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Sex Differences in the Play Behavior of Yearling Yellow-bellied Marmots

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With 6 figures

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Abstract

Play in yearling yellow-bellied marmots (*Marmota flaviventris*) was studied under non-manipulative field conditions in the Upper East River Valley of Colorado. The behavior patterns constituting play were described and illustrated and 12 specific hypotheses related to sex differences were tested. The results of these tests were used to evaluate the adaptive significance of play by comparing two major functional hypotheses: motor training and social cohesion.

Introduction

Rodent play is rich in its behavioral variety, yet its investigation has been largely neglected (FAGEN 1981). A review of play in this order is premature (HOLE & EINON 1984). Although a comparative synthesis must wait until the number of detailed descriptive treatments and quantitative analyses of play increases, play has increasingly been recognized as an important evolutionary problem (BEKOFF & BYERS 1985).

Our purpose is three-fold: first, to describe and illustrate all yearling yellow-bellied marmot behavior that occurred during, or temporally close to, any bout of play; second, to test various hypotheses related to sex differences within this age-class; third, to interpret the results of these tests in light of two major hypotheses proposed to explain the possible adaptive significance (hereafter referred to as function) of play: motor training and social cohesion. These two hypotheses are largely distinct, but they are not mutually exclusive. The question is not whether social play provides repetitive exercise or early social experience, but whether

these effects of play confer a selective advantage that led to play's evolution (BEKOFF & BYERS 1981).

The motor training hypothesis suggests that play enhances the development of bone remodeling, muscle hypertrophy, cardiopulmonary capacity, and neuromuscular coordination (BYERS 1980; BEKOFF & BYERS 1981). Proposed effects of such developments include increased strength, endurance, and socially competitive skill levels (SYMONS 1978; FAGEN 1981; SMITH 1982). The social cohesion hypothesis suggests that play enhances the formation, strengthening, and maintenance of social bonds among conspecifics (reviewed in BEKOFF & BYERS 1981; FAGEN 1981; SMITH 1982; POOLE 1985). This hypothesis also suggests that delayed dispersal in certain groups may be associated with play (BEKOFF & BYERS 1985).

Study Animal and Predictions

Yellow-bellied marmots (*Marmota flaviventris*) are ground-dwelling sciurids forming matrilineal female groups to which a territorial male may attach to form a harem (ARMITAGE 1986). Females within a matriline exhibit cohesive behaviors and may cooperate to exclude unrelated female conspecifics (ARMITAGE 1986). The behavioral ecology of this species has been thoroughly studied (ARMITAGE 1962, 1984, 1986; ARMITAGE & JOHNS 1982), and the play behavior of juveniles was reported in some detail (NOWICKI & ARMITAGE 1979). Play rarely occurs between age-classes and virtually never occurs between adults (ARMITAGE 1962). Young rarely disperse; about 50 % of female yearlings and essentially all male yearlings do (DOWNHOWER & ARMITAGE 1981). Examples of locomotor-rotational and object play were never observed; consequently, "play" and "social play" are synonyms for this species.

If play evolved in this species primarily as a mechanism to develop physical strength, endurance, and fighting skills (1) both females and males should play frequently, but males should play more than females and should choose partners with whom they can play most forcefully because male fitness is much more strongly linked to territorial defense than is female fitness; (2) self-handicapping (BEKOFF 1978; FAGEN 1981) to facilitate play with weaker individuals should be infrequent, resulting predominantly in same-sex play, because interactions with partners of much lesser or greater strength would not stimulate as much physical development as interactions with partners of comparable strength (reviewed in SYMONS 1978; FAGEN 1981).

If play evolved primarily as a mechanism to develop, strengthen, and maintain social bonds and to delay dispersal, (1) females should play frequently relative to males because females form matrilineal social groups and female yearlings are philopatric, (2) self-handicapping should be relatively common, resulting in mixed-sex play, because females and males interact frequently as adults and the nature of their encounters is often amicable (cohesive).

Methods

Study Area and Population

The yearling yellow-bellied marmots studied were located in the East River Valley of the Gunnison National Forest near the Rocky Mountain Biological Laboratory, Gothic, Colorado (elevation 2900 m). All yearlings occupied a single burrow system at Locality 4 (described in detail in ARMITAGE 1974).

All 13 animals were marked with a unique set of stripes or blots with non-toxic fur dye that enabled each to be readily identified. Trapping, handling, and marking procedures were elaborated elsewhere (ARMITAGE 1974). Sex was determined by measuring the distance from the center of the anus to the posterior base of the genital tubercle (anogenital distance). This distance was 8–13 mm for females, ($\bar{X} = 10$ mm, $N = 7$) and 22–30 mm for males ($\bar{X} = 26$ mm, $N = 6$).

Neither paternity nor maternity of these yearlings could be unequivocally determined. Most likely one male fathered all the animals. They were born in and lived in the same burrow system in 1980, they were closely related (two mothers were 4-year-old sisters and the third was a 2-year-old daughter of one of the sisters), some were undoubtedly full siblings, and all were extremely familiar with each other (ARMITAGE 1986). Among social ground squirrels familiarity probably is more important than relatedness in mediating amicable interactions among conspecifics (ARMITAGE 1982; MICHENER 1983). Consequently, we assumed that the actual degree of genetic relatedness between any two individuals was an insignificant factor in this study.

Three adult females, the same individuals that bore the yearlings in 1980, and an adult male formed the social group with whom the yearlings associated. During the study period (June 1–July 13, 1981) the number of yearlings at the study site decreased, forming seven discrete periods of stable group composition. This change in population structure was considered during statistical analyses (ALTMANN & ALTMANN 1977). Although 6 yearlings were still present during the second week of July, play was so infrequent that the study was terminated. Play among yearlings rarely occurs after mid July.

Data Collection and Analysis

Behavior was observed during peak activity periods (6.00–10.00 h and 16.00–19.00 h MDT; ARMITAGE 1962) with a 40–80 \times telescope, situated approx. 250 m across the river valley from the colony. Illustrations were based primarily on photographs and cine film. A scan sample (ALTMANN 1974), noting behavior and location, was taken every 15 min unless preempted by an occurrence of play. All notes were recorded on cassette tape. With practice, dyadic play interactions could be continuously monitored both qualitatively (predetermined motor patterns) and quantitatively (duration of each pattern). Two or more temporally overlapping dyadic interactions rarely occurred. Under these circumstances the information gathered was usually restricted to location and group composition. Occurrences of triadic and tetradic encounters were noted.

Development of the play-related ethogram was an exercise in pattern detection and pattern classification, and was ultimately based on intuition and gestalt perception (see SCHNEIDER et al. 1984). We focused particularly on the position of each individual's trunk, head and limbs, relative to the other member of the dyad. By estimating spatial relations on a rather coarse scale we developed a mutually exclusive and exhaustive classification of play and play-associated (all non-play motor patterns occurring temporally proximate to any play patterns) behavior. This classification enabled us to preserve frequency and sequence of behaviors as well as the duration and time spent in various behaviors. We designated a focal animal during all interactions (although we shifted this focus to its partner at times to provide a more complete record of playful synergy), yet we applied behavior-contingent rather than time-contingent starting and stopping rules. This procedure may be most appropriately termed "focal-pair sequence sampling of all occurrences of play and play-associated behaviors" (see sections V, VI, and VII in ALTMANN 1974).

Although adults occasionally interrupted the activities of the yearlings, a reasonably unbiased sample was obtained because (1) both playing and non-playing individuals moved in and out of view across the entire study site, and (2) the yearlings consistently and frequently came in contact with one

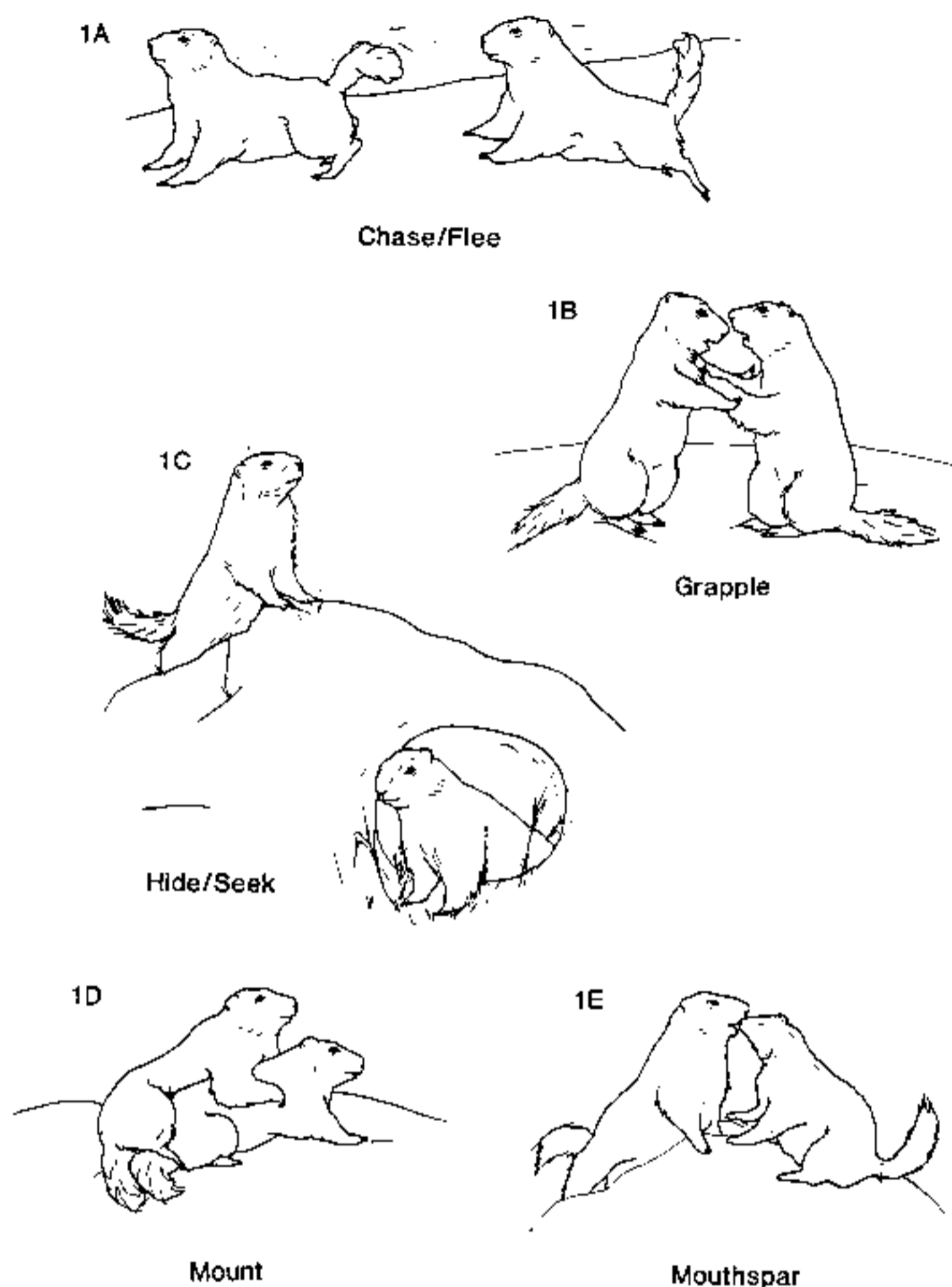


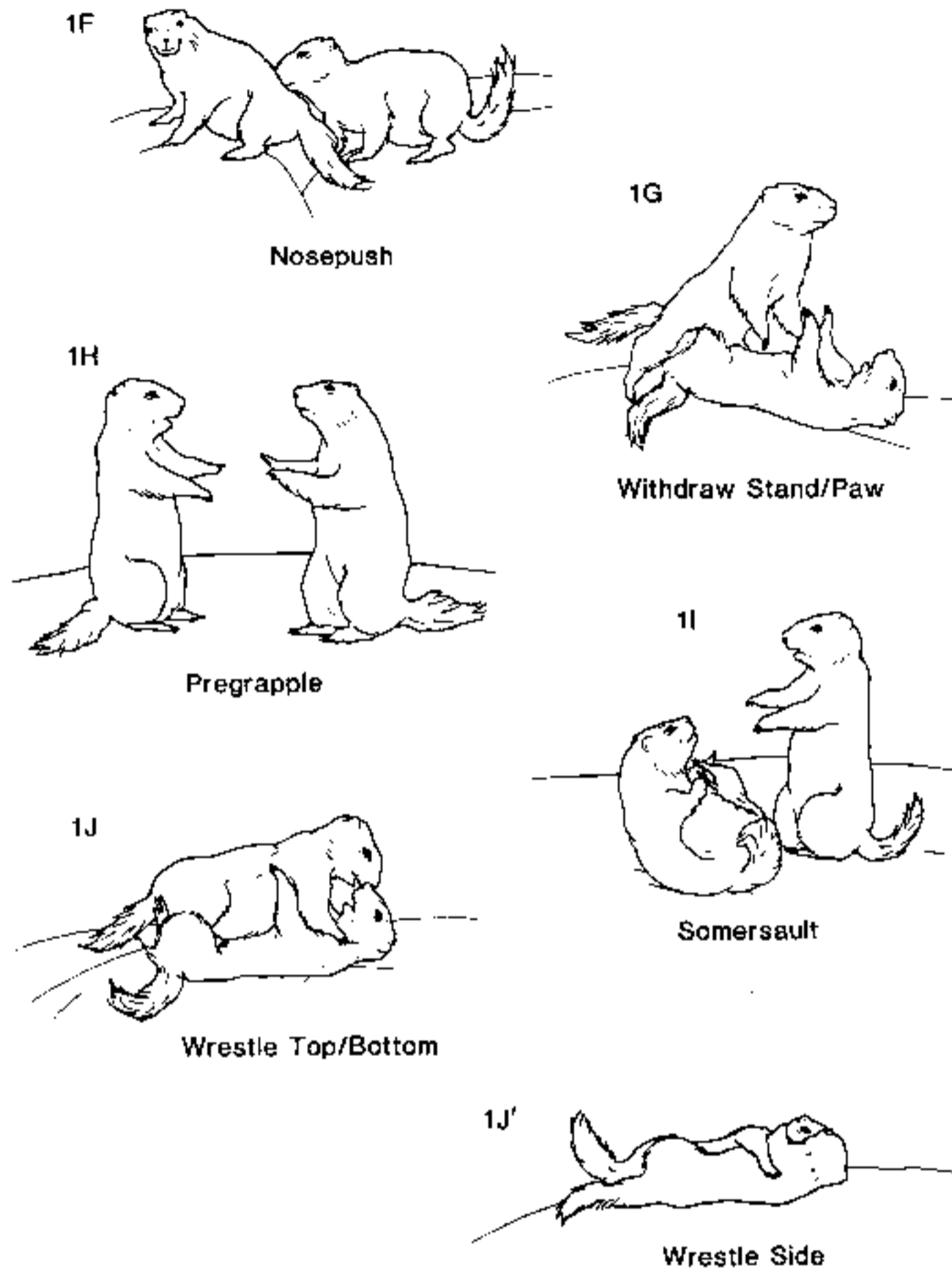
Fig. 1: Play motor patterns (see text)

another because practically all non-foraging activities were focused at the immediate burrow system area (FRASE & ARMITAGE 1984). Commonly all yearlings occurred within a few m of each other during several census periods each day. Consequently, as long as a given animal was known to be present in the population, we assumed that it had all of the other yearlings available as play partners.

Results

Play-related Ethogram

We placed the 18 motor patterns observed in this study into three main categories: play, transition events, and play-associated patterns. Chase/flee, hide/seek, grapple, mouthspar, pregrapple, and wrestle were included as unambiguous examples of play; i.e., "play markers" (CHALMERS 1978) because they (1) involved reciprocity, (2) frequently appeared exaggerated in their form, (3) often involved play signals, (4) lacked submissive or threatening behaviors, and (5) occurred back-to-back with variable order and temporal sequencing, frequently punctuated by bouts of escaping, withdrawing, and approaching. Classifying mount,



nosepush, paw, and somersault as play was problematic because each lacked reciprocity of "true social interaction" (MÜLLER-SCHWARZE 1978). Transition events occurred between two play bouts. Play associated patterns frequently occurred in other social contexts.

A play bout was defined as a series of play motor-patterns performed between two individuals. A non-play bout was similarly defined, but it was composed of play-associated motor-patterns. Play bouts were scored as ended when one or both of the two players withdrew from the other without any immediate chase/flee or hide/seek behavior.

Play bouts tended to occur in clusters called "superbouts" (MACHLIS 1977). A superbout is a series of play and non-play bouts, each punctuated by the other, and organized into a relatively dynamic and cohesive temporal-spatial context. Superbouts were scored as ended when one or both of the two players interacted with a third animal or neither partner made any immediate (in 98 % of the cases, within 60 s) effort to approach the other after one had withdrawn.

Although structural and functional descriptions of behavior are logically distinct (HINDE 1970; FAGEN 1974), they are difficult to separate in practice (SMITH

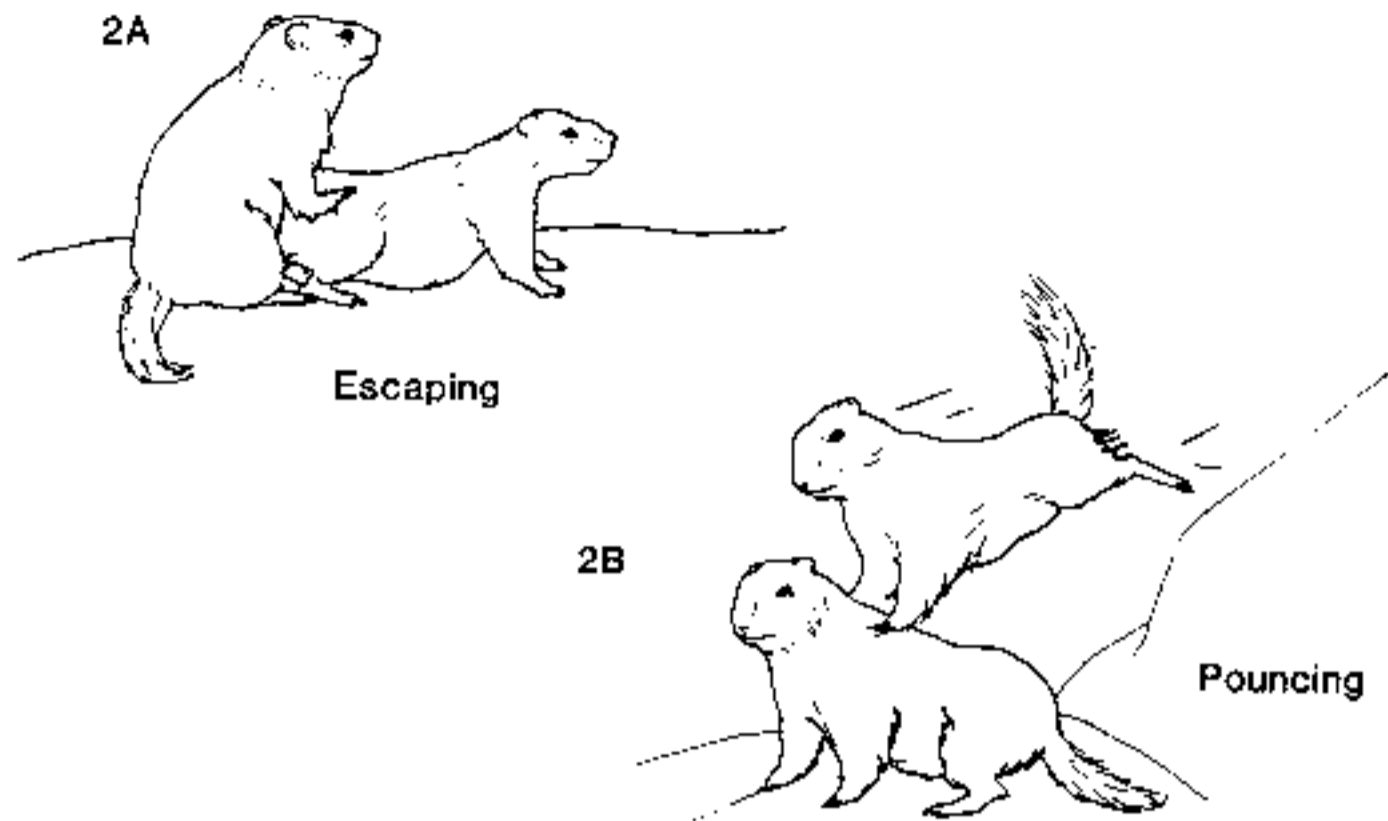


Fig. 2: Transition motor patterns (see text)

1982). Consequently, we supplemented the following definitions (based mainly on structural characteristics) with illustrations (Figs. 1—3).

1. Play Motor Patterns

- A. *Chase/Flee*: Animals do not face each other and are some distance apart; both move rapidly, and one directly follows the other (Fig. 1A).
- B. *Grapple*: Animals face each other and make contact with forepaws while vertically oriented on hindlegs alone or on hindlegs and rump (Fig. 1B).
- C. *Hide/Seek*: Animals are some distance apart and usually concealed in some way from one another; following is typically indirect and of variable speed (Fig. 1C).
- D. *Mount*: Animals generally face the same direction in a dorsal-ventral position, both prone or semi-prone, and one at least partially on top of and frequently posterior to the other; neither lordosis nor thrusting was observed (Fig. 1D).
- E. *Mouthspar*: Animals face each other quadrupedally, quickly and repeatedly contacting parts of the other animal's head, neck, and chest with an open mouth; forepaw-trunk contact occurs occasionally (Fig. 1E).
- F. *Nosepush*: From a quadrupedal position one animal pokes, prods, or shoves the other by extending its head, neck, and shoulders forward; contact was directed at various parts of the body, but especially posteriorly; eye-to-eye contact between the two animals did not necessarily occur (Fig. 1F).
- G. *Paw*: Rapid, repetitive movement of forepaws and occasionally hindlegs by an animal in a supine position, while a proximate animal in a standing or sitting position looks away; the animal on its back looks directly at the other animal (Fig. 1G, see also "Withdraw").
- H. *Pregrapple*: Animals face each other some distance apart while vertically oriented on hindlegs alone or on hindlegs and rump; distance precludes contact (Fig. 1H).
- I. *Somersault*: Leaping, flipping, or rolling in which one animal generally turns its heels over its head while the other animal at least visually follows it from a

proximate sitting, standing, or upright position; occasionally both animals performed this motor pattern concurrently; never observed outside a social context (Fig. 1I).

- J. *Wrestle*: Animals are in constant contact and often face the same direction in a ventro-ventral position while horizontally oriented; rapid extension and flexion of legs occurs frequently as does contact with open mouths variably directed at partner; during top/bottom wrestling, the top animal is prone, the bottom supine; during side/side wrestling, both animals are on their sides (Fig. 1J').

2. Transition Motor Patterns

- A. *Escaping*: A momentary change in relative position during top/bottom wrestling that involved the disengagement of the animal wrestling on the bottom from its partner (Fig. 2A).
- B. *Pouncing*: A momentary change in relative position that involved one animal suddenly jumping on another; top/bottom wrestling commonly followed this event (Fig. 2B).

3. Play-Associated Motor Patterns

- A. *Allogroom*: One animal licks or nibbles various parts of another animal's body; forepaw-trunk contact may co-occur (Fig. 3A).
- B. *Approach*: One animal walks or occasionally runs directly toward a stationary or relatively stationary animal (Fig. 3B).
- C. *Autogroom*: Animal licks or nibbles various parts of its own body (Fig. 3C).
- D. *Greet*: Animals generally face each other and naso-nasal contact occurs (Fig. 3D).
- E. *Social Investigation*: one animal orients its head toward various parts of the other animal, but especially his neck and anogenital regions; actual contact did not necessarily occur (Fig. 3E).
- F. *Withdraw*: One animal breaks physical or visual contact with the other and increases the distance between them by sitting or standing (Fig. 1G, see also "Paw"), walking away (Fig. 3F), or running away (Fig. 3F').

Bout Characteristics

83 h of observation resulted in four tetradic, 15 triadic and 268 dyadic play encounters. A total of 5523 dyadic motor patterns made up 882 play bouts and 822 bouts of non-play, and these 1704 bouts constituted 240 superbouts. The average superbout lasted 145 s and contained 3.7 play and 3.4 non-play bouts. Non-play bouts occurring within a superbout had a median duration of 5 s, whereas periods of non-play between superbouts (for a given pair of animals) had a median duration of nearly 19 min (1137 s). Based on frequency, superbouts consisted primarily (92.5 %) of 7 motor patterns: chase/flee, grapple, wrestle, escaping, pouncing, approach, and withdraw. 6 motor patterns made up 93.5 % of the interaction time: chase/flee, grapple, hide/seek, wrestle, approach, and withdraw. Consequently, all other motor patterns, including all play patterns not

considered to be play markers, constituted only 6.7% of the duration of the superbouts (Table 1). Although the mean values for bout characteristics were based on pooling repeated observations from the same individuals, pooling has virtually no effect on estimates of mean values (MACHLIS et al. 1985).

Sex Differences in Play

Females and males engaged in far fewer superbouts with opposite-sex partners than expected ($\chi^2 = 50.4$, $df = 2$, $p < 0.001$). Males participated in far more superbouts with other males than expected by chance. Females preferred to play with other females and at rates somewhat higher than expected.

Of the superbouts where the initiator was known, females initiated fewer superbouts than expected, while males initiated more superbouts than expected ($\chi^2 = 4.6$, $df = 1$, $p < 0.05$).

Females initiated fewer superbouts with males, while males initiated more superbouts with males than predicted by chance ($\chi^2 = 16.6$, $df = 1$, $p < 0.001$). Differences between the observed and expected frequencies of superbout initiation by females toward females and males toward females were minor (Fig. 4).

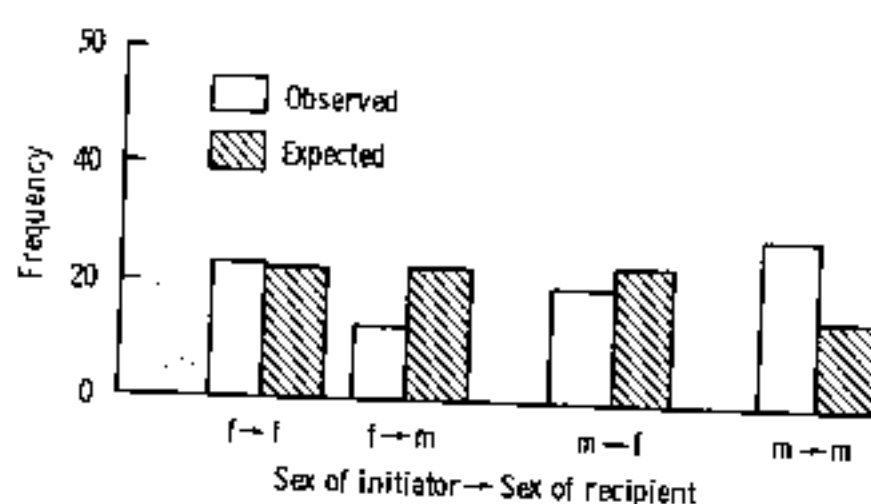


Fig. 4: Frequencies with which female (f) and male (m) yearlings initiated superbouts of play with female and male partners

The duration of female:female (f:f) and male:male (m:m) superbouts did not differ (Mann-Whitney test, SIEGEL 1956; $z = 1.39$, $N_1 = 75$, $N_2 = 82$, $p = 0.16$).

The numbers of play bouts per superbout for females and males were: $\bar{X} = 3.8$ play bouts per superbout (pb/sb), S.D. = 4.36 and $\bar{X} = 4.5$ pb/sb, S.D. = 5.65, respectively. The difference was not significant (Mann-Whitney test; $z = 0.07$, $N_1 = 75$, $N_2 = 82$, $p = .47$).

Nor was there any difference between the total proportion of time engaged in actual play motor patterns to the total interaction time for f:f and m:m sex-classes (Arcsine transformation test for the equality of two percentages (SOKAL & ROHLF 1969; $t = 0.9$, $p = 0.37$). These proportions (f:f = 0.75, m:m = 0.68) were calculated by dividing the sum of all play bout durations by the sum of all superbout durations. Superbouts involving periods of time in which both animals were temporarily out of view were excluded from this analysis. A preliminary test showed no difference between the sex-classes with respect to the probability of a given superbout containing such an interval ($\chi^2 = 0.5$, $df = 1$, $0.5 > p > 0.3$).

Unidirectional separation was by far the most commonly observed mechanism by which a superbout ended. Consequently, we defined the terminating animal as the first partner to withdraw from the last play bout of a superbout.

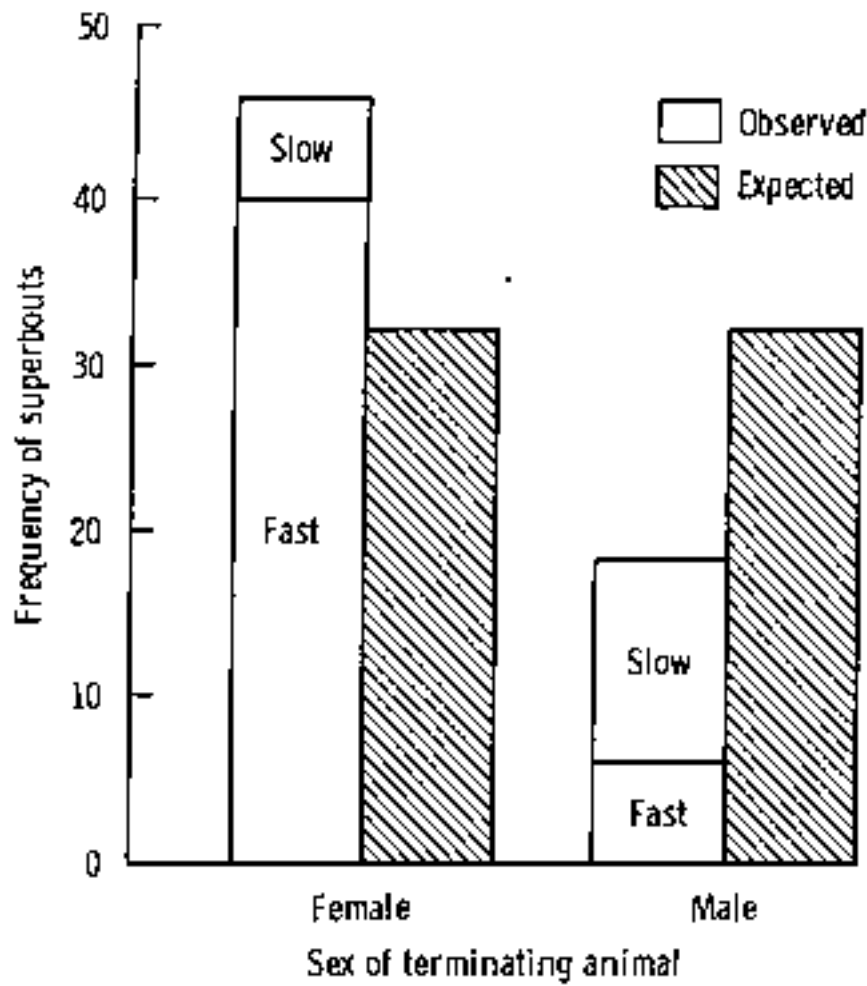


Fig. 5: Comparison of the frequency and speed with which female and male yearlings terminated mixed-sex superbouts of play

Females terminated more superbouts than expected by chance, while males terminated fewer (Fig. 5, $\chi^2 = 12.3$, $df = 1$, $p < 0.001$). Superbouts were terminated either relatively slowly (walking away, standing or sitting) or relatively fast (running away). Females usually terminated a superbout in a relatively fast way, males in a relatively slow way (Fig. 5; $\chi^2 = 18.4$, $df = 1$, $p < 0.001$).

We assumed that either animal could terminate a mixed-sex superbout at virtually any time, and that the probability of a particular play motor pattern occurring just prior to the terminating behavior should be a function of the percent of play-bout time occupied by the motor pattern during mixed-sex play. In other words, if females spent 29 % of their play time grappling with males, we expected 29 of 100 female terminations to be preceded by grappling.

We based our probabilities on 229 play bouts. In order to minimize the number of cells with unreasonably small expected frequencies, all play positions were combined into one of the following three mutually exclusive and exhaustive categories based on the relative temporal-spatial posture of the two animals: Top/Pursuit (e.g., wrestle-top, mount-top), Bottom/Retreat (e.g., wrestle-bottom, mount-bottom) and Side/Neutral (e.g., wrestle-side, grapple). Females did not terminate mixed-sex superbouts at random ($\chi^2 = 6.0$, $df = 2$, $p < 0.05$): they withdrew more often than expected from the bottom/retreat position (especially wrestle-bottom and mount-bottom) and less often than expected from the top/pursuit position. On the other hand, males terminated superbouts randomly with respect to relative position ($\chi^2 = 0.5$, $df = 2$, $0.8 > p > 0.7$).

The transition motor pattern, pouncing, was dominated by males during mixed-sex superbouts. Males were responsible for nearly 70 % (36/53) of the total pounces (Arcsine transformation test for the equality of two percentages ($t = 1.9$, $p = 0.06$)). Pouncing always occurred as a transition from one bout to another during a superbout.

The transition motor pattern escaping always followed "wrestle-bottom" during an asymmetric play bout. Hide/seek occurred too infrequently to be analyzed. In 83 mixed-sex superbouts, males directed asymmetric play motor

Table 1: Number of occurrences, rate (number of occurrences per pair-h), and mean duration (in s) of each dyadic play and play-associated motor pattern for entire study for all animals. We calculated frequencies and rates for states by treating the onset of each state as an event (ALTMANN 1974: 231), and used formula (8) to determine the 3825.8 pair-h of observation (ALTMANN & ALTMANN 1977)

Dyadic motor pattern	Number	Rate (No./pair-h)	Mean Dur. (s)			
1. Play motor patterns						
A. Chase/Free	202	.053	5.0			
B. Grapple	1077	.282	5.3			
C. Hide/Seek	24	.006	58.8			
D. Mount	56	.015	8.2			
E. Mouth spar	38	.010	4.3			
F. Nose push	39	.010	7.2			
G. Paw	20	.005	6.2			
H. Pregrapple	51	.013	2.1			
I. Somersault	89	.023	2.7			
	Bottom/Top	1307	.342	7.7		
J. Wrestle	1391	.364	7.5			
	Side/Side	84	.022	3.6		
2. Transition motor patterns						
A. Escaping	817	.214	0.0			
B. Pouncing	213	.056	0.0			
3. Play-associated motor patterns						
A. Allogroom	6	.002	13.7			
B. Approach	344	.090	4.0			
C. Autogroom	26	.007	6.4			
D. Greet	57	.015	3.6			
E. Social Investigation	7	.002	9.3			
	Sit or Stand	576	.151	8.4		
F. Withdraw	Walk	1066	.279	.034	6.1	3.8
	Run	361	.094		3.2	

patterns (chase/flee, mount top/bottom, and wrestle top/bottom) significantly more often at females than the reverse (Arcsine transformation test; chase/flee: $t = 5.4$, $p < 0.001$; mount top/bottom: $t = 4.2$, $p < 0.001$; wrestle top/bottom: $t = 4.1$, $p < 0.001$). For all motor patterns the female was significantly more likely to be found in the bottom or flee position, the male, in the top or chase position (Fig. 6).

Role reversals were scored whenever the animals exchanged top and bottom positions in wrestling at any time within a given play bout. Wrestling between two males involved a significantly higher percent of bouts that contained at least one role reversal than wrestling between mixed-sex or f:f partners (Arcsine transformation test f:m vs. m:m, $t = 3.3$, $p = 0.001$; f:f vs. m:m, $t = 2.3$, $p = 0.02$). No statistical difference in role reversal occurred between f:f and f:m play ($t = 1.2$, $p = 0.23$). An analysis of juvenile sex-classes revealed identical

presence of adults, etc. Therefore, we expected considerable variation in play. However, our purpose was not to examine individual differences but sex differences. Because play with a specific set of partners under controlled environmental conditions cannot be structured in a field study of a wild population, we pooled all data. Most of the analyses described above were non-parametric tests of frequency data. It is unknown to what degree pooling affects the reliability of such tests (MACHLIS et al. 1985).

Discussion

Description and Distinction

Mount, nosepush, paw, and somersault were not included in the ethogram as play markers primarily because they lacked reciprocity. Mounting (referred to more generally as sexual play) often occurred outside a playful context; that is, not temporally intermixed with play markers. Neither mounting nor nosepushing seemed to incorporate play signals such as the open-mouth play-face (POOLE 1978; SYMONS 1978). Consequently, mounting in immature marmots may be of questionable relevance to a treatment of play, an idea consistent with rat studies (HOLE & EINON 1984). On the other hand, play markers immediately followed nosepushing a significantly higher % of the time than all other behaviors combined ($p < 0.001$), substantiating our subjective impression that nosepushing served to stimulate a reluctant animal to play.

Pawing and somersaulting always occurred within a playful context and seemed to be frequently accompanied by the open-mouth play-face. Although the scarcity of pawing precluded its statistical analysis, this behavior appeared to be used by an animal on its back to entice its recently withdrawn partner to continue playing. Like nose-pushing, somersaulting was immediately followed by a play marker significantly more often than not ($p < 0.001$), indicating that the somersaulting animal invited more play.

Some researchers distinguished levels of competitiveness or aggressiveness as these levels relate to play-fighting; terminology in this area is confusing. For example, in rats (HOLE & EINON 1984), the terms rough and tumble play (R&TP) and not-very-serious-fighting (NVSF) were used; in polecats (POOLE 1966, 1973), aggressive play and companion fighting; and in rhesus macaques [HARLOW (as cited in POIRIER & SMITH 1974)], rough and tumble play, approach-withdrawal play, and aggressive play.

HOLE & EINON (1984) argued that the differences between R&TP and NVSF are real, though subtle, and that each should be treated as a separate category of behavior. To some extent this distinction may be valid for yellow-bellied marmots, although a thorough quantitative analysis of it would be difficult in the field. While neither juvenile (NOWICKI & ARMITAGE 1979) nor yearling play was ever seen to escalate into true aggression, superbouts sometimes seemed to begin in a more bouncy and exuberant way than they ended. At other times the intensity of the interaction seemed to maintain its original level. In any case, while future researchers should be aware of such distinctions, it seems somewhat artificial to restrict the use of the term, play, to only R&TP.

Polygyny and Play

If play provides motor training for adult agonism, then the motor training hypothesis predicts that males should play more with males than with females, choose partners with whom they can play most forcefully, and self-handicapping should be infrequent. If play develops social cohesion, then females should play more with females than with males and self-handicapping should be relatively common. Furthermore, because females form social groups, frequent play of three or more females should occur.

Motor training as a function of play in yearlings was supported by the following: males preferred playing with males; females initiated no more or less play with other females than expected, yet avoided initiations with males; males initiated more play with other males than expected and initiated play with females as expected; during mixed-sex play females terminated more superbouts than males, and they did so by running away after having been on the bottom or in a retreat position; males pounced on females more than the reverse; during asymmetric play the male most often assumed the top or chase position; and during wrestling bouts, role reversals occurred most often between two males.

Role reversal is widely cited as a characteristic of play (see FAGEN 1981) although the results presented here are somewhat difficult to interpret in a straightforward way. We found, as did NOWICKI & ARMITAGE (1979), that with the exception of male:male dyads, a lower percent of bouts contained role reversals than not. In contrast to other interpretations (STEINER 1971; HOLF & EINON 1984) we conclude that because of this sex difference, the more competitive the play-fighting, the greater the number of role reversals. While an alternative interpretation exists, that the animal on top reduced its efforts and allowed itself to be flipped, the first interpretation, that the animal on the bottom increased its efforts to get on top, is more reasonable given the evidence for sex differences during asymmetric play.

None of the results unambiguously supported social cohesion as a function of play. Females preferred playing with females, but that could result from a very high preference of males for playing with males; in effect, leaving no choice to females. The lack of any preference to initiate play with other females is contrary to what would be expected from the social cohesion hypothesis. Furthermore, the number of individuals involved in a play interaction at any one time was predominately limited to two (268 dyads to 19 triads and tetrads). Dyadic play often occurred following the break up of these ephemeral triadic and tetradic encounters. Because there were seven female yearlings, the opportunity to form social play groups was present, but there is no evidence that females did so.

Several lines of evidence indicate that the evolutionary fitness of play is more significant for males than for females. All play is social play and homosexual play is preferred over heterosexual play. Females clearly avoided initiating play interactions with males; when mixed-sex play did occur, the female most often terminated the superbout. The probable cause of these two conditions follows: males tended to dominate females during asymmetric play; males frequently pounced on females; females usually terminated superbouts by running away

from the male, and the proximate cause of this withdrawal was most likely due to the female being in a bottom or retreat position. The overall inference, then, is that males played too "rough" for females, and as a consequence, females avoided initiating play with them.

This same relationship occurs among adult marmots. Throughout the summer males frequently approach females with a "sex-grasp" (ARMITAGE 1974) that is similar to mounting among juveniles and yearlings. Females frequently rebuff the male with an open mouth threat which may be followed by mouthsparring. The female often rises to the pre-grapple position; grappling usually follows and a brief wrestle results in the female becoming supine and the male pinning the female by placing his forepaws on her shoulders (the wrestle top/bottom position, Fig. 1J). When the animals disengage, the female escapes.

Male:male agonistic encounters in which fighting occurs are rare and brief. Fighting is characterized by behaviors reminiscent of wrestle and chase/flee. The male/female and male/male behavior of adults that have behavioral patterns similar to those observed in play all occur in agonistic or social dominance contexts. Because female play has the same motor patterns as male play, female play may also be related to agonistic behavior. Although fighting among females is rare, experience from play may contribute to a female's eventual dominance status in a matriline. Play may bear on sexual behavior because the play pattern "mount" occurs in sexual behavior (ARMITAGE 1965), but mounting behavior is also associated with dominance. No other behaviors between adults contain patterns similar to play motor patterns.

In conclusion, play in yellow-bellied marmots occurs in a dyadic social context and primarily contains motor patterns that are similar to those observed among adults during agonistic encounters. We suggest that individuals prefer to play with partners of similar ability as evidenced by relatively infrequent interactions between age-classes or sex-classes. The usual termination of mixed-sex play by the female and the struggling by males to attain and maintain the top position during wrestling bouts provide further evidence that self-handicapping is not the rule and that males regularly test the limits of their abilities. Females engage in play less often and in a less dominating way than do males because the fitness costs associated with an adult losing a fight are much lower for females than males. It seems unlikely that play prepares animals for dispersal in that animals playing infrequently do not form social bonds and leave their natal group (BEKOFF & BYERS 1985). Among marmots, males play more frequently than females and all males disperse regardless of how much they play. Therefore, we propose that play evolved in this species as a mechanism by which physical development, especially in terms of its effects on competitive skills, is enhanced. Furthermore, we suggest that this enhancement is primarily a neuronal-behavioral process. If social dominance and the coordination of agonistic behavior are facilitated in this way, then play inevitably also serves to develop physical fitness. Whether physical fitness is an intended or unintended side effect becomes moot.

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