BEHAVIORAL DEVELOPMENT IN BIGHORN SHEEP: A COMPARISON OF

POPULATIONS INHABITING DESERT AND NORTHERN

ENVIRONMENTS

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ABSTRACT

The development of social behavior was studied in three natural populations of bighorn sheep. All populations exhibited the same behavioral repertoires, but the utilization of specific behaviors among both infants and adults differed between populations. It is suggested that differences in the adult utilization of behavior patterns results, in part, from behaviors used during infancy. In turn, the social and physical environments affect the development of subsequent behavior patterns in sheep older than lambs. Desert sheep (in southern California) used more mounting behavior than sheep from the other two populations (British Columbia and eastern Oregon), presumably because they matured sexually almost a year earlier. Sheep in the British Columbia population used different behavior patterns more frequently, perhaps as a consequence of interactions experienced in larger bands. Additionally, playful interactions were reduced due to physical hazards in the desert environment, but they were at least nine times as frequent in the British Columbia population.

Play in large groups resulted in the utilization of more different

kinds of behavior patterns. These behavioral findings are interpreted ecologically as consequences of inhabiting environments that differ socially and physically.

INTRODUCTION

Although social behavior is an important and central aspect of the biology of a species, it is not always ranked among the highest priorities for study by wildlife biologists. Nevertheless, it seems that, in order to comprehend better "why animals do what they do" or "occur where they do," an understanding of social behavior and even developmental aspects of behavior must be attempted. Furthermore, the dynamic nature of social systems should also be considered. Understanding the behavior of a species is equally as important as understanding its movements, foraging strategies, or patterns of reproduction when trying to gain insight into its "basic biology."

Few studies of ungulate ethology have contrasted behavioral development in natural allopatric populations that span large portions of a species geographical range. Such comparative studies under natural conditions are important in assessing the role of the environment upon behavior and also in understanding the evolution of social systems.

Bighorn sheep, Ovis canadensis, are ideally suited for a comparative study of behavioral development because they present a number of biologically interesting problems. For instance, parturition is asynchronous in desert populations and lambs may be born at any time of the year (Hansen, 1965; Simmons, 1969), whereas in northern or mountain populations the parturition season is more synchronous (Geist, 1971). Also, group sizes

are considerably smaller in the desert than they are in more northern and resource productive habitats (see Simmons, 1969; Leslie, 1977; Hoeffs, 1975).

Given these differences in environmental conditions, I was interested in exploring the following questions: (1) How does social behavior develop? (2) What environmental (social and/or physical) factors influence social ontogeny?, and (3) What is the adaptive significance for the differences?

METHODS

Study Populations California bighorn sheep, O.c. californiana, were studied in the Chilcotin-Cariboo region of the central interior of British Columbia from May through November, 1976. A second population of California big-horns was studied on Hart Mountain, in the Great Basin Desert of eastern Oregon from May to August, 1977. These sheep were transplanted from the

Chilcotin to Hart Mountain in 1954, and, at the time of the transplant, numbered 18. Currently the population size in the transplanted population is about 200. Sheep in this region became extinct around the turn of the century. The last study population was located in the Santa Rosa Mountains in the Colorado Desert of California. These sheep are commonly called desert or peninsular bighorn, O.c. cremnobates. The sheep population in these arid, insular mountains is estimated at 250 (Merrit, 1974). They were studied from January through April, 1977. Further details of the habitats, climate, and study populations are found in Berger (1978).

Data Collection. Data on sheep behaviors were collected by stalking and observing sheep in the field on almost a daily basis. I observed sheep in the Chilcotin for 896 hours, those at Hart Mountain for 293 hours, and those in the desert for 454 hours. Behaviors and social interactions (see ethogram) were recorded into a cassette tape deck and later transcribed, or they were taken directly onto note cards.

Male and female sheep may be sexed visually on the basis of horn and body size differences (Geist, 1968, 1971). However, at a young age when no dimorphism occurs, lambs may be sexed by one of three methods: (1) Male lambs urinate from a standing position while females squat. This method of sexual determination was used most frequently as other methods were not always as accurate. (2) Testes may be visible in males. However, if testes are not visible, it does not necessarily preclude the possibility that a lamb is not a male. (3) Once horns develop, male horns usually grow at a faster rate than females, and they are thicker and flare more widely. Since observation of lambs was often at a considerable distance and accurate determination of sexes was not always possible, the data

presented in this paper represent those situations in which I was certain of sexual identities.

Analyses. All statistical analyses of the differences between percentages (probabilities) were performed using the Brandt and Snedecor method when there were two or more samples (see Snedecor, 1956; section 9.9) and the arcsin transformation method for testing the equality of two percentages (suggested by Sokal and Rohlf, 1969: 607). This latter method generates a test statistic, t_g, which may then be compared with a normal deviate (area under the normal curve).

Ethogram. For bighorn sheep, 17 behavior patterns have been categorized and described by Geist (1971:134-143). This ethogram may be enlarged to include at least six more behaviors. Below, I list and describe the behaviors that I quantified.

SEXUAL PATTERNS

1. Mount. see Geist (1971). Mounting is the only overtly sexual pattern used by sheep.

CONTACT PATTERNS

2. Head butt. see Geist (1971).

3. Clash. see Geist (1971).

4. Touch. Two sheep that lower their heads and place them in contact with another. No pushing occurs and their heads remain in contact for at least one second.

5. Push opponent. Two or more sheep that push with their heads, their rumps, or sides, of other sheep.

THREAT PATTERNS

6. Threat jump. "This is an intention movement to clash" (Geist, 1971:143). Threat jumps are often sufficient to discourage an opponent from fighting and no further contact ensues.

7. Horn threat. "...this is an intention movement to butt and as such is a true weapon threat" (Geist, 1971: 142-143). Sheep lower their heads in a position so that they may be in a position to butt an opponent.

8. Head threat. Young sheep that have not yet developed their horns will lower and orient their heads in the same way as when horn threats are performed.

    The above three patterns are indeed threats as Geist (1971) correctly pointed out, because: (i) when dominant individuals threaten subordinates, they retreat and little or no contact occurs; and (ii) when threats are insufficient to discourage the approach(es) of other sheep, contact patterns follow.

DISPLAY PATTERNS

9. Low stretch. see Geist (1971). A display of horns performed by lowering the head.

10. Twist. see Geist (1971). A display of horns performed by lowering and twisting one's head.

11. Present. see Geist(1971) A horn display performed by raising one's head and lifting the horns.

12. Front leg kick. see Geist (1971). "...is linked to the display threats of sheep, such as the low stretch, present, and twist; it is virtually a contact display threat" (Geist, 1971:139). Since front leg kicks are not a contact pattern such as butting, and probably serve to convey information about body size (as do horn displays for horn size (Geist, 1968), I have categorized front leg kicks as a display pattern.

    Walther (1974) recognized that threat and dominance displays in horned ungulates may often be similar but argues that they merit distinction because basic differences also exist. For example, in bighorn sheep, threats indicate readiness for fighting by directly utilizing ones horns and placing them in a position for contact. In contrast, displays are not actively conveying a threat (although a subordinate individual may feel threatened by the presence of a dominant sheep) and displaying individuals are not oriented in a fighting position.

ROTATIONAL PATTERNS

13. Neck twist. This pattern is more exaggerated than a head shake (Geist, 1971) and it is often used in playful interactions. Neck twists are common to lambs, yearlings, and rams.

14. Gambol. Gambols entail jumping with all 4 legs off of the ground in a somewhat vertical direction. The body axis is rotated and twisted in midair. Both ewes and lambs have gamboled so high that they fell

over backwards. The oldest ram observed gamboling was about 6 years old.

15. Heel kick. Heel kicks entail jumping off of the ground and simultaneously kicking both rear legs or heels. Byers (1977) described an apparently identical motor act in ibex kids.

All of the above mentioned behavior patterns, except displays, occur during play. Rotational movements function as play signals (Berger, 1978).

RESULTS

Sex and Age Differences in Behavioral Development. Males generally used more threat, contact, sexual, and display patterns than did females (Figure 1). There were no significant differences (arcsin proportions test) in the per cent utilization of patterns used by male and female lambs. These data indicated a trend in which male lambs were more likely to engage in all patterns other than rotational movements (see discussion) than female lambs. Displays were infrequently observed in females of all ages and for males they developed only after two months of age (Figure 1).

Behavioral Development in Different Environments. The week (age) of first appearance of different motor patterns in lambs is given in Table 1. Generally, behaviors appeared at similar ages in all populations, except that two display patterns occurred about three months earlier in desert sheep than they did in Chilcotin sheep. The most probable reason displays were not observed in some populations was because I departed from those study sites before lambs developed those patterns of behavior (i.e., they were too young).

The relative frequencies of behavior patterns observed in this study are shown for lambs in Figure 2; for yearlings, ewes, and Class I rams in Figure 3. Desert lambs engaged in significantly more contact and sexual patterns than did Chilcotin lambs (see Table 2 for a summary of statistical

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Table 1. Age of appearance of different motor actions in lambs. A minimum of 5 observations of a specific pattern was necessary. NO= not observed in lambs

LOCALITY

PATTERN OF BEHAVIOR	MOTOR ACT	desert	transplant	Chilcotin
CONTACT	head butt	———one week———	"	"
	clash	"	"	"
	touch	"	"	"
	push opponent	"	"	"
THREAT	head threat	———one week———	"	"
	threat jump	"	"	"
ROTATIONAL	neck twist	———two weeks———	"	"
	gambol	———one week———	"	"
	heel kick	"	"	"
SEXUAL	mount	———one week———	"	"
DISPLAY	low stretch	3 months	NO	6 months
	front leg kick	2½ months	NO	6 months
	twist	NO	NO	7 months
	present	NO	NO	NO

Table 2. Summary of tests of equality of two percentages for relative frequencies of behavior patterns observed in lambs, yearlings, ewes, and Class I rams. DES = desert; TRANS = transplant; CHIL = Chilcotin. * = p<.05; ** = p<.01; *** = p<.001; numbers = t_s (test statistic - see statistical analyses). NS = no significance (see also Figs. 2,3).

		CONTACT	THREAT	ROTATIONAL	SEXUAL	DISPLAY
LAMBS	DES vs CHIL	*** 4.48	** 3.13	*** 4.75	*** 5.62	—
	DES vs TRANS	NS 1.27	*** 3.68	*** 5.42	NS .86	—
	CHIL vs TRANS	*** 4.90	NS .93	*** 5.80	*** 4.76	—
YEARLINGS females	DES vs CHIL	* 2.19	*** 6.72	*** 4.90	—	—
	DES vs TRANS	NS 1.80	* 2.31	NS 1.75	—	—
	CHIL vs TRANS	* 2.08	** 2.61	*** 5.61	—	—
YEARLINGS males	DES vs CHIL	NS .48	*** 5.07	NS .36	NS 1.08	** 2.72
	DES vs TRANS	* 2.20	** 2.96	NS 1.44	* 1.90	NS .96
	CHIL vs TRANS	* 2.29	*** 3.90	NS 1.68	* 2.16	NS 1.74
EWES	DES vs CHIL	*** 6.00	* 2.49	*** 6.31	—	NS 1.68
	DES vs TRANS	NS .86	** 2.91	* 2.29	—	* 1.90
	CHIL vs TRANS	*** 6.19	* 2.02	** 3.14	—	* 1.85
CLASS I RAMS	DES vs CHIL	** 2.95	* 2.27	NS .38	*** 4.70	*** 5.76
	DES vs TRANS	*** 3.39	NS .49	NS .79	NS .77	*** 5.43
	CHIL vs TRANS	** 3.26	NS 1.08	NS .60	** 3.10	NS 1.23

CLASS I RAMS + MALE YEARLINGS

	SEXUAL
DES vs CHIL	*** 4.72
DES vs TRANS	** 3.12
CHIL vs TRANS	NS 1.73
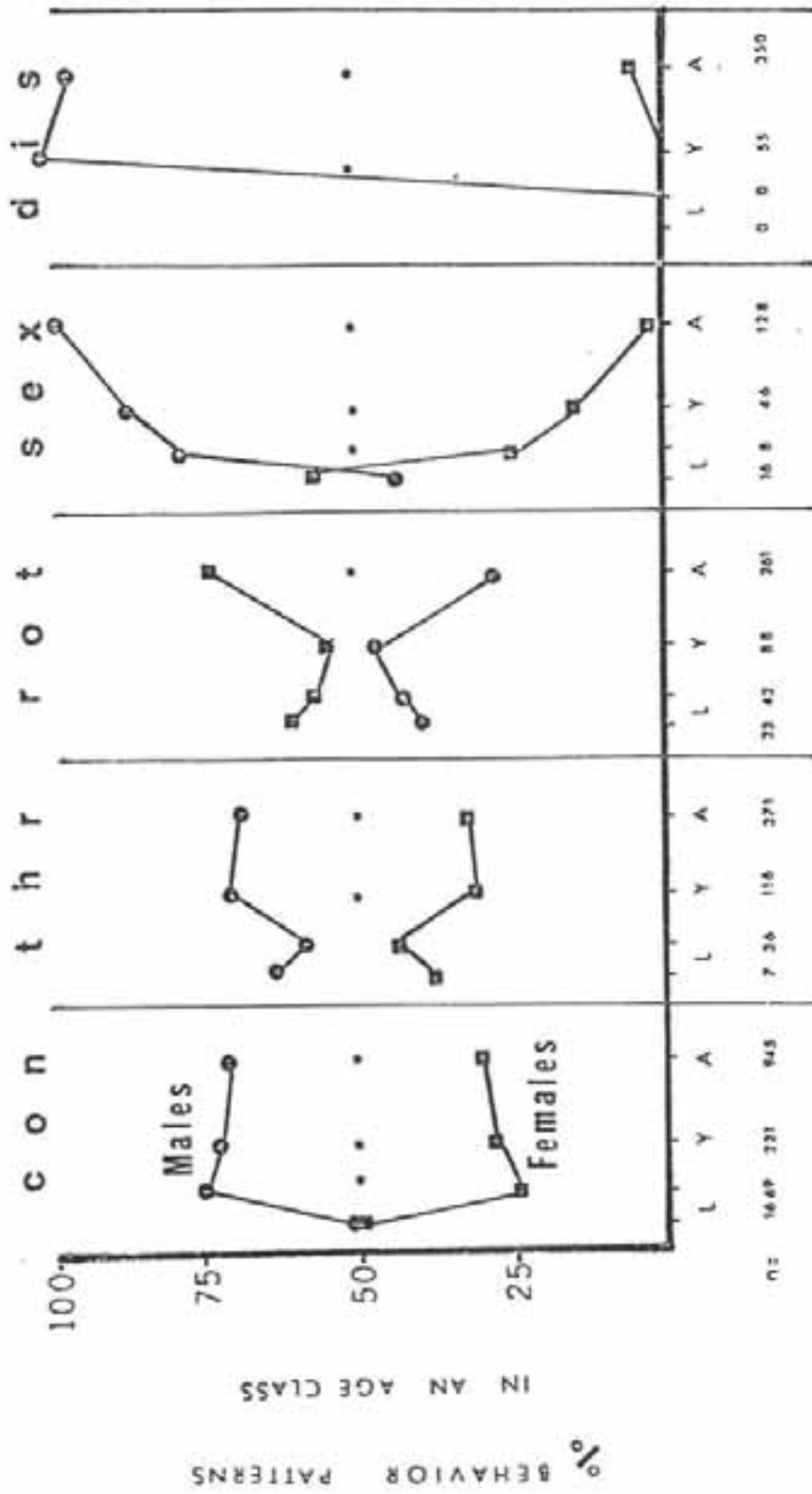
FIGURE 1. Sex and age differences in the development of behavior patterns in bighorn sheep. CON = contact patterns; THR = threat; ROT = rotational; SEX = sexual; DIS = display. L = lambs (two data points are shown for lambs; those occuring before two months of age and those after this age). Y = yearlings; A = adults (ewes and Class 1 rams). Asterisks indicate stratified significance at the p 0.05 level (aresin transformation - see statistical analyses).

analyses for Figures 2 and 3). Conversely, lambs from the Chilcotin utilized significantly more rotational and threat patterns.

Generally, threat, contact, and sexual patterns occurred more frequently in desert yearlings, ewes, and Class I rams than they did in Chilcotin Sheep. More specifically, the major significant ($p < 0.05$) differences for male sheep may be summarized as follows:

(1) desert males (=yearlings + Class I rams) mounted more often than Chilcotin equivalents.

(2) desert males (as above) engaged in more threat and contact patterns than did Chilcotin equivalents:

(3) Chilcotin males (as above) used more display patterns than did their desert equivalents.

For females, the major significant differences ($p < 0.05$) may be summarized as follows:

(1) Chilcotin females (=yearlings + ewes) used more rotational patterns than did desert females;

(2) desert females (as above) utilized more threat and contact patterns than did Chilcotin females. Also, in all populations, females utilized more rotational and less sexual and display patterns than males (Figures 1, 2, and 3).

Behavioral Diversity. Various sized groups engaged in play (see Berger, 1978 for a categorization of play). This activity was characterized by the utilization of motor patterns from different contexts (e.g., headbutting, mounting, chasing, jumping, etc.). In addition to those patterns listed in the ethogram, rubbing and nuzzling (see Geist, 1971) occurred during play. Sequences of play began when three or more individuals engaged in some form of exaggerated locomotor-rotational or contact activity, and it

FIGURE 2.   Histogram illustrating the per cent relative frequency of behavior
patterns used by three populations of bighorn lambs. For any given
population, per cent relative frequency equals the total number of
motor acts per behavioral pattern divided by the total number of
motor acts for all behavioral patterns. D = desert population (n=572);
T = transplant population (n=572); C = Chilcotin population (n=1,144).
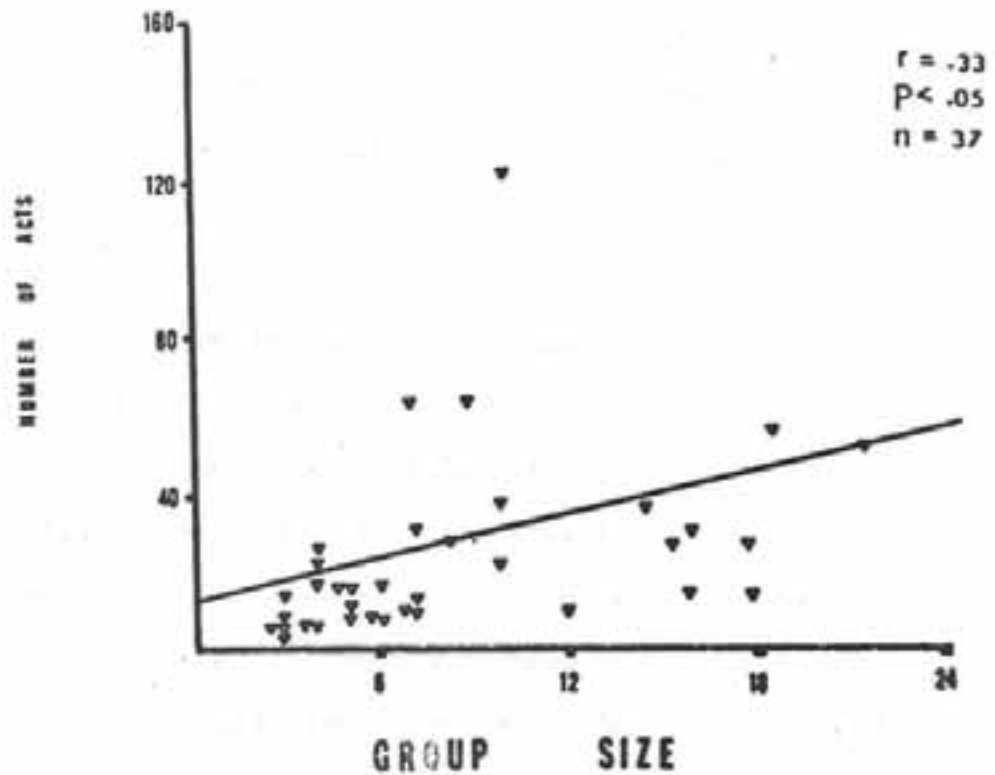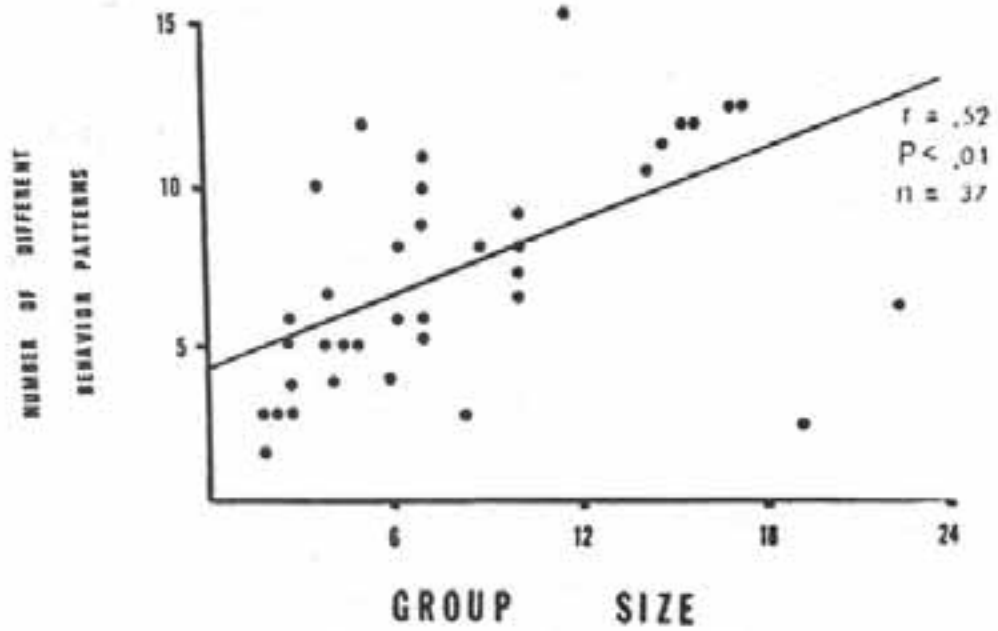
NUMBER OF DIFFERENT BEHAVIOR PATTERNS

r = .52
P< .01
n = 37

GROUP   SIZE

NUMBER OF ACTS

r = .33
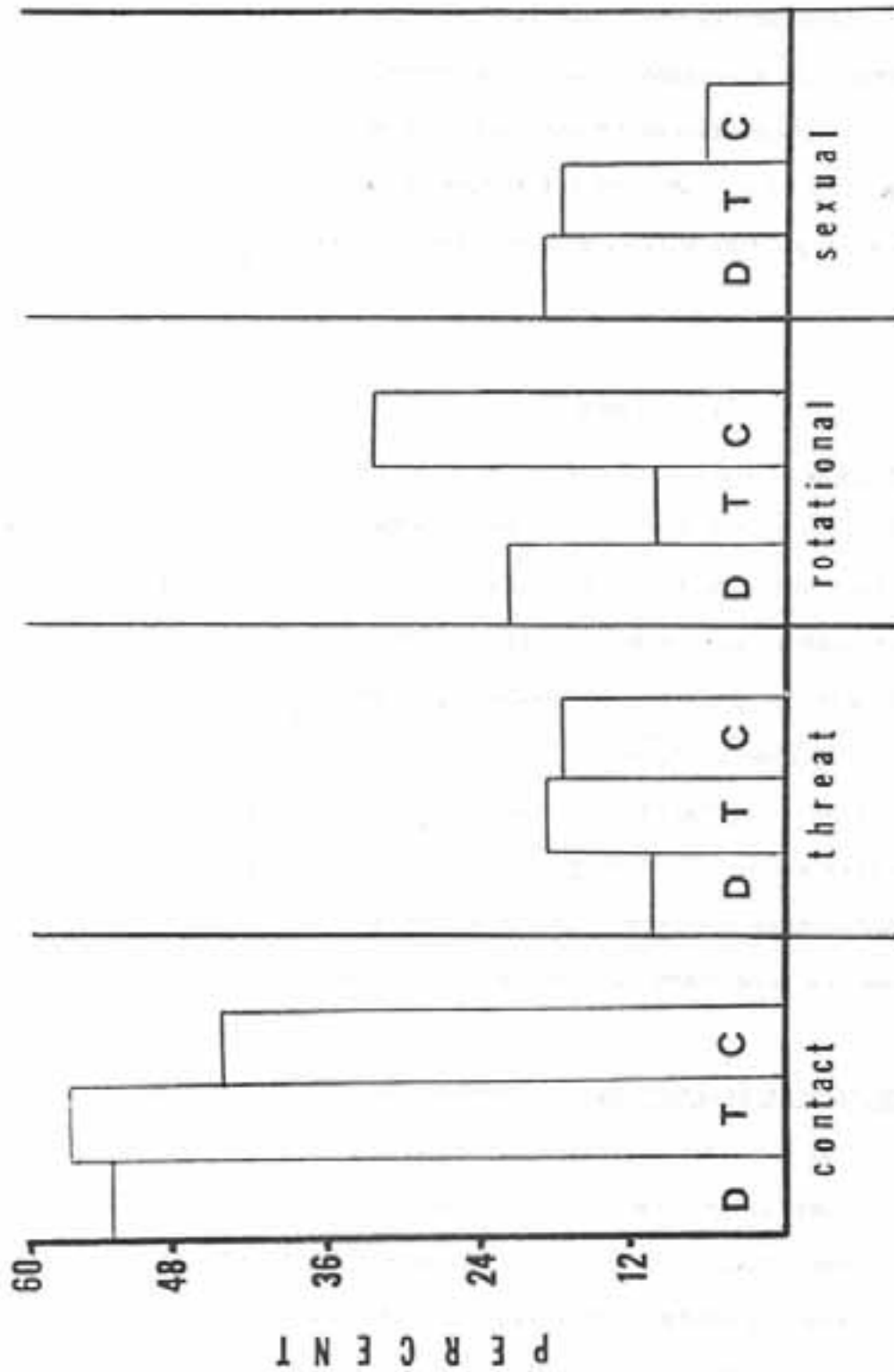P< .05
n = 37

GROUP   SIZE

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FIGURE 3. Histogram illustrating the per cent relative frequency of behavior patterns used by various sex and age classes of three populations of bighorn sheep. Within any given population, the per cent relative frequency of occurrence of a behavior and for a particular sex or age class is calculated in the same manner as it is in figure 2. Rams equal Class 1 rams only. D = desert (n=1,120); T = transplant (n=465); C = Chilcotin (n=1,026).

terminated when less than three individuals persisted in these actions. During play, a direct relationship was found (r=0.52; p<0.01; n=37) between group size and the number of different behavior patterns that occurred in lambs (Figure 4). Also, a significant correlation (r=0.33; p<0.05; n=37) existed between the number of players and the number of acts within a sequence. That is, the more players within a group, the greater the number of acts that occurred.

DISCUSSION

Development of Motor Acts. Male and female lambs showed no significant differences in the frequency of motor pattern development probably as a result of small sample sizes (due to the difficulty in correctly identifying lamb sexes). Males tended to use more contact, threat, and sexual patterns than did females. Studies of primates (Baldwin and Baldwin, 1971; Kummer, 1971; LeResche, 1976), ungulates (Sachs, 1976; Byers, 1977), and rodents (Poole and Fish, 1976) also indicated that sexual dimorphism exists at early ages. In American sheep, Blood et al., (1970) and Bunnell and Olsen (1976) showed that males gain weight more rapidly than females. My data illustrate that behavioral dimorphism coincides with differences in growth rates.

Social Ontogeny in Different Environments. Geist (1971) stated that bighorn lambs are capable of butting, clashing, threat jumping, and mounting soon after birth. In each of my three study populations, one-week old lambs displayed these patterns. Population differences did, however, exist in the development of display patterns by males. Desert male lambs used the low stretch and front leg kick at a younger age (about 3 months) than
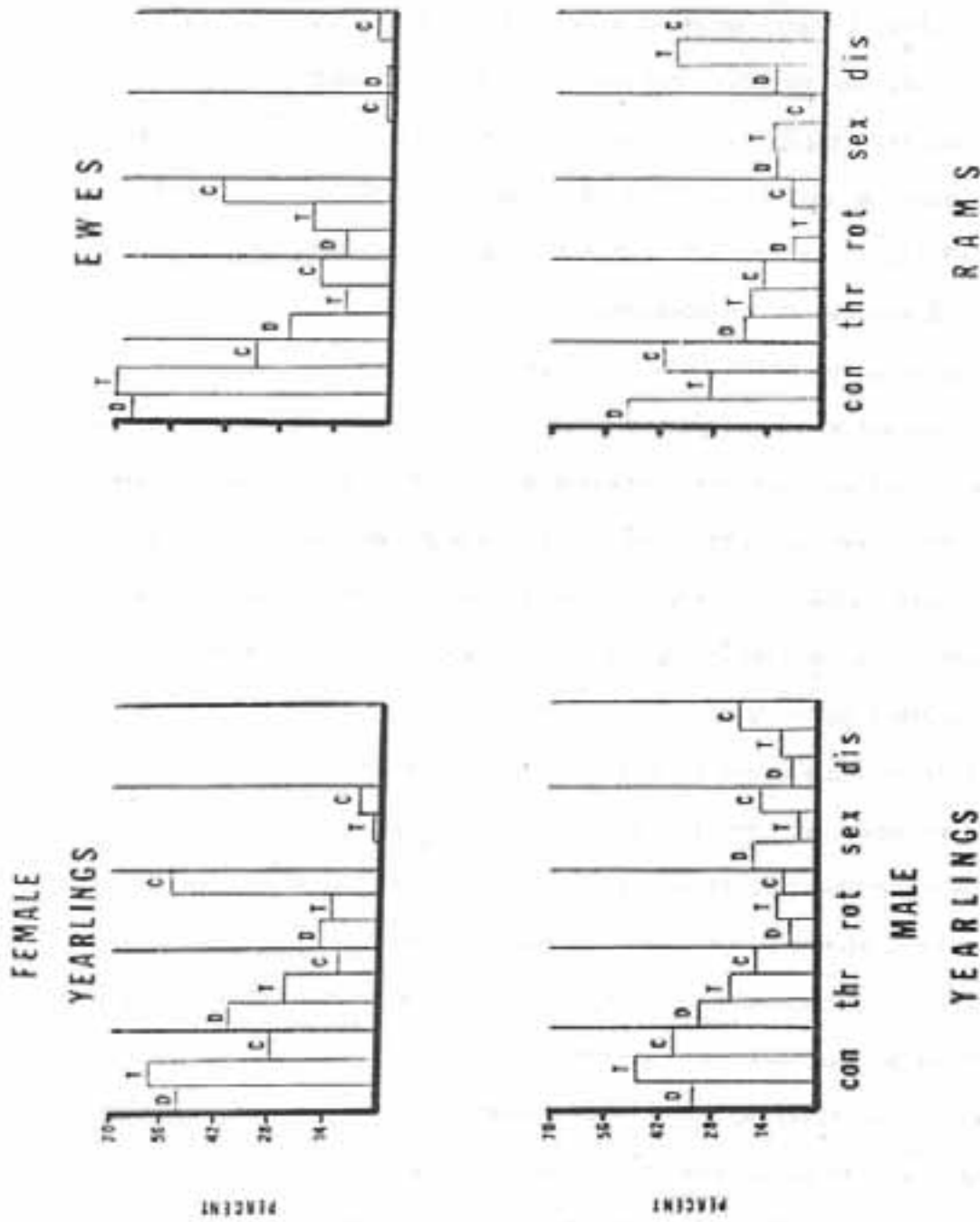
FIGURE 4. The relationship between group size and the number of different behavior patterns that occurred during lamb play sequences; and the same relationships but for motor acts within a sequence.

did Chilcotin male lambs. Other than display patterns, behavioral ontogenies followed a similar time course for populations in all environments. However, the frequency of utilization of behavior patterns was very different between environments (Figures 2 and 3). Desert lambs and desert males (= male yearlings + Class I rams) mounted more often than did their peers in the Chilcotin. Also, desert lambs and older sheep (yearlings, ewes, and Class I rams) used less rotational movements than Chilcotin sheep. Since desert sheep engaged in less social and locomotor play than did Chilcotin sheep (Berger, 1978), it is not surprising that these movements occurred less frequently in the desert population.

Two more important population differences existed. First, desert lambs used more contact patterns than Chilcotin lambs, yet the former threatened less often. Contact patterns represented more than 50% of the patterns used by desert lambs. 'Apparently desert lambs were behaviorally less diverse than Chilcotin lambs. In other words, desert lambs had the same behavioral repertoires as Chilcotin lambs, but individuals in the desert were less likely to perform as many different patterns. Second, desert yearlings (of both sexes), ewes, and Class I rams used more contact patterns than Chilcotin sheep of equal sex and age classes. (In contrast, Chilcotin lambs threatened more than desert lambs.) Also, desert sheep larger than lambs displayed less often than their Chilcotin equivalents.

In sum, then, lambs as well as older sheep from all three environments were characterized by the same behavioral repertoires, but desert sheep were behaviorally less diverse. They used fewer different patterns but in greater frequencies than Chilcotin sheep which used all their patterns but not as frequently. For instance, desert males used threat and contact

patterns whereas Chilcotin males utilized threat and contact patterns less often but displayed more frequently (Figures 2 and 3). Hence, between environments, there was an inverse relationship between the frequency of occurrence of threats and displays.

Behavioral Development and Diversity. Several questions may now be asked regarding these population differences in social development: (1) Why was sexual behavior more prominent in desert lambs and older males? (2) What factors caused behavioral diversity to be greater in the Chilcotin? (3) Why did desert sheep play less? (4) What benefits may be accrued by more behaviorally diverse individuals?

Desert sheep grow faster and mature sexually (at about 1½ years of age) approximately one year earlier than sheep from northern environments. These regional differences appear to be genetically mediated (Berger, 1978). Since natural selection has most likely favored early puberty in desert sheep, it is not surprising that more mounting occurs at earlier ages in desert sheep than it does in northern or mountain populations. Data are not yet available on hormone levels of different aged desert sheep, but it may be possible that desert males possess higher androgen levels which may, in turn, lead to more mounting. Turner (in prep) found that desert males are born more precocial than mountain lambs and, in the former, teste descension occurs at about 2-3 weeks of age. In mountain lambs, testes descend at about 3 months.

Although Chilcotin sheep matured sexually at a later age than sheep in the Santa Rosa Mountains, they played more. Geist (1971), Shackleton(1973), and Horejsi (1976) found that more playful lambs occurred in high-quality sheep populations which were characterized by well fed, fast growing, and

early maturing (defined by these authors as independence) individuals as opposed to the opposite characteristics in low-quality populations. Berger (1978) provided data that suggested sheep from the Santa Rosa Mountains were better nourished than those from the Chilcotin. Why, then, did desert sheep play less than Chilcotin sheep, thus contradicting Geist's predictions of population quality?

Berger (1978) suggested that play occurred less often in the Santa Rosa study population due to lack of suitable "playgrounds," hazards of the physical environment, and a less complex social environment (e.g., group size). Furthermore, it was suggested that greater food dispersion in the desert resulted in smaller and more widely dispersed foraging bands. Consequently, lambs spent more time alone (time not with peers or adults) and were independent at an earlier age than were transplant or Chilcotin lambs.

The social environment (group size), not surprisingly, may indeed be an important variable in the development of social patterns of behavior. Figure 4 showed that, when lambs played in larger groups, more different behavior patterns occurred than when play resulted from interactions in smaller groups. Even if the number of distinctly different behavior patterns observed was a function of more individuals available for observation, the fact remains that yearlings, ewes, and Class I rams from the Chilcotin still utilized greater behavioral repertoires than did their conspecifics from environments with smaller average group sizes (Berger, 1978). Also, more acts per sequence were incorporated into play when groups were large (Figure 4).

Since group sizes in the desert are small (Berger, 1978; Simmons, 1969) and lambs may be born at any time of the year (Hansen, 1965), those individuals born in a desert environment may not be exposed to nearly as complex

a social environment as those born in mountain or northern habitats (where group sizes are larger and parturition is more synchronized). Baldwin and Baldwin (1971, 1977) found that squirrel monkeys (saimiri) in large groups played more extensively than those in small groups. A similar situation has been observed in gibbons (hylobates); little play occurred in infants presumably due to small group sizes and individual differences in body size and strength (Ellefson, 1967). Other field and laboratory studies of primates have confirmed the idea that individuals raised in enriched social environments tend to be behaviorally less retarded than those reared in socially impoverished environments (see Hinde and Spencer-Booth, 1967; Hinde, 1974; Mason, 1961a, b; 1962). The social environment, as has been amply demonstrated, plays a large role in infant behavioral development.

In desert environments, bighorn sheep lambs are not only faced with few peers but also those of differing sizes and ages. Contact play occurred infrequently between lambs of different ages and body sizes (Berger, 1978). In Death Valley, California, probably the most arid environment inhabited by sheep in North America, Welles and Welles (1961) reported small group sizes and no nursery bands. Social play may be very infrequent in such an extreme environment.

Interpretations of Demic Differences in Behavioral Ontogenies. I interpret demic differences in behavioral ontogenies in terms of ecological factors rather than genetic differences. It appears that desert sheep were behaviorally less diverse than other sheep populations due to a number of factors that included small group size, less social facilitation, and less play. These last factors most likely were a result of a precarious physical environment, while the first factor was due to the distribution of food resources. The difference in sexual behavior between my northern and south-

ern study populations is probably a result of selection pressures for early sexual maturation in the desert environment.

In contrast to desert sheep, those in the Chilcotin used the full range of their behavioral repertoires. There are several factors that may be responsible for the increased behavioral diversity in these sheep. First, they matured sexually about a year later than those from the Santa Rosa Mountains (Berger, 1978). In many mammals, prolonged sexual maturity allows for greater learning and social experience(s) (Hinde, 1974; Wilson, 1975). Second, large groups (above a minimum size) provide more complex social environments (Anderson and Mason, 1974; Goy and Goldfoot, 1973). Third, Chilcotin sheep inhabited physical and social environments that were more conducive for play. Although, to my knowledge, it has never been demonstrated experimentally that additional play leads to the increased utilization of different motor actions, play nevertheless most probably allows individuals to refine motor skills (Rasa, 1973; Eisenberg and Le-hausen, 1972; see also Bekoff, 1976; Fagen, 1976).

One might expect natural selection to favor those individuals inhabiting complex social environments (e.g., larger groups) to develop more sophisticated communication systems (i.e., visual, vocal, etc.) in order to signal more efficiently. Marler (1975, 1976) found that primates inhabiting larger and more constant groups possessed more graded signals. For Chilcotin sheep, too, it would also appear to be adaptive for individuals to communicate by utilizing as many behaviors as possible. The four display patterns, for which I provided data, are distinctly different from one another, and, although gradations do occur for each pattern, the patterns do not grade into one another (except for the low approach and twist; see Geist, 1971). Certainly, selection will favor those individuals that

are more adept at communicating regardless of group size. But, in large groups, individuals who can communicate an intended message with the most precision will experience less ambiguity in reception.

In summary, the differences in behavioral ontogenies in different environments are illustrative of "open behavioral programs" (see Mayr, 1974). Adaptation and function must be scrutinized most carefully before being attributed to biological phenomena (Hinde, 1975; Tinbergen, 1965; Williams, 1966). It thus appears that, although bighorn sheep subspecies possess a species typical behavioral repertoire (Geist, 1974), environmental conditions influence greatly and modify the time course(s) that social development follows. Furthermore, this study illustrates (as has been pointed out clearly by Wilson, 1975) that behavior is indeed labile and varies in different ecological settings. Before generalizations about the nature of species specific social development are valid, different populations under contrasting ecological conditions must be studied.

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