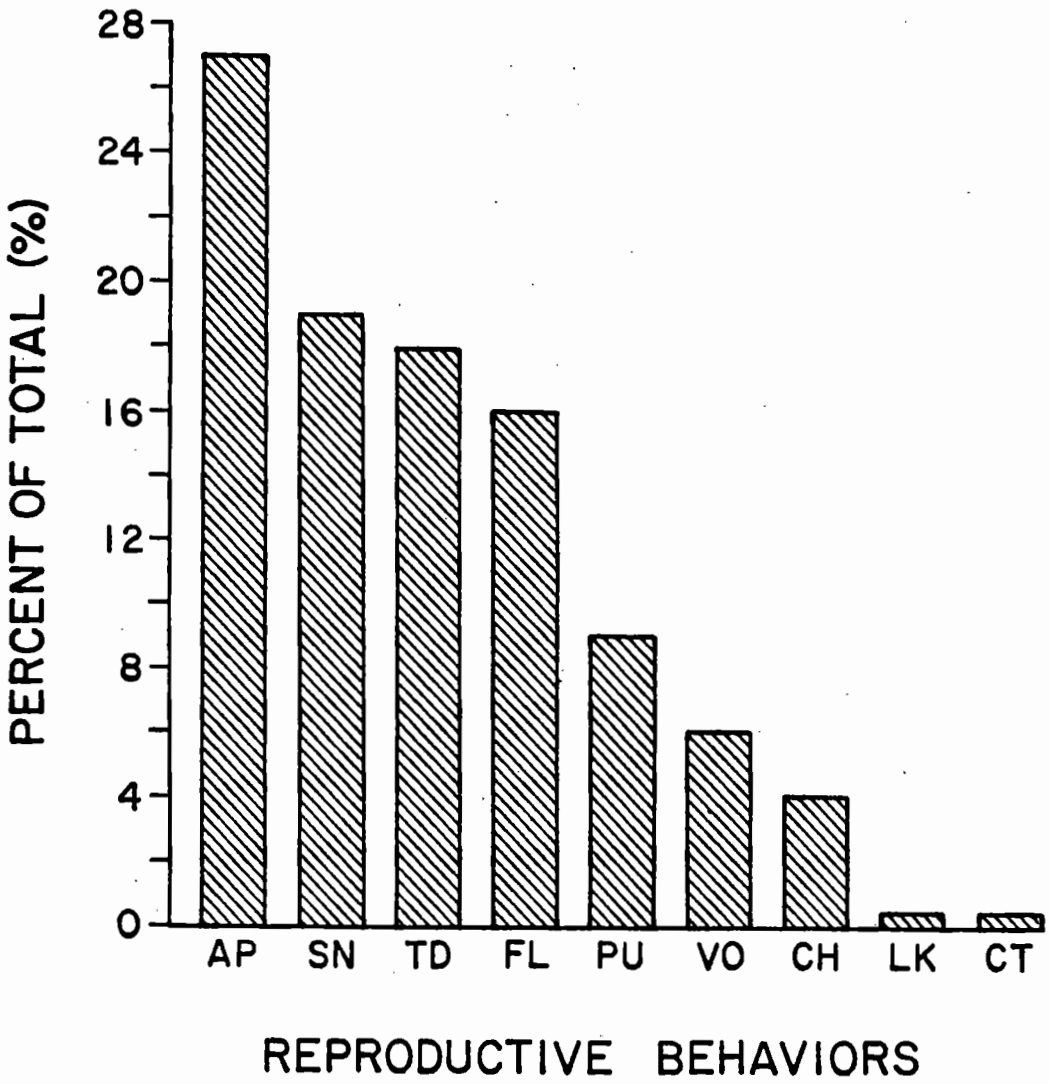

Figure 4. Histogram of 9 male reproductive behaviors observed during the 1985 rutting season. See Table 2 for behavior abbreviations.

are based on a total of 255 reproductive behaviors. Approach (27% of total), sniff (19% of total), and tend (18% of total) behaviors occurred most frequently, whereas lick and contact were observed infrequently (0.5% of total).

Reproductive behavior rates (Table 3) were highest for bucks #31 (3.37 behaviors/hr.) and #28 (3.17 behaviors/hr.) and lowest for bucks #13, #21, #22, #23 (0 behaviors/hr.) (Appendix A).

Antler Correlations With Aggression Rates, Reproductive Behavior Rates, And Dominance

In the antler point hierarchy bucks #19 (10 points) and #28 (9 points) were highest, and bucks #20, #22 (2 antler points) were lowest. For antler size, bucks #4, #5, #26, and #28 were at the top of the hierarchy (very large antlers), and bucks #20, #21, #22, #23, #24, #25, and #33 at the bottom (small antlers) (Table 3).

Even though the antler size and antler point hierarchies strongly correlated with each other, only the antler size hierarchy correlated significantly with aggressive behavior rates (Table 4). Hierarchies that correlated significantly with both antler point number and antler size were based on rates of reproductive behaviors and dominance rank (Table 4). However, non-significant correlations occurred between the sparring rate hierarchy and both antler point number and size hierarchies (Table 4).

Table 4. Spearman correlation matrix (r_s and r^2) for six hierarchies: Point Number (PN), Antler Size (AS), Aggressive Behaviors (AB), Sparring (SP), Reproductive Behaviors (RB), and Dominance (D).

	PN	AS	AB	SP	RB	D
PN	--					
AS	0.94/0.89[d]	--				
AB	0.33/0.11	0.41/0.17[b]	--			
SP	-0.20/0.04	-0.23/0.05	0.22/0.05	--		
RB	0.49/0.24[c]	0.49/0.24[c]	0.39/0.15[a]	-0.02/0.0004	--	
D	0.43/0.18[a]	0.53/0.28[c]	0.52/0.27[c]	-0.15/0.02	0.10/0.01	--

[a] $0.025 > P > 0.01$

[b] $0.01 > P > 0.005$

[c] $0.005 > P > 0.0005$

[d] $P << .0005$

Aggression And Dominance Correlations With Reproductive Behavior Rates

A significant correlation occurred between the aggressive behavior and dominance hierarchies but not between the dominance and sparring hierarchies (Table 4). Aggressive and reproductive behavior hierarchies were significantly correlated (Table 4). However, the reproductive behavior hierarchy did not significantly correlate with the sparring or dominance hierarchies (Table 4).

Even though there were eight hierarchy comparisons that were significantly correlated (Table 4), much variation remained unexplained as indicated by r^2 values. The exception was the comparison between antler point number and antler size, with only 11% of the variation not accounted for. For the other comparisons, 72% to 85% of the variation remained unexplained.

Female Choice

Female responses towards male approaches include: avoid (N = 91), tolerate (N = 38), urinate (N = 15), and aggression (N = 5) (Table 5). Females avoided males by either walking (N = 72), jumping (N = 3) or running away (N = 5). Females ran away from bucks in the 2 and 4 point antler classes most frequently (56% of total). Tolerate responses involved a female staying in the immediate vicinity of an approaching buck (N = 38). This behavior was observed during male tending (N = 10), contact

Table 5. Female responses towards male approaches.

Point #	2	4	5	6	7	8	9	10	
Avoid	7	22	5	4	16	30	6	1	N = 91
Tolerate	0	0	1	6	3	22	4	2	N = 38
Urinate	0	0	0	0	3	10	1	1	N = 15
Aggression	0	5	0	0	0	0	0	0	N = 5
# of bucks in each antler point class	1	6	1	5	5	13	1	1	N = 33

(N = 2), lick (N = 3), approach (N = 12), and sniff behaviors (N = 11). Only female urinate responses during tending were recorded. Bucks in the 8-10 antler point class were successful 33% of the time in eliciting a urination response. Females responded aggressively by chasing males (N = 3), kicking their front legs at them (N = 1) or placing their ears back (N = 1). all aggression was directed at four point yearlings.

Female responses to each antler point class could not be analyzed due to small frequencies. Bucks were therefore grouped into two classes: large-antlered bucks included those with 8 or more points and small antlered bucks had fewer than 8 points. Female avoid and tolerate responses to bucks in these classes were analyzed with a Chi-square test to determine if female responses were independent of the antler characteristics of bucks. This test showed that females tolerated large-antlered bucks and avoided small-antlered bucks more frequently than expected by chance (X^2 = 11.69, d.f. = 1, 0.010 > P > 0.005).

Female sniff (N = 22) and approach (N = 10) behaviors showing interest towards males (Table 6) were combined and similiarly analyzed with a Chi-square test. There was no evidence that females were interested in bucks with a particular antler size (X^2 = 2.5, d.f. = 1, n.s.).

On 14 November 1984, I observed a copulation, preceeded by six mounting attempts by an 8 point buck with the largest antlers and body size in the area. The rush-courtship strategy

Table 6. Female behaviors showing interest towards males.

Point #	2	4	5	6	7	8	9	10	
Approach	0	0	1	1	2	6	0	0	N = 10
Sniff	0	2	3	1	3	12	0	1	N = 22
# of bucks in each antler point class	1	6	1	5	5	13	1	1	N = 33

rather than tending was observed. Afterwards, this buck approached and sniffed two other females and performed a flehmen followed by an antler thrash.

Aggressive And Reproductive Patterns

Weekly sparring rates for 1984 and 1985 are shown in Figure 5. Although sparring data in 1984 were only collected through November 14, two sparring peaks occurred. Sparring rates peaked during the fourth (0.36 matches/hr.) and fifth weeks (0.27 matches/hr.) and were lowest (0 matches/hr.) during the first and seventh weeks. In 1985, sparring observations through December 28, showed that rates peaked during the fourth week (0.23 matches/hr.) and were lowest (0 matches/hr.) at various times before and after.

For the 1985 rutting season, weekly aggression rates (behaviors/hr. and sparring matches/hr.) and weekly reproductive behavior rates/hr. are shown in Figure 6. Aggression rates were highest during the fourth (0.14 behaviors/hr.) and tenth week (0.14 behaviors/hr.) and lowest (0 behaviors/hr.) during weeks 3, (0.19 behaviors/hr.), 11 (0.16 behaviors/hr.) and 13 (0.16 behaviors/hr.). Reproductive behaviors were not observed (0 behaviors/hr.) during weeks 12 and 14.

The relationship between daily aggressive and reproductive behavior rates and herd composition each observation day were tested by correlation analysis (Table 7). Correlations were

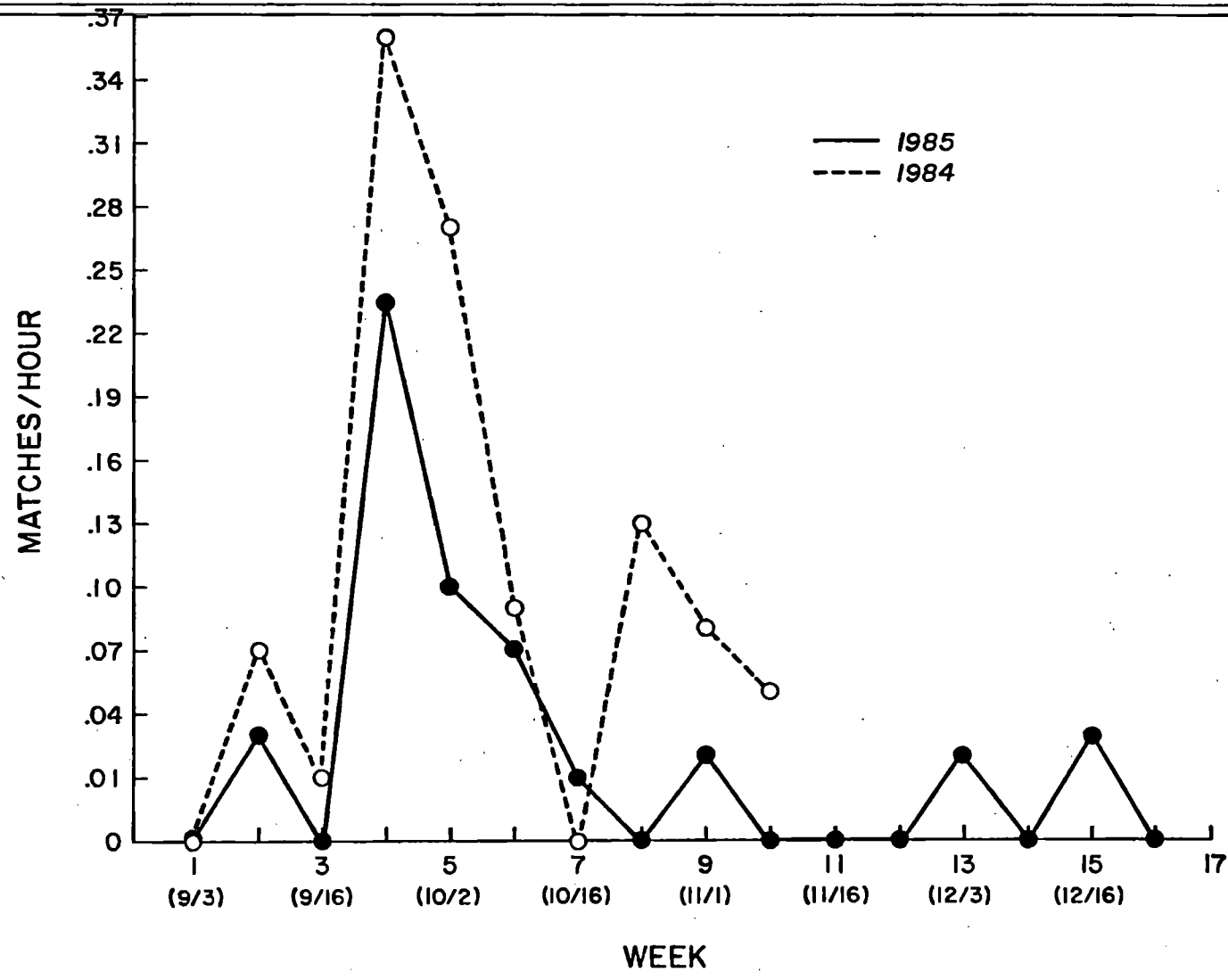

Figure 5. Number of sparring matches observed per hour of observation in 1984 and 1985.

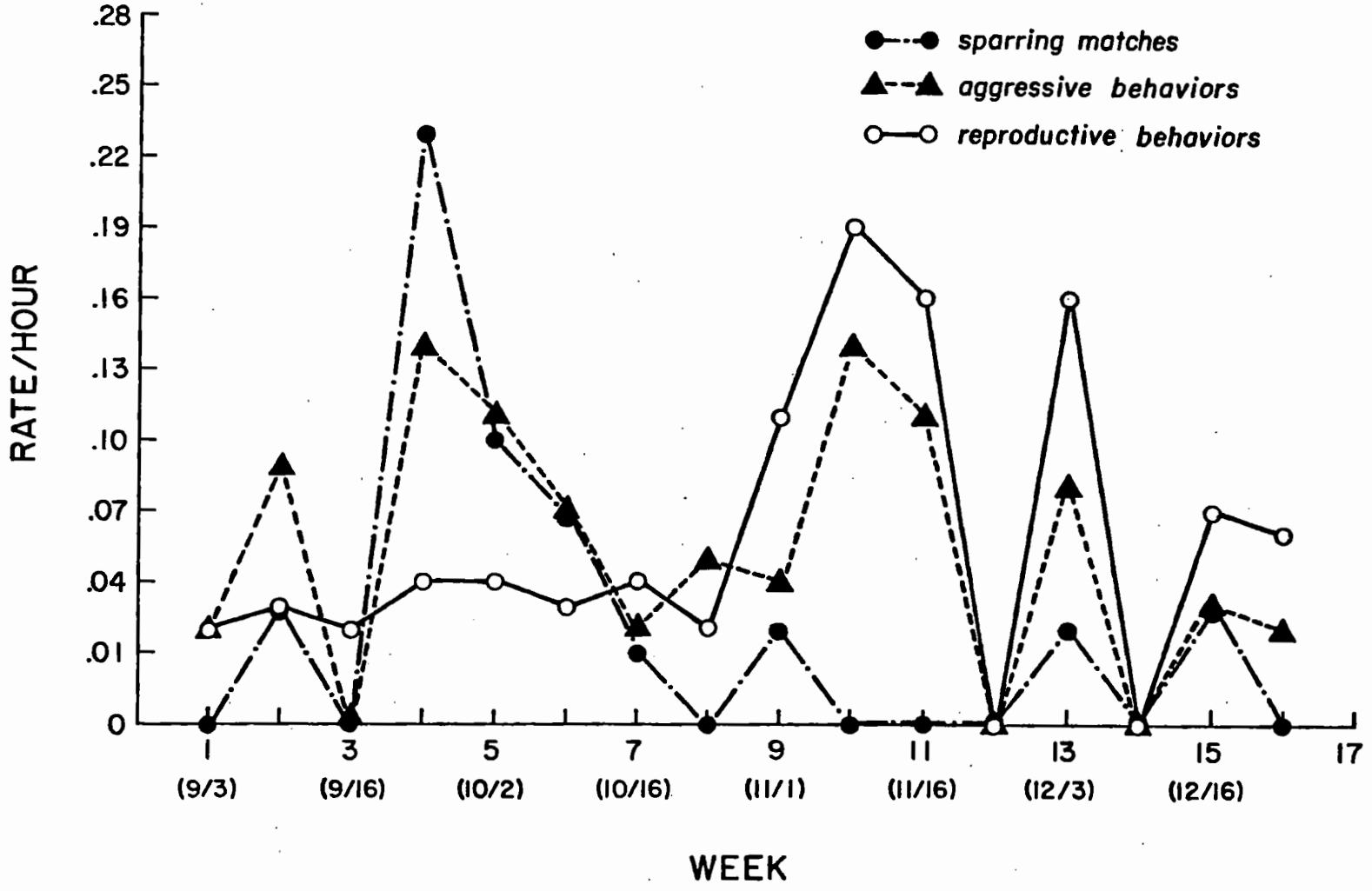

Figure 6. Number of sparring matches, aggressive behaviors, and reproductive behaviors observed per hour of observation during the 1985 rutting season.

Table 7. Correlation analysis of daily herd composition and rates of sparring, aggressive, and reproductive behaviors (N = 59).

	Males		Females		Total	
Sparring	r = 0.47	P = 0.0002	r = 0.36	P = 0.01	r = 0.39	P = 0.002
Aggressive Behavior	r = 0.25	P = 0.06	r = 0.21	P = 0.12	r = 0.19	P = 0.15
Reproductive Behavior	r = -0.12	P = 0.36	r = -0.11	P = 0.43	r = -0.12	P = 0.36

nonsignificant between daily aggression rates and daily reproductive behavior rates and the number of males, females, and total deer present. However, correlations were significant between sparring rates and the total number of males, females, and deer present.

CHAPTER IV

DISCUSSION

Recognition Of Bucks

Recognition of males permitted comparison of individual aggression, sparring, and reproductive rates in relation to antler point number and size. Hierarchies were constructed for the males by ranking individual performance rates for these behaviors. Analyses comparing the hierarchies indicated that in several cases they were not significantly correlated. These results suggest that researchers must be careful about generalizing the results obtained from studies based on only one kind of behavior hierarchy.

Aggressive Behaviors

In mule deer, certain aggressive behaviors such as antler thrash, rub-urinate and vocalizations may function to advertise social status as well as physiological condition to both males and females. Pheromones released during the antler thrash and rub-urinate revealed sex, age and individual differences when chemically analyzed by chromatography (Walther, 1984). In my study, these behaviors were performed by the most dominant bucks, confirming the findings of other investigators (Kucera,

1978; Geist, 1981).

Sparring may occur in order to initiate buck rutting condition (Dasman and Tabor, 1956), establish the dominance hierarchy prior to actual breeding (Dorrance, 1966; Linsdale and Tomich, 1953; Kucera, 1978; Koutnik, 1983; Wachtel et al., 1978; Hirth, 1977), distribute males to assure that dominant bucks breed first and most often (deVos et al., 1967), and provide experience for younger bucks (Koutnik, 1983; Kucera, 1978; Wachtel et al., 1978; Hirth, 1977). Because bucks with the largest antlers did not spar, this suggests that antler size rather than direct contact may provide useful information to others about individual strength.

Fights occurred infrequently and represented only 2.1% in 1984 and 2.5% in 1985 of all sparring matches recorded. This is similar to the findings of Wachtel et al. (1978) who reported that only 2.2% of all contests escalated into fighting. This is not surprising because fights can be damaging. In mule deer, Geist (1986) found that 15% of all bucks observed over two years had injuries resulting from fights.

The fact that most aggressive encounters were settled by aggressive behaviors (60% of total) rather than by sparring or fights, supports the suggestion by Maynard Smith and Parker (1976) that asymmetric cues may be used to settle contests before they escalate into fights. Settling conflicts with asymmetric cues, such as antler and body size, might therefore be an evolutionarily

stable strategy (ESS) resulting in higher reproductive fitness (Maynard Smith and Price, 1973).

Reproductive Behaviors

The purpose of some courtship or reproductive behaviors, such as tending is to stimulate females to urinate so that males can detect their reproductive status (Walther, 1984; Geist, 1981), to pursuade females to tolerate male approaches, and to synchronize the internal sexual state of both partners (Walther, 1984).

Approach and sniff male behaviors were recorded most frequently. Because copulations are difficult to observe (Kucera, 1978; Koutnik, 1978; Bowyer, 1986), tending, lick, and contact behavior frequencies may predict a male's reproductive success. A male strategy for maximizing his reproductive success may involve tending a group of females. This courtship strategy occurs infrequently; I observed it once during the 1984 rutting season, and it has also been observed by others (Robinette, 1977; Hirth, 1977).

Vocalizations may excite females during courtship (Geist, 1981) but, as in aggressive behaviors, may also advertise to females dominance status and/or physiological condition (Clutton-Brock et al., 1982). In this study, courtship vocalizations performed by bucks tending does were most frequently given by the three most dominant bucks (47% of total), thus supporting this notion. Copulation attempts by subordinate bucks (who performed

contact and lick behaviors) did not involve courtship vocalization. This may be a subordinate strategy to avoid the attention of, and possible displacement by, dominant bucks nearby.

It has been suggested that male dominance displays (such as antler thrash and rub-urinate) that are used in agonistic encounters are also performed by ungulate males during courtship in the same or modified form (Walther, 1984). During my study, I observed bucks perform the flehmen followed by antler thrash (N = 3) and rub-urinate (N = 3), thus suporting the above idea. Females may therefore prefer the same male traits that increase success in male-male competition.

Dominance Definitions

Cervid studies have used different criteria and methods for determining dominance. Dominance rank has been most frequently calculated by recording the outcomes of all agonistic encounters (including sparring) (Ozoga, 1972; Brown, 1974; Townsend and Baily, 1981; Miller, 1974; Kucera, 1978; Bowyer, 1986; Muller-Schwarze, 1972; Barrette and Vandal, 1985; Epsmark, 1964). However, Koutnik (1983) established a dominance hierarchy in mule deer by excluding antler threats and sparring. Others have counted the number of individuals beaten (Ozoga, 1972) and weighted their rank according to the ranks of their contestants by using fights (Clutton-Brock et al., 1979) or aggressive displays (Clutton-Brock et al., 1984) as the criteria for dominance.

In this study, the definition by Clutton-Brock et al. (1979) was greatly modified. Perhaps in this form it may not provide accurate information about mule deer dominance and the relationship to reproductive behavior rates.

The results obtained in this study clearly show that for the same population of bucks, hierarchies based on sparring and aggressive behavior rates do not significantly correlate. Thus, the definition of "dominance" is not always comparable from paper to paper. This may explain some of the contradictions found in the literature. Examples are discussed below.

Antler Correlations With Aggression, Reproductive Behavior Rates And Dominance

A significant correlation between antler size and aggressive behaviors suggest that bucks with the largest antler size have higher aggressive behavior rates than bucks with smaller racks. Older, more experienced bucks may be more efficient at associating asymmetric cues (antler and body size but not antler point number) with strength and/or fighting ability during agonistic interactions. At the same time, nonsignificant correlations between antler point number and size and sparring indicate that individual sparring rates may be somewhat independent of antler size. This may indicate that bucks spar either to gain experience (younger bucks) or reassess fighting ability (older bucks) that may change from one rutting season to the next. Bucks

in an antler class may be establishing position or attempting to raise rank.

Significant correlations of antler point number and size with reproductive behavior rates show that bucks with the largest antler size have higher reproductive behavior rates and suggest that they may have greater reproductive success. In the genus Odocoileus, the few copulations observed were all performed by bucks with the largest antlers (Kucera, 1978; Hirth, 1977; Bowyer, 1986; personal observation). Several other studies have also shown a correlation between antler (or horn) size and reproductive success (Clutton-Brock et al., 1979; Geist, 1971).

A significant correlation between antler size and the dominance hierarchy shows that large-antlered bucks are also most dominant, as defined by Clutton-Brock et al. (1979). It is likely that other definitions of dominance will not always result in rank correlations with antler size. Geist (1981) stated that dominance in mule deer could not be assessed by antler size, but my results suggest that perhaps it can. In a recent study of dominance in mule deer, defined as the number of aggressive encounters won, Bowyer (1986) also found a correlation with antler size.

Dominance also correlates with horn size in Bighorn sheep (Geist, 1971) and antler size in caribou (Rangifer tarandus caribou) (Barrette and Vandal, 1985). In red deer stags, antler size determines dominance hierarchy positions (Topinski, 1974;

Clutton-Brock et al., 1979), and loss of antlers reduces social rank (Lincoln, 1972). However, Appleby (1982) reported that dominance rank in red deer stags was not correlated with antler size but instead with body weight and age. In elk (C. canadensis) social status varies with antler size (Geist, 1982), which may in turn be used by older experienced bulls to estimate social rank (Bubenik, 1982).

In the present study, ages of bucks were not known and quantitative data on body size were not collected, so these variables were not correlated with antler point number and size. In general, antler point number and size is correlated with both age (Linsdale and Tomich, 1953; Anderson and Medin, 1969) and body size (Clutton-Brock et al., 1980; Bowyer, 1986; Anderson and Medin, 1969).

Aggression And Dominance Correlations With Reproductive Behavior Rates

The results of this study indicate that high rates of aggressive behavior, although not high sparring rates, may correlate with high dominance positions, high reproductive behavior performance rates, and thus, possibly higher reproductive success. However, dominance rank does not significantly correlate with reproductive behavior rates. Dominance, as previously pointed out, is here defined as the sum of both sparring and aggressive interactions in respect to the index used by Clutton-

Brock et al. (1979). Yearlings were excluded from the dominance hierarchy because their positions were inaccurate. For example, buck #33 (who only competed with other yearlings) had a dominance score of 2.0 (Appendix A) that placed him above buck #1, an eight-pointer in position 11. Other workers defining dominance differently may find significant correlations with reproductive behavior.

One reason for the great amount of unexplained variance occurring among the hierarchy comparisons may be the age and body size differences among individual bucks within the same antler point or antler size class. Other factors involving individual differences may also contribute to unexplained variance, but one can only speculate as to what they are.

Female Choice

For ungulates, there are few quantitative data showing that females prefer males with large antlers or horns (Clutton-Brock et al., 1982; Geist, 1971). Even though it has been suggested that females in the genus Odocoileus are allowed little choice (Michael, 1968; Linsdale and Tomich, 1953), my results suggest that females do prefer bucks with the largest antlers. Female avoid and tolerate responses towards male approaches provide supporting eveidence (Table 5).

Several studies have found that females usually avoid male approaches (Walther, 1984; Linsdale and Tomich, 1953)

whereas Geist's (1981) observations indicate some degree of female tolerance during tending. In my study, females tolerated bucks during other behaviors as well including contact, lick, approach, and sniff.

Another female response that may also indicate preference for certain males is urinating for a tending buck. Other workers have suggested that females may urinate to distract or avoid harassment from males, who stop to perform the flehmen (Geist, 1981; Hirth, 1977). In this study, the significance of females urinating in response to male courtship approaches is not clear. I suggest that the urination response is not used by females to avoid males (since they were not observed running off) but instead as an encouraging response towards bucks they preferred. Because bucks with the greatest number of antler points (8-10) were most successful in eliciting a urinating response, it strongly suggests that certain bucks may be preferred by females for mating.

All female aggression was directed towards 4 point yearling bucks. Aggression towards immature yearling males was also described by Linsdale and Tomich (1953). Females may either be protecting their fawns or may prefer not to mate with younger bucks.

To my knowledge, there are no other quantitative data available on females showing interest and encouragement towards certain males, even though sniffing of males by females (Linsdale

and Tomich, 1953; Geist, 1981) and females approaching bucks (Hirth, 1977) have been previously described. Females sniffed males when they walked by or when they were approached. Buck rump and forehead regions (both have pheromone glands) were frequently sniffed and may reveal important information about individual status.

The question as to why females may prefer a particular and/or dominant buck requires further discussion. Geist (1981) suggests a female may prefer dominant bucks in order to: 1) maximize her chances of producing equally competent sons, 2) minimize her offspring's chances of acquiring deleterious genes, and 3) acquire the male's physiological efficiency for her offspring.

Kodrik-Brown and Brown (1984) proposed a "truth in advertising" hypothesis stating that sexual selection favors costly phenotypic traits (such as antlers) that honestly advertise a male's genetic quality. Specifically, antler symmetry, size, and shape may advertise valuable genes for daughters and sons (Trivers, 1985). Therefore, by increasing the genetic fitness of her offspring, a female also increases her fitness. Although the genetic basis for female choice in deer has not been assessed, new findings in other animal studies suggest possibilities. For example, in a natural population of lady birds (Adalia bipunctata) a single dominant gene controlled female choice (Majerus et al., 1986).

Aggressive And Reproductive Patterns

Both Geist (1981) and Koutnik (1983) reported that seasonal sparring rates peaked both before and after breeding. This was not confirmed by my results. In 1984 sparring data were not collected past the beginning of November. In 1985 unusually cold weather may have accounted for the zero sparring rates recorded, as well as the absence of a second sparring peak. Even though further investigation is required, I suggest that both sparring peaks usually occur before breeding. It would be advantageous to establish or reestablish dominance positions by sparring before breeding, so that more energy would be available for reproduction.

When weekly reproductive behavior rates were at a peak (during week 10), aggressive behavior rates were low, and sparring was not observed. Even though aggression is neccessary to assert dominance during breeding, conflicts were settled without direct contact (sparring or fights).

Daily aggressive and reproductive behavior rates were independent of the herd composition, whereas sparring rates were highest when the greatest number of males, females, and total number of deer were present. Perhaps, large numbers of deer stimulated sparring behavior because the winners of sparring matches were noticed by many males and females, who then could assess male strength, associated antler size, and social status.

CHAPTER V

CONCLUSION

In a polygynous mating system, such as that of the mule deer, a male's reproductive success is dependent on the number of females with which he mates. Males compete with each other for access to females. This may favor large antler and body size, which are generally correlated with age. Antler size and number of points may honestly advertise genetic fitness and, as a result, may also be important in intersexual selection where females can chose the best male for breeding. Results suggest that antlers (point number and size) are the product of both intrasexual selection and intersexual selection and may have evolved to maximize both male and female reproductive success.

Antler point number and/or size may be used to predict the following information about individual status: aggressive behavior rates, reproductive behavior rates, dominance, and possibly female preference for particular bucks. Even though these correlations were significant, a great amount of variance was unaccounted for.

Antler size but not antler point number may predict individual aggressive behavior performance rates but neither predicts sparring rates. Specifically, bucks with the largest

antler size may use aggressive behaviors most often rather than sparring during agonistic encounters. This suggests that older bucks are more efficient than younger bucks at associating asymmetric cues (such as antler and body size) with fighting ability without resorting to physical contact. This greater ability by older bucks may be gained with age and/or experience.

Antler point number and size also predicts individual reproductive behavior rates. Larger antler size or point number may indicate potentially greater reproductive success. Older bucks tended females more frequently than younger bucks. Since this behavior best predicts imminent copulation, the results suggest that older bucks are able to obtain access to the greatest number of females for breeding. That younger bucks were not observed tending females may be due to a combination of low dominance position (established by agonistic encounters) and female choice.

Antler point number and antler size correlated with dominance whereas reproductive behavior rates did not. This may be the result of calculating dominance scores with a modified form of the index of Clutton-Brock et al. (1979) or of excluding yearlings from the hierarchy.

That females have mating preferences in mule deer may be supported by their tolerate response predominantly towards approaches by males with large antlers or number of antler points. This suggests that antlers may be used by females to assess male

dominance status and/or genetic quality.

Antler size along with other morphological and behaviorial traits probably advertise dominance status to both males and females. Further investigation of female mule deer responses towards particular males is necessary in order to verify the significance of antlers in intersexual selection.

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Appendix A. Dominance scores and behavior rates for 33 individual bucks: Dominance-aggressive behavior (D^a), Dominance-sparring (D^b), Dominance-aggressive behavior and sparring (D^{a+b}), Aggressive Behavior (AB), Sparring (SP), and Reproductive Behavior (RB).

I.D.#	D^a	D^b	D^{a+b}	AB	SP	RB
1	1.75	1.30	1.90	1.58	2.17	0.59
2	0.10	1.00	0.07	0.24	0.24	0.24
3	0.57	1.25	0.60	0.46	0.40	0.40
4	12.00	1.00	14.00	2.29	0	2.00
5	6.50	3.70	4.80	0.91	1.13	0.23
6	1.00	3.00	2.60	0.13	0	0.13
7	1.00	3.30	3.40	0.20	1.00	0.60
8	0.20	5.00	0.57	0.70	0.70	1.40
9	17.00	2.17	2.75	0.66	0.46	0.20
10	0.43	0.20	0.30	0.57	1.57	1.07
11	1.33	0.25	0.63	1.93	0.43	2.68
12	1.00	0.50	0.47	0.45	0.21	0.25
13	3.00	1.00	1.00	1.65	0	0
14	9.00	6.67	7.80	2.07	2.07	1.71
15	0.21	0.71	0.12	0.62	1.08	0.24
16	0.42	1.33	0.67	1.23	3.97	0.43
17	0.20	1.00	1.00	0	0	0.87
18	1.80	1.17	2.50	2.93	1.31	1.06
19	3.00	1.00	3.00	0.13	0.13	0.50

Appendix A. (continued)

I.D.#	D^a	D^b	D^{a+b}	AB	SP	RB
20	-	-	-	0.24	1.63	0.56
21	-	-	-	0.32	1.34	0
22	-	-	-	0	0.14	0
23	-	-	-	0.13	0.65	0
24	-	-	-	0.31	0.69	0.08
25	-	-	-	0	0	0.20
26	6.00	1.00	7.00	1.90	0	0.63
27	0	0	0	0.36	0	1.09
28	20.00	1.00	26.00	3.86	0	3.17
29	0.20	0.33	0.13	0.35	1.06	1.41
30	0.22	0.58	0.42	0.24	0.38	0.29
31	0.14	1.00	0.14	0	0	3.37
32	0.08	0.09	0.04	0	6.79	0.26
33	-	-	-	6.00	2.67	0.67